THE ORGANIZATION OF SESSILE GUILDS ON PIER PILINGS

by

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FRONTISPIECE: A piling of Edithburgh pier encrusted with sponges and other sessile invertebrates

The photograph includes the sheet-like sponge *Crella* sp. (black areas at the top and bottom of the piling) which is the most abundant species in the sessile guild on the pilings. Other sponges shown in the photograph include

SP1 *Aplysilla rosea* (pink mass on the right side of the piling)

SP47 *Chondropsis* sp. (irregular yellow-orange areas)

SP50 *Tedania* sp.a (orange mound-like colonies)

SP13 *Callyspongia* sp. (grey-purple projections on lower right)

SP5 Red encrusting sponge (scattered red patches)

The orange colony protruding from the piling on the upper left is the bryozoan, B1 *Celleporaria fusca* and the similar shaped grey colony protruding from the piling on the upper right is the bryozoan, B2 *Celleporaria valligera*. The encrusting grey colony adjacent to and under the lower end of the perspex ruler is the colonial tunicate, T18 *Didemnum* sp.b.

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SUMMARY

The structure and organization of two subtidal sessile guilds at the southern end of the Gulf of St. Vincent in South Australia were investigated. The guilds were located on the pilings of piers at Edithburgh and Rapid Bay.

In both sessile guilds the majority of species were relatively sparse, occupying a small percentage of the substratum while one species was by far the most abundant and occupied a large percentage of the substratum. At Edithburgh this was an encrusting sponge, *Crella* sp., and at Rapid Bay it was an encrusting stony coral, *Culicia* sp.

In addition to these two species both guilds were mainly composed of various sponges, tunicates and bryozoans. The relative competitive abilities of certain of these species as well as two serpulid species were assessed using estimates of overgrowth ability, growth rate, life span and growth form. The results of this assessment were discussed in relation to the abundances of the different phyletic groups at each site.

This assessment, experimental removal of *Culicia* sp. from some areas of piling at Rapid Bay and observations made during the development of the sessile guild at Rapid Bay on artificial panels suggested that the initial attainment of high abundance by *Culicia* sp. was due, primarily, to long life span and resistance to overgrowth and larval recruitment by other species. *Culicia* sp. colonized the artificial panels in very low numbers and the growth of new recruits was slow. Consideration of the

Perch, *Goniistius vizonarius*, was observed to be a major predator of *Didemnum* sp. a.

The number, identities and abundances of species did not show continuous or drastic changes in either sessile guild over the duration of the study period. This stable structure was attributed mainly to the fact that the majority of species in these guilds had long life spans. These facts were discussed in relation to recent generalizations about fouling communities mainly composed of species with short life spans. Three hypotheses were proposed to explain why there were more long-lived species in the guilds at Edithburgh and Rapid Bay than in the fouling communities considered by others. From the available evidence it was tentatively concluded that the larger size and longer period of submergence of the substrata at Edithburgh and Rapid Bay favoured longer lived species.

DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma at any University, and to the best of my knowledge contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

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1.0 INTRODUCTION

1.1 Community Organization

The term "community" refers to a collection of interacting organisms in a prescribed area or habitat (Whittaker 1972, Krebs 1972, Ricklefs 1973). Often this general definition is elaborated according to the way in which the user imagines biological communities might function. For example, some authors state that the species in a community have a common evolutionary history (Connell and Orias 1964, Goodman 1975). However I will use the term community only in a general sense to avoid confusion.

Communities have a "structure" in the sense that they are composed of different species which are arranged in different patterns. The number, identity, abundance and distribution of different species in a community are commonly recognized as aspects of this structure (Krebs 1972, Caswell 1976, Menge 1976). Theories of community "organization" have been concerned almost exclusively with the processes that produce this structure (e. g., reviews by Goodman 1975, Connell 1975, Whittaker 1975, Caswell 1976, Osman and Whitlach 1977).

Many of these theories attempt to explain the development of specific types of community organization and structure over evolutionary time (e. g., Hutchinson 1959, Margalef 1963, 1969, Odum 1969, Sanders 1968, 1969, Whittaker 1969, 1972). However, there is a growing body of literature which is concerned with identifying those factors and processes which are important in community organization in an ecological time scale, that is a period of,

say, years or centuries, which is short compared to the time likely to be required for speciation (e. g., Paine 1966, 1971, 1974, Dayton 1971, Grant 1977, Menge 1976, Buss and Jackson 1979, Harris 1978, Karlson 1978, Keough and Butler 1979, Osman 1977, Sutherland 1976, 1978, Addicott 1974, Maguire et al. 1968). It is the set of theories and generalizations which have been derived from these studies which is pertinent to the investigations reported in this thesis.

Most discussions of community organization on an ecological time scale emphasize the importance of predation, competition and physical disturbance and particularly interactions between these three factors (Paine 1966, Levin and Paine 1974, 1975, Connell 1975, 1978, Menge and Sutherland 1976).

Many investigations have demonstrated that the action of predators ameliorates competition between their prey allowing more species to co-exist in one locality than would exist in the absence of that predation (rocky intertidal: Paine 1966, 1969, 1971, 1974, Dayton 1971, 1975, Menge 1976, 1978, Lubchenco 1978, Lubchenco and Menge 1978, Peterson 1979; subtidal hard substrate: Day 1977, Russ In Press; corals: Porter 1972, 1974; tropical rainforest: Janzen 1970). In each of these cases one or more species of predators feed preferentially on one or more "competitive dominants". A competitive dominant is defined as a species which is able to increase its share of some resource at the expense of most other species in the community which require the same resource. In the absence of some controlling factor, such as predation, which suppresses its abundance

it is able to exclude other species from the habitat. It may be able to monopolize the resources completely.

Lubchenco (1978) proposed that the role a predator will play in community organization will depend on the competitive ability of its preferred prey. In communities where a competitive dominant is not the preferred prey predation would be expected to reinforce the effects of competitive dominance. That is, more species would be expected to exist in the locality in the absence of that predation. Several investigations support this proposition (Day 1977, Glynn 1976, Lubchenco 1978).

In communities where there is no competitive dominant predation may have one of two effects. Addicott (1974) demonstrated that predation decreased the number of species in protozoan communities in pitcher plants. Alternatively, Dayton and Hessler (1974) give some evidence suggesting that generalized predation of the deep-sea benthos enhances species diveristy. As far as I am aware there is no comprehensive conceptual model which explains why or under what circumstances predation may have these two different effects in the absence of competitive dominants. However it is worth noting that Addicott (1974) has discussed the factors that may determine how community structure will respond to predation and concluded that predation could not increase species numbers under any circumstances unless there were strong competitive interactions between the prey.

Physical disturbance has also been found to play a significant role in community organization (Dayton 1971, Connell 1975,

Osman 1977, Grant 1977, Lubchenco and Menge 1978, Glynn 1976). In the marine communities on hard substrata studied by Dayton (1971), Connell (1975), Osman (1977), Grant (1977) and Lubchenco and Menge (1978) localized physical disturbance such as wave shock periodically clears areas which are then available for invasion by new recruits. After an initial rise the numbers of species in these areas decrease over time as one or more competitive dominants monopolize the areas. Thus these disturbances permit a greater number of species to co-exist in one locality than would be found there without any disturbance (for further discussion see Section 4.1). Glynn (1976) also reports that extreme tidal exposures off the Pacific coast of Panama devastate corals on reef flats, particularly the competitively dominant corals. This has a diversifying effect on the reef flat assemblage.

In a series of investigations in the rocky intertidal communities of the New England coastline Menge (1976, 1978a, 1978b) demonstrated that physical disturbance affected the efficiency of the gastropod predator, *Thais lapillus*, and thus modulated its role in community organization. At localities exposed to wave shock the efficiency of this predator decreased (Menge 1978a). Thus at these localities it was unable to prevent its preferred prey, *Balanus balanoides* and *Mytilus edulis* which were competitive dominants from monopolizing the space. However at localities where the predator was protected from wave shock and desiccation it was able to reduce the abundance of these competitive dominants (Menge 1978a, b). Thus a greater

number of species co-existed at protected sites than at exposed sites.

As Menge (1976) pointed out the results of his investigation concur with the key predictions of the models of community organization by Connell (1975) and Menge and Sutherland (1976). Both models predict that communities in situations of comparatively low environmental stress will be structured largely by predator-prey interactions while those in situations of high environmental stress will be structured by competitive interactions. In particular Connell (1975) maintains that predation will in general be more intense in less stressful environments and thus competitive exclusion should be prevented more often in these situations.

Stress has many diverse forms (for examples see Grime 1977, Vermeij 1978) and as can be seen from the proceeding paragraphs the concept may encompass phenomena commonly termed disturbance. Nevertheless the two terms, stress and disturbance, are usually defined separately (Grime 1977, Vermeij 1978, Whittaker and Goodman 1979). In this thesis I will use Menge and Sutherlands' (1976) definition of environmental stress, that is "the frequency that physical environmental conditions approach or exceed the physiological tolerance limits of an organism." I shall define disturbance as any event which directly causes the destruction of animal or plant biomass (Grime 1977, Vermeij 1978). From this point of view the intertidal environment is clearly more stressful than the subtidal environment (Jackson 1977a). Thus according to the models of Connell (1975) and Menge and Sutherland (1976)

predation will play a greater role in community organization in the subtidal compared to the intertidal.

Several authors have demonstrated that predators can play a significant role in structuring subtidal sessile communities (hard substrata: Day 1977, Russ In Press, Paine 1976; coral reefs; Porter 1972, 1974 Brock 1979; benthic sponges: Dayton et al. 1974). However this does not appear to be a universal pattern. Predation appears to have very little influence on community structure in a coral reef community (Porter 1974) temperate or subtropical fouling communities (Sutherland 1976, Sutherland and Karlson 1977, Keough and Butler 1979) and the sessile community of a cryptic coral reef environment (Hartman and Goreau 1970, Jackson et al. 1971, Jackson and Buss 1975, Buss and Jackson 1979).

Since predation is often a very important factor in the organization of intertidal communities (e.g. see review by Paine 1977) not all comparisons between the intertidal and subtidal communities investigated up to date would support the predictions of the models of Connell (1975) and of Menge and Sutherland (1976).

It may be that these formulations cannot be successfully applied to comparisons between habitats. Between the intertidal and subtidal regions there are likely to be major differences in the pools of species which can potentially be a part of communities on hard substrata particularly if comparisons are made between different biogeographic regions. There is no guarantee that absolute measurements of environmental stress, that is the values of various environmental parameters such as temperature,

salinity, oxygen levels, p.H., will correspond to the subjective measurements made by different species (Whittaker and Goodman 1979). A given habitat may be stressful to some species but not others (for examples see Vermeij 1978 pp. 182). Accordingly an explanation for differences between the organization of communities in different habitats may require an understanding of evolutionary processes as well as ecological processes. Since it is not the aim of this introduction to discuss theories dealing with community organization on an evolutionary time scale I shall not examine this point further except to note that evolutionary history may limit the application of generalizations based mainly upon an understanding of processes on an ecological time scale.

It is also significant that these subtidal communities in which predation was not an important structuring agent lacked a competitive dominant, whereas those in which predation was an important organizing factor did contain one. Thus it may also be inappropriate to make comparisons between communities which do not both possess competitive dominants. A more thorough understanding of the effect of predators in the absence of competitive dominants is required before this matter can be resolved.

In the absence of an obvious organizing process such as predation, physical disturbance or competitive exclusion knowledge of the life-history patterns and/or the biological peculiarities of the species in a community may lead to explanations of community organization (e.g. Sutherland 1976, Sutherland and Karlson 1977, Jackson and Buss 1975, Buss and Jackson 1979, Buss 1976).

For example, in the cryptic coral reef environments of Jamaica many species co-exist in a benign environment where predation is low. It is argued that they can co-exist because of the existence of competitive networks (i.e. Species A outcompetes Species B and Species B outcompetes Species C but Species C outcompetes Species A.) (Jackson and Buss 1975, Buss and Jackson 1979). Along similar lines Porter (1974) suggests that competitive exclusion is retarded in the Caribbean coral reefs even in high density situations where there is little physical or biological disturbance because no one species excels in all aspects of interspecific competition. Alternatively studies of continuous sponge communities on the walls, floors and roofs of submerged caves in the Mediterranean Sea suggest that the high diversity and stability of such assemblages may be a result of "cooperation phenomena" (Sara 1970, Rutzler 1970). The term "cooperation phenomena" refers to survival during overgrowth and epizooism which reduces the potentially deleterious effect of interspecific interactions between sponges.

Recent evidence has demonstrated that many fouling communities (i.e. communities made up of sessile organisms on hard substrata in the marine subtidal zone) in temperate and subtropical localities are characterized by continuous and unpredictable changes in the numbers and abundances of species over time (Sutherland 1976, Sutherland and Karlson 1977). Sutherland and Karlson (1977) propose that three aspects of the life-histories of the species in these communities work together to produce

this variation in community structure. These are short life span, variable recruitment and the unequal ability of species to invade occupied substratum and resist larval recruitment. In these communities free space is vacated frequently because the life spans of most species are a year or less and is often invaded by a species different from the previous occupant. Thus community structure changes continually (see Chapter 7 for further explanation.)

Conversely Frank (1968) suggests that the long life-spans of the most abundant species in forest communities may be responsible for the "stability"* of those assemblages. Similarly Connell (1976) suggests that the long life-spans of many corals may be responsible for the stability of coral reefs.

Finally it is noteworthy that several of the recent studies and models concerning the process of succession emphasize the importance of life-history characteristics of individual species (e.g. Drury and Nisbet 1973, Horn 1976, Connell and Slatyer 1977 and Noble and Slatyer In Press). In such models knowledge of various life-history characteristics (e.g. reproductive capacity, growth rate) of species adapted to grow in different environments is used to predict the series of species replacements during succession.

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*Throughout this thesis the term stability refers to the variability over time in the following components of community structure; the number of species, the identity of species and the abundances of species. It is recognized that this will be a function of factors extrinsic and intrinsic to the community. This definition carries no causal connotations and is a specific usage of the constancy concept of stability defined by Orians (1975). There are many other meanings of stability (e.g. see Margalef 1969, Holling 1973, Whittaker 1975, Orians 1975) which are not implied here.

1.2 This Study

Recent investigations suggest that there are two factors in addition to those considered in the preceding section which have a significant effect on the structure of fouling communities. These factors are substrate size and substrate age.

At several localities the length of submersion of pieces of substrata has been shown to have a significant effect on the identity and abundance of the sessile species established on them (Jackson 1977a, Osman 1977, Karlson 1978, Harris 1978, Anger 1978, Russ In Press). Additionally Jackson (1977a) and Keough (pers. comm.) have found that there are significant differences in the number of recruits per unit area in a given time on different sized substrata. Moreover Jackson (1977a) suggests that species with certain types of life histories will preferentially colonize substrata of a particular size.

The fouling communities most often investigated in the past decade have been those which developed on submerged artificial plates (e.g. Sutherland 1974, 1975, 1976, 1978, Sutherland and Karlson 1973, 1977, Osman 1977, Jackson 1977b, Day 1977, Anger 1978, Russ In Press). The generalizations concerning the structure and organization of fouling communities in temperate and subtropical localities (detailed in Section 1.1) have arisen mainly from Sutherland's (1974, 1975, 1976) and Sutherland and Karlson's (1973, 1977) investigations of the fouling community at Beaufort, North Carolina. These investigations were carried out on small unglazed ceramic tiles (232cm in area) which were never submerged for longer than four years. Furthermore the

other investigations to which Sutherland (1976) and Sutherland and Karlson (1977) refer in order to support their analysis were also conducted on artificial plates. In view of the fact that substrate size and age may affect community structure the generalizations drawn from such studies may not apply to fouling communities on very large substrata such as pier pilings or natural rock faces which have been submerged for many years.

This dissertation is a study of two sessile guilds (i.e. fouling communities excluding mobile organisms; see Section 2.3) located on the pilings of two piers (Edithburgh pier and Rapid Bay pier) in the Gulf of St. Vincent in South Australia. In both cases the guilds under investigation have had access to the pilings for 15 years. In order to determine the structure, dynamics and some aspects of the organization of these two sessile guilds two approaches were used.

Firstly a continual non-destructive census of each guild was carried out for two years on non-manipulated areas of the pilings. This procedure provided data on the structure and dynamics of both sessile guilds (Section 2.4). It also provided data concerning some aspects of the life-histories and competitive adaptations of the common species and phyletic groups which were found in the sessile guilds (Chapter 3).

Secondly, field experiments were conducted at each pier in order to gain insights into the organization of each sessile guild.

At Edithburgh pier the reoccupation of artificially cleared patches on the pilings was investigated in two field experiments

with the aim of identifying some of the factors influencing the abundance of the phyletic groups and species in natural patches (Chapter 4). The role of predation in sessile guild structure was also investigated by means of a predator exclusion experiment using cages (Chapter 6).

At Rapid Bay pier the process of sessile guild development was investigated in order to identify and describe the process by which a particular species in the sessile guild had become so overwhelmingly abundant (Chapter 5). Artificial panels were employed for this experiment. The role of this species in sessile guild structure was examined further in a removal experiment on the pilings (Chapter 6). Lastly, the role of predation in sessile guild structure was investigated in a caging experiment (Chapter 6).

The results of this investigation have also been used to test the generalizations made by Sutherland (1976) and Sutherland and Karlson (1977) about the structure and dynamics of fouling communities in temperate subtropical localities (Chapter 7). Further, they show how life history patterns may determine community stability.

2.0 THE SESSILE GUILDS AT EDITHBURGH AND RAPID BAY

2.1 The Study Sites

Two piers in the Gulf of St. Vincent in South Australia were used as study sites.

Edithburgh pier ($137^{o}45'E$ $35^{o}5'S$) is located on the western side of the gulf (see Fig. 2.1). The wooden structure seen today (Photograph 2.1) extends 173 metres in an easterly direction out from a low rocky cliff. Field work was restricted to the outer half of the pier (see Fig. 2.2) which was originally built in 1900. Additions and repairs made to the pier in 1931 were the last to involve the pilings chosen for study. The timber used for the pilings has a compact straight grain and is most probably one or more of the following *Eucalyptus* species, *E. marginata* (Jarrah), *E. fibrosa* (Red Ironbark) and *E. paniculata* (Grey Ironbark). Most pilings are roughly cylindrical in shape ranging in diameter from 30cms. to 40cms. The sandy sea floor slopes steadily down away from the low rocky cliff with depth ranging from 4.5m below Mean Lower Low Water (M.L.L.W.) at the middle of the pier to 5.5m at the end. To the south of the pier lies a dense bed of the sea grass *Posidonia australis* var. *angusta* Hook. To the north and east of the pier this gives way to algae, mainly *Scaberia argardhii* (Greville) and numerous razor shells, *Pinna bicolor* Gmelin. Underneath the pier there are large numbers of *Pinna bicolor* and the scallop *Chlamys asperrimus* (Lamarck) and moderate numbers of the solitary tunicates *Phallusia depressiuscula* (Heller) and *Ascidia gemmata* Sluiter which grow out of the old dead razor shells and amongst the occasional heaps of rubble seen under-

neath the southern side of the pier.

Rapid Bay pier (138°11'E 35°31'S) is located in a broad northerly facing bay on the eastern side of the gulf (see Fig. 2.1). It is an industrial pier employed to load limestone from the nearby quarry on to ships. The original wooden structure which extends in a northerly direction into the bay for 395 metres (Photograph 2.2) was built in 1942. Field work was restricted to the steel "tee head" section which was installed in 1960. This consists of six "dolphins," three each side of a central platform, connected by walkways (see Fig. 2.3). The steel pilings were fabricated from two RSJ sections seam welded together producing an I shaped piling 42cm.x 25cm. in cross section (see inset in Fig. 2.3). They were originally treated with flame descaler, wire brushed, "seachrome" primed and coated with bituminous tar before immersion. The whole "tee head" section stands in nine metres of water at M.L.L.W. and no piling has been replaced below the low water line since the original installation. Sea grass beds, mainly *Posidonia australis* var. *angusta* surround this part of the pier giving way to a bare sandy bottom littered with limestone debris, concrete blocks and various pieces of steel cable and railing underneath the pier. To protect the steel pilings from corrosion in the tidal range a Cathodic Protection device is used. A D.C. Voltage is supplied to the steel structure from a 415/6 volt Transformer/Rectifier. The negative supply side is connected to the steel structure while the positive supply side is connected to anodes suspended in the water under the pier.

Although both piers are located geographically in gulf

waters Rapid Bay is exposed to wave action from the Northwest and is subject to oceanic swells. Edithburgh on the western side of the gulf is protected from these conditions largely because it is sheltered by land from the prevailing Southwest winds. Conditions have been rough enough at Rapid Bay on several field trips to make SCUBA diving impossible. Since this was never the case at Edithburgh during the three years of field work subjective impressions support the proposition that Edithburgh pier is the less exposed study site.

Both sites are moderately warm and temperate. Water temperatures range from approximately 20°C in January and February to approximately 12°C in July and August.

To minimize spatial variations in the physical parameters light and water turbulence at each site I restricted my study areas to those pilings not flanking any edge of either pier. The two central rows of pilings supporting the outer half of the Edithburgh pier (Rows b and c in Fig. 2.2) and the groups of six pilings central to each dolphin of the Rapid Bay pier (see Fig. 2.3) were chosen for the study. The light meter readings from an underwater camera were uniformly low in these areas. I further restricted my study to a two meter wide band of the pilings beginning .5m from the sea floor. Phenomena due to sand scour at the base of the pilings and increasing light intensity and water turbulence near the tops of the pilings were thus excluded from the study.

2.2 General Field Methods

All field work was done using SCUBA and a total of 300

hours was personally spent underwater for the three year period of the study from April 1975 to April 1978. Diving conditions were in general fair to good at both sites with wave amplitude rarely exceeding .5 metres and visibilities of four to six metres. Conditions were usually worst in late winter and early spring (August and September) with visibilities sometimes reduced to less than a metre and rough seas making entry into and emergence from the water difficult, especially at Rapid Bay.

Data were collected using photographic techniques. A Nikonos II underwater camera fitted with an electronic flash was used to photograph all monitoring and experimental quadrats on the pilings. An underwater tripod was designed and built (see Photograph 2.3) to optimize the accuracy and speed at which the camera could be positioned underwater to photograph the appropriate quadrats. The camera fitted into the apex of the tripod such that any object falling within the two dimensional area circumscribed by the outer ends of the three tripod arms could be photographed at a precisely fixed distance. This eliminated, to a large extent, operator errors of focus and alignment which accrued when the camera was aimed by hand at the area to be photographed.

Ektachrome ASA 64 colour transparency film was used for all data photographs. All quadrats were photographed at a distance of .8 metres with an aperture setting of f8 and a shutter speed of 1/60 second.

This method of data collection yielded permanent photographic records which could be interpreted and analysed later

in the laboratory. It also made it possible to non-destructively census the same area, *in situ*, on successive dates. Methods for interpretation of the transparencies are detailed in Section 2.4.2.2.

2.3 Species in the Sessile Guilds

In the most commonly used definition of a fouling community (Sutherland 1975, Sutherland and Karlson 1977, Sutherland 1978) attention is focused on the "foundation species," "the group of critical species which define much of the structure of a community " (Dayton 1972). The criteria to select these species are:

1. ability to attach to the primary substratum (Dayton 1971). In this case the primary substratum is the pier piling surface.
2. 10% occupancy of primary or secondary substratum in at least one sample taken from the designated area (Sutherland 1974).

This definition excludes all totally epizootic and ephiphytic species and mobile species. Mobile species were not included in this definition because they had little effect on the abundance of the sessile species in the system under study (Sutherland and Karlson 1977).

At the beginning of this investigation it was not known which, if any, mobile species at either study site would have a significant effect on the abundances of any of the sessile species because it was the first time an assemblage of this type had been investigated in South Australia. Later short term investigations of the effect of four common asteroids *Coscinasterias calamaria* (Gray), *Patiriella brevispina* H. L. Clark, *Petricia vernicina* (Lamarck), *Tosia australis* Gray, on the struc-

ture of the epifaunal community at Rapid Bay pier suggest that these mobile species, at least, have little effect on the abundance of common sessile species at this pier (Keough and Butler 1979). However my own observations together with longer predator exclusion trials (see Chapter 6) suggest that one or more predatory species including the magpie perch *Goniistius vizonarius* (Saville-Kent) had a significant effect on the abundance of various tunicate species at both piers.

The recent generalizations about fouling communities (Sutherland and Karlson 1977) originated mainly from Sutherland's work with experimental plates at Beaufort, North Carolina. In some of the earlier work (Sutherland 1974) grazing by fish appeared to be an important factor in community development however in a more recent paper (Sutherland & Karlson 1977) it was stated that fish were only occasionally important determinants of community structure. One other species, a sea-urchin, which could have been a significant determinant of community structure was excluded from the experimental system. Although this is not the case for either of the South Australian communities I shall, for the sake of consistency define the primary objects of my study as those two collections of species adhering to the piling substrate within the two study areas. This definition excludes all mobile species and species only seen attached to others. It will include all sessile species, regardless of abundance, recorded in any of the photographic sampling schedules that are described in this dissertation excluding those species which were only observed on artificial plates and on experimentally caged sites. The latter species are listed and discussed in

Chapter 5 and Chapter 6 respectively. I have rejected the 10% occupancy criterion because some species which always occupied less than 10% of the space in the quadrats used in the above sampling schedules had a larger mean percentage cover than other species which were distributed very patchily within the study areas and occasionally occupied more than 10% of the space in a quadrat.

These two collections of species are made up of one trophic level and are guilds of sessile species which are both part of the larger, more complex communities with several trophic levels, inhabiting the general pier environment. A guild is functionally defined as a group of species within a community which have become adapted to some related set of factors (Root 1974). I also acknowledge that one or more members of the larger communities may be important determinants of the structure of these sessile guilds (see Chapter 6). Thus, I am concentrating on groups commonly called "fouling communities" but I shall refer to them henceforth as "sessile guilds".

Due to the lack of taxonomic knowledge of many marine invertebrate groups in Australia some of the sessile animals lack specific identification. This is particularly true of the sponges; of the 1,000 species of Demospongia described in South Australia last century it is considered impossible to put a name to any but a few dozen species (Bergquist and Skinner In Prep.). All species have been given a code number and voucher specimens have been lodged in the marine laboratory of the Zoology Department at the University of Adelaide. In the cases where there was no specific or generic identification of species it is possible

that sibling species were grouped together as one species or that one species has been treated as two.

The members of the two sessile guilds are listed in Table 2.1. Thirty-five species were recorded at Edithburgh and 56 at Rapid Bay. The two sites had 27 species in common. *Chlamys asperrimus*, *Galeolaria caespitosa*, *Galeolaria hystrix*, *Filograma implexa*, *Cnemidocarpa etheridgii*, *Polycarpa pennunculata* and *Asci dia thompsoni* are the only solitary forms listed.

2.4 Sessile Guild Structure and Dynamics

2.4.1 Introduction

The nature and number of species in a community and the abundances of those species are the most commonly examined aspects of biological communities (Caswell 1976). The trophic relationships between the species are also considered by some (e.g. Margalef 1963, Krebs 1972, Caswell 1976 and May 1977) to be an integral part of any description of community structure.

The two sessile guilds under investigation are made up of one trophic level. Accordingly the object of this section is to describe the first three aspects of structure for the sessile guilds within the two study areas using the parameters described in Section 2.4.2.3. Because these parameters vary with time it is not merely "structure" (as if it were a static description) that is being examined but also "dynamics".

2.4.2 Methods

2.4.2.1 Sampling Procedure

Sixteen 20cm.x 30cm. permanent quadrats on the pier

pilings were photographed at approximately monthly intervals at both sites over a period of two years (see Table 2.2 for the precise sampling dates).

At Edithburgh the position of each quadrat was chosen in the following manner. The surface of each piling within rows b and c (see Fig. 2.2) was divided lengthwise into four equal rectangular sections facing North, East, South, and West respectively. Each section was given a number and quadrats were then allotted to any of these sections using a random number table with the restriction that there was only one quadrat per column of pilings (see Fig. 2.2).

At Rapid Bay eight quadrats were located on the East Arm of the tee head and eight quadrats on the West Arm of the tee head (see Fig. 2.3). Each of the pilings within the defined study area on each arm was given a number and quadrats were then allotted to any of those pilings using a random number table. On each arm two quadrats were allocated to face 1, face 2, face 3 and face 4 of the pilings (see Inset in Fig. 2.3) respectively.

At both sites the height of the quadrats within the two metre wide band (see Section 2.1) corresponded to the elevation of the diver (which was variable and considered to be random) on arrival at the piling when the first samples were taken. So that quadrats could be relocated accurately on successive visits the centre of the bottom edge (20cm. in width) of each quadrat was marked. At Rapid Bay this was done with a knot tied in a piece of nylon rope strapped around the piling. At Edithburgh a small wooden block was nailed to

the piling in the appropriate place.

2.4.2.2 Processing the Samples

Percentage cover rather than biomass, numbers of individuals or productivity is often used to measure species abundance in fouling communities (for example see Sutherland 1974, 1975, 1978). The use of numbers of individuals is generally precluded in such communities due to the preponderance of colonial forms. However, it is not immediately obvious why percentage cover should be favoured over the other two measurements. Biomass and productivity are commonly used to measure species abundances in terrestrial plant communities (e.g. Wells 1971,McNaughton and Wolf 1971). Whittaker (1965) maintains that productivity (dry weight of organic matter produced per unit area per unit time) is the best single measure of species abundances in terrestrial plant communities because it simultaneously expresses the biological activity of a species and indicates the share of the environmental resources of the community it utilizes. In this way the measure reflects functional aspects of the community such as engergy flow as well as structural aspects.

All sessile animals and plants in fouling communities share two potentially limiting resources;

(1) primary space: the substratum onto which they attach and
(2) the aquatic milieu around them from which they gain physical resources and organic nutrients (Dayton 1971).

The utilization of the space resource can be directly measured using percentage cover while productivity would indicate the

rate at which species utilized the other resources in their aquatic environment. Biomass is usually highly correlated with productivity in certain agricultural plant communities (Pechanec and Pickford 1937b, Wells 1971), however changes in P/B ratios during succession (Margalef 1963, 1968, Odum 1969) indicates that different species in certain natural communities have different P/B ratios. Biomass may therefore be a biased estimate of productivity.

One aim of this investigation is to determine which processes have a significant effect on the structure of the two sessile guilds. Since competition for resources particularly primary substratum is known to be an important structuring agent in sessile communities (e.g. Paine 1966, 1971, 1974, Dayton 1971, Sutherland 1974,1975, 1978, Menge 1976, Osman 1977, Jackson 1977b) an estimate of species abundances in terms of percentage cover and productivity (or at least biomass) would provide the most useful description of community structure.

The estimation of productivity and biomass would have involved either harvesting quadrats precluding the use of permanent plots essential for recording certain competitive interactions (see Chapter 3) and community flux (see Section 2.4.2.3) or compiling a "bank" of standard reference photographs (Wells 1971) from which the productivity and/or biomass of colonies in a sample transparency could be estimated. The latter method was attempted but the construction of a "bank" proved to be so time consuming that it was abandoned. Therefore in this study percentage cover has been used to measure species abundances.

Only those parts of a colony or individual which were adherent to the piling surfaces were measured as cover. For all species except *Callyspongia* sp., *Sycon* sp., solitary tunicates, *Podoclavella cylindrica, Chlamys asperrimus* and algae this area was the two dimensional projection of the colony or individual seen in the transparencies. *Callyspongia* sp. has a runner-like growth form which adheres to the piling only at certain points. The areas of these points of contact were measured by examination of colonies in the field. *Sycon* sp., *Podoclavella cylindrica,* and the species of algae had upright bushy growth forms and are attached by a "stalk" to the piling. Observations made in the field indicated that the contact area of the "stalk" did not vary linearly with the two dimensional projections of the colonies in any of these species. Although these observations did suggest it was positively correlated with colony size there was considerable variation in mean contact area between colonies of similar sizes (range of .25cm^2 - .7cm^2 for all sizes). Accordingly I recorded each colony of these species as having a contact area of .5cm^2 (.08% of a 600cm^2 quadrat) although this is likely to be an overestimate of the actual mean contact area. Since all these species were very rare (Appendices Ia and Ib) this approximation was not thought to seriously affect interpretation of the results. For the same reasons I recorded each individual of the scallop *Chlamys asperrimus* as having a contact area of .5cm^2. This was also a rare species (Appendices Ia and Ib).

Each of the solitary tunicates was either roughly ovoid or spheroid in shape with a flattened area on its test where

it was attached to the piling. These areas were roughly circular with a diameter approximately 1/3 of the total height of the tunicate. These areas were drawn in by eye on the tracings of the transparencies.

The transparencies were projected onto white paper and the colony outlines were traced. The area occupied by each colony was measured using a polar compensating planimeter and the percentage cover for each species in the quadrat was calculated from these figures. A series of test runs using irregularly shaped areas of various and known sizes indicated that the planimeter was accurate to $\pm 5mm^2$. Thus the error involved in measuring areas of less than $1cm^2$ was greater than ±5%. Accordingly I used a transparent piece of graph paper divided into $1mm^2$ squares to measure areas less than $1cm^2$ in size. All percentage cover data presented in this thesis was calculated using the preceding methods.

Most species could be identified easily from the transparencies due to distinctive colour and colony morphology. Occasional difficulties arose with very small colonies. These were surmounted either by reference to transparencies on subsequent dates when the colonies had grown or by close examination of the colonies in the field. There were two exceptions to this. The two *Galeolaria* species were difficult to distinguish, both in the field and in transparencies. For this reason individual abundances for these two species are not given. In the results sections they have been included under one heading, *Galeolaria* spp. (TW3/4). Because of their extremely low abundance in both sessile guilds (see Appendices Ia and Ib) this was not thought to

affect seriously the interpretation of results.

Processing of transparencies proved to be very time consuming and therefore only quarterly samples (marked with * in Table 2.2) were used.

2.4.2.3 Calculations and Analysis

2.4.2.3.1 Diversity

Researchers frequently use various diversity indices to summarise large amounts of information about the numbers and abundances of species within a community (Wilhm 1968). Most of the common indices of species diversity (e.g. see Heip and Engel 1974) combine two components of diversity: 1. the number of species and 2. equitability or evenness of distribution of individuals among the species. I have chosen to treat these two aspects of diversity separately by estimating species number, S, the simplest measure of species diversity (Osman and Whitlach 1977) and species evenness, J, using the Shannon-Weiner index (see Pielou 1966a, 1966b, 1975) shown below.

$$H = \Sigma pi \log_2 pi \text{ where}$$

$$pi = \text{proportion of the ith. species,}$$

$$\text{and } J = H/\log_2 S.$$

Species number and species evenness were calculated for each sample date at both sites using the mean percentage cover data in Appendices Ia and Ib. This gave one estimate of species number and species evenness, denoted S' and J' respectively (Pielou 1975) for each sample date at each site. These estimates have been plotted against time for both Edithburgh and Rapid Bay in Fig. 2.4.

The accuracy of these estimations in respect to the actual species number and species evenness of the two sessile guilds will depend upon how well the parent populations are represented in the two samples of 16 quadrats (Pielou 1966a,b). To assess this I have plotted S vs. number of quadrats and J vs. number of quadrats (see Pielou 1966b) for both sites on September 1976 and March 1977 (see Fig. 2.5). The explanation for the choice of these dates may be found in Section 2.4.3.1. I have also used the calculations for the species evenness vs. number of quadrat curves to calculate estimators of J' defined as

$$\hat{J} = \hat{H}'/\log_2 S$$

$$\hat{H}' = \bar{h} = 1/(z - t + 1) \sum_{k=t}^{z} h_k$$

$$h_k = (M_k H_k - M_{k-1} H_{k-1})/ M_k - M_{k-1}$$

where

S = total number of species in the parent population

z = total number of quadrats

t = the number of quadrats after which the species evenness vs. quadrat number curves becomes horizontal

k = number of quadrats, k=1,2,3 ....., z.

M_k = total cover of all species in the first k combined quadrats

H_k = estimate of H based on k quadrats.

(Pielou 1966b) at both sites for these two sample dates. A Mann-Whitney U-test was used to test whether there was a signi-

ficant difference between sites in the estimators of J' at these two sample dates.

2.4.2.3.2 The Distribution of Species Abundances

The distribution of species abundances, expressed as a percentage of the substratum occupied and as a percentage of the total available substratum was calculated for all sample dates common to the sampling schedules at both sites (Appendix Ic). The data was grouped in 1% class-intervals, i.e. 0.00 - 0.99, 1.00 - 1.99, etc. to 99.00 - 99.99. The class interval of 1% was chosen arbitrarily. The distributions of species abundances have been plotted for both Edithburgh and Rapid Bay on the September 1976 and March 1977 sample dates in Fig. 2.6. The Smirnov test (Conover 1971 pp. 309-314) was used to judge whether the distribution of species abundances of the two sites at different sample dates could be regarded as the same (see Pielou 1975 pp. 61-65). Further statistical comparison is detailed in the results section.

2.4.2.3.3 Percentage Cover

The mean and standard deviation of percentage cover was calculated for each species at each sample date at both sites (Appendices Ia and Ib).

The mean and standard deviation of percentage cover were plotted against time for

(i) species which attained a mean percentage cover calculated from the 16 quadrats of at least 1% on at least one sample date.

(ii) All species present (Total cover).

(iii) Each phyletic group which attained a mean percentage cover calculated from the 16 quadrats of at least 5% on at least one sample date (total cover for each phyletic group.)

The total cover at Edithburgh was statistically compared to that at Rapid Bay on the seven sample dates common to both sites using a Mann-Whitney U-test (Siegel 1956).

2.4.2.3.4 Community Flux

Community flux, defined by the formula

$$\sum_{j=1}^{m} \frac{/xjt2 - xjt1/}{t2 - t1}$$

where xjt = percentage cover of species j at time t
t2>t1 measured in days
m = total number of species.

(Sutherland 1975) was also calculated. This calculation was made using the arithmetic mean of percentage cover averaged over the 16 quadrats and for each individual quadrat for standard 90 day intervals at each site.

When arithmetic means are used the resulting value is considered to be an estimate of the total amount of space given up plus the total amount of space acquired by the various species in the community in a given time period (Sutherland 1975). Thus it is an index of the total amount of variation in the abundances of all species over time.

Examination of successive transparencies of the permanent quadrats at both sites indicated that many species did not lose or acquire space simultaneously in all quadrats. However it did

suggest that in the majority of cases colonies of the same species lost and acquired space simultaneously within quadrats. For this reason if community flux is calculated for each individual quadrat and averaged over the 16 quadrats the resulting value is an estimate of the total amount of space given up plus the total amount of space acquired by colonies and individuals rather than species. I interpret community flux calculated in this way in this situation as an index of the turnover (i.e., change in occupancy over time) of the space resource.

The community flux for each individual quadrat is tabulated in Appexdix Id. The community flux calculated using the arithmetic means and the mean and standard deviation of the community fluxes calculated for each individual quadrat are plotted against time for both sites in Figure 2.13.

For each type of community flux statistical comparisons were made between sites using the Mann-Whitney U-test. In each case estimates of community flux made on successive sample intervals were viewed as independent and were treated as though they represented a sample of independent estimates for the whole study period. Strictly speaking this is not the case because the estimates for successive sample intervals are made using the same quadrats. However due to events such as senescence, colonization and overgrowth the composition of quadrats often changed considerably in the interval between sample dates thus the assumption of independence may not be seriously in error.

2.4.3 Results

2.4.3.1 Diversity

With the *Galeolaria* spp. counted as one, 33 species were recorded in the sampling schedule at Edithburgh and 50 species recorded in the sampling schedule at Rapid Bay (see Appendices Ia and Ib). Thus one species at Edithburgh, *Dysidea fragilis* and five species at Rapid Bay, the Light grey finger sponge (SP60), *Botrylloides nigrum*, *Botrylloides* sp., the Opaque orange encrusting tunicate (T3) and the Pink encrusting tunicate (T38) which were defined as members of the sessile guilds in Section 2.3 were not recorded in these samples. These species were extremely rare elements of the sessile guilds and contributed very little to their physical structure thus their omission in the following analysis was considered unimportant.

S', the total number of species recorded in the quadrats at one sample date, at Rapid Bay was always greater than that at Edithburgh (Fig. 2.4A). Regrettably this difference cannot be tested statistically because of the nature of the data. The curve of species number vs. quadrat number becomes less steep as quadrat number increases (Fig. 2.5A,B) but it does not ever become horizontal at either site. This fact coupled with the observation that rare species not recorded in any of the quadrats on certain dates were still present within the study areas suggests that S' is an underestimate of the total number of species in the sessile guild at each site. However since S' at Rapid Bay always represented less than 83% of the total number of species recorded during the sample period compared to 90% at Edithburgh the total number of species will be underes-

imated by S' more at Rapid Bay than at Edithburgh. For this reason I maintain the evidence is sufficient to assert that the sessile guild at Rapid Bay was more diverse in terms of species number than the sessile guild at Edithburgh for the period of the sampling schedule.

Calculation of species evenness J' required that the diversity index H' be divided by $\log_2 S$ where S equalled the total number of species in the population from which the sample was taken (See Section 2.4.2.3.1). Following the preceding discussion the best estimate of this was considered to be the total number of species recorded during the sampling schedule (33 for Edithburgh and 50 for Rapid Bay) rather than S'.

J', the evenness with which species abundances were distributed in the quadrats at one sample date, at Rapid Bay was always less than J' at Edithburgh (Fig. 2.4.B). The species evenness vs. quadrat number curves calculated for the September 1976 and March 1977 sample dates at both sites became horizontal after seven quadrats and four quadrats respectively (see Fig. 2.5C,D). This showed that J', calculated using 16 quadrats, was a reliable estimate of J at both sites. In the September 1976 samples the values of J' from the two sites are most similar (see Fig. 2.4B) and so this represents the case where J is least likely to be significantly different between sites. $\hat{J}'$, the estimator of J', was found to be significantly higher at Edithburgh than Rapid Bay for both the September 1976 and March 1977 sample dates (See Table 2.3). In view of this result further comparison of J' at all sample dates, which would

have involved a large amount of laborious calculation, was not considered necessary. This result is sufficient to show that species abundances at Edithburgh were distributed more evenly than those at Rapid Bay for the period of the sampling schedule.

2.4.3.2 The Distribution of Species Abundances

The distributions of species abundance at both sites superficially resemble the logarithmic series. (Fisher, Corbet and Williams 1943) where most species have minimal abundance. At both sites for all sample dates the lowest class of abundance (0.00 - 0.99) contained the largest number of species irrespective of the way in which abundances were expressed (see Fig. 2.6, and Appendix Ic). Additionally at both sites there was always one species whose abundance was very much greater than all the others and over half the species had an abundance of less than 2% each. The data shows that most species at both sites were rare, individually occupying a small percentage of the substratum, with one species occupying a comparatively large percentage of the substratum. For abundances expressed as a percentage of the occupied substratum there was a significance difference (.05 probability level) between the distributions of species abundances of the two sites for five of the seven sample dates (Table 2.4). On all occasions the deviation between the distributions was in the same direction. Rapid Bay always contained a greater proportion of rare species but a smaller proportion of less rare species than Edithburgh (see Appendix Ic). This suggests that there was a real difference between the distributions of species abundance, when ex-

pressed as a percentage of occupied substratum, at the two sites. This is even more likely because the Smirnov test is conservative when the number of species is less than 40 in one sample and the number of species is different in each sample (Siegel 1956, Conover 1971) which was the case for each comparison.

For abundances expressed as a percentage of the total available substratum there was a significant difference (.05 significance level) between the distributions of species abundances of the two sites for only three of the seven sample dates (Table 2.4). On the basis of this result alone I do not feel I can make a conclusive statement about the similarity or difference of the distributions when species abundance is expressed as a percentage of the total available substratum. It is noteworthy, however, that the deviation between the distributions was always in the same direction as for the former comparison (Appendix Ic).

As pointed out in Section 2.4.2.3.3 of the methods the data from separate dates at either site were not independent. However as was explained there an assumption of independence between dates may not be seriously in error. If this assumption is made the seven probabilities from the Smirnov tests can be combined to give one probability (Sokal and Rolf 1969 pp. 621-624). The resulting figure can be regarded as the probability of observing the original seven probabilities when there was no significant difference between the distributions of species abundances at the two sites. In both cases this probability is far less than .05 (for abundances expressed as a percentage of the occupied substratum $x^2_{(14)} = 39.2$, $P < .005$, for abundances expressed

as a percentage of the total available substratum $x^2_{(14)} = 33.84$, $P<.005$). This suggests that there was a real difference in the distributions of species abundance calculated in either fashion between sites. A greater proportion of species individually occupied a smaller percentage of the occupied substratum and the total available substratum at Rapid Bay that at Edithburgh.

2.4.3.3 Percentage Cover

A significantly greater proportion (.05 significance level) of the substratum was occupied at Rapid Bay than at Edithburgh for the seven sample dates common to both sites (Table 2.5 Fig. 2.7). Most of the unoccupied space at Rapid Bay was the skeletal remains of *Culicia* sp. rather than bare piling (see Appendix Ib). With the exception of the odd bryozoan skeleton unoccupied space at Edithburgh was bare piling.

Four phyletic groups; sponges, tunicates, bryozoans and cnidarians (represented by one species only, *Culicia* sp.) occupied the major proportion of the space resource at both sites. All the other species together not belonging to these four phyletic groups occupied less than .5% of the space on each sample date at both sites (Appendices Ia and Ib).

The mean percentage cover of sponges ranged between 40% and 65% at Edithburgh during the sampling period compared to 11% - 16% at Rapid Bay (Fig. 2.8). Sponges were the most abundant group at Edithburgh.

The mean percentage cover for bryozoans was very low at Rapid Bay being always less than 1.5% compared to Edithburgh

where it fluctuated between 8% and 15% during the sampling period (Fig. 2.8).

The mean percentage cover for tunicates ranged between 21% and 5% at Rapid Bay and 15% and 1% at Edithburgh. The fluctuation in mean abundances of tunicates at Edithburgh appears to be seasonal with maximum values reached in June and minimum values in December (Fig. 2.8). This trend is also apparent in the mean percentage cover for three colonial tunicates at this site (Fig. 2.10). This is not the case for tunicates at Rapid Bay; instead the mean percentage cover for this group declines during the sampling period (Fig. 2.8).

Culicia sp. was the most abundant species at Rapid Bay with mean percentage cover ranging between 55% and 75%. At all times during the study it occupied more space at Rapid Bay than all the other species put together. At Edithburgh it was very much less abundant with mean percentage cover ranging between 2% and 6% (Fig. 2.8). Sixteen of the 33 species at Edithburgh and 15 of the 50 species at Rapid Bay attained a mean percentage cover of at least 1% during the study period.

At Edithburgh eight of the 18 sponge species attained this value. *Crella* sp. had the highest mean percentage cover (ranging between 20% and 25%) at every sample date (Fig. 2.9). Since it was at least twice as abundant as any other sponge in the sample on all sample dates it was clearly the most abundant sponge in the sessile guild. It was also twice as abundant as any other species in the sample (Fig. 2.9 and Fig 2.10) thus it was also the most abundant species in the

sessile guild. *Aplysilla rosea* and *Mycale* sp. had similar (between 7% and 12%) mean percentage covers, consistently higher than those of all other species in the sample, with the exception of *Crella* sp. after the September 1976 sample date (Fig.2.9 and Fig. 2.10). The other five sponge species *Aplysilla sulphurea, Callyspongia* sp., *Chondropsis* sp., the Red encrusting sponge (SP5) and *Lissodendoryx* sp. considered here did not at any sample date attain a mean percentage cover of more than 6% in the sample.

Only five of the 22 sponge species at Rapid Bay attained a mean percentage cover of at least 1%. Two of these, the Green encrusting sponge (SP4) and *Aplysilla rosea,* had higher mean percentage covers (ranging between 2% and 5.3%) at all sample dates than did the other three sponges (Fig. 2.11). With the exception of the Red encrusting sponge (SP5) in March 1978 the other three sponges did not attain a mean percentage cover of more than 1.5% for the entire sample period (Fig. 2.11). This suggests that the Green encrusting sponge (SP4) and *Alypsilla rosea* were the most abundant sponges in the guild at Rapid Bay.

Four of the seven bryozoan species at Edithburgh attained a mean percentage cover of greater than 1% but none of the six bryozoan species did so at Rapid Bay. *Celleporaria fusca* had mean percentage covers ranging between 4.5% and 6% which were always higher than those for *Celleporaria valligera* which ranged between 2% and 4.5% (Fig. 2.10). *Celleporaria pigmentaria* and the Mustard encrusting bryozoan (B7) had mean percen-

tage covers which were always less than those of the other two species with one exception, December 1976 when the mean percentage cover of *Celleporaria pigmentaria* was slightly higher than that of *Celleporaria valligera*. This suggests that *C. fusca* was more abundant in the sessile guild than *C. valligera* and both were more abundant than *C. pigmentaria* and the Mustard encrusting bryozoan (B7).

Three of the five and 10 of the 15 tunicates at Edithburgh and Rapid Bay respectively attained a mean percentage cover of greater than 1%. At Edithburgh all the three tunicates, *Botrylloides leachii, Didemnum* sp.a and *Didemnum* sp.b showed a peak in abundance in the winter of 1976 (Fig. 2.10). Observations made in successive transparencies of a single quadrat indicated that colonies of these three species settle in December, January and February, grow to a maximum size in June, July and August and die off in October and November. This is also true of *Podoclavella cylindrica*. A seasonal trend in abundance is not obvious in the graphs for *Botrylloides leachii* and *Didemnum* sp.a at Rapid Bay (Fig. 2.12) although colonies of these species showed the same patterns of settlement timing, growth and senescence as those at Edithburgh. None of the tunicate species at Rapid Bay attained a maximum mean percentage cover greater than 5% and there did not appear to be any consistent differences between species for the sample period (Fig. 2.12). All three species of tunicate at Edithburgh did attain a maximum mean percentage cover greater than 5% but as with Rapid Bay there did not appear to be any consistent differences

between species (Fig. 2.11).

All species with the exception of *Culicia* sp. at Rapid Bay had very large standard deviations always bigger than the mean values (Figs. 2.9, 2.10, 2.11, 2.12 Appendices Ia and Ib). This indicated that the distribution of these species within the study areas was extremely uneven in relation to the size of the quadrat used. This drastically reduces the power of any statistical test for the significance of the trends and differences discussed above. In some cases, by assuming approximate independance between dates one could pool across times by a method such as that of Sokal and Rolf (1969 pp. 621-624). This amounts to taking note of the consistency of the differences through time although they may not be statistically significant at one time. It would still be unwise to make too much of the results of such a test. Here, I wish to make nothing more than the above statements about what is suggested by the data, with the additional observation that in no case did the mean percentage cover of any species show wild and unpredictable fluctuations over time, i.e. no one species dominated the guilds for a period and then suddenly became very rare. (Figs. 2.9, 2.10, 2.11, 2.12, Appendices Ia and Ib).

2.4.3.4 Community Flux

Community flux calculated from the arithmetic means (Fig. 2.13) did not differ significantly between sites (Mann-Whitney U-test N1=8, N2=7, U=27 P=.478), indicating that the total amount of variation in the abundances of the species in the sessile guilds at Rapid Bay and Edithburgh was the same. Simi-

larly community flux calculated for individual quadrats (Fig. 2.13) did not differ significantly between sites (Mann-Whitney U test N1=8, N2=7, U=20 P=.198) indicating that the rate of turnover of the space resource was equivalent at both Rapid Bay and Edithburgh.

It is noteworthy that for every sample interval at both sites community flux calculated using the arithmetic means is considerably lower than the mean of community flux calculated from individual quadrats (Fig. 2.13). Since the two types of community flux were derived from exactly the same data there is no statistical test readily available to assess the significance of this difference. However the figures do suggest that while a great deal of substratum may be "changing hands" in each quadrat it need not be accompanied by an equivalent amount of variation in species abundances averaged over a number of quadrats.

2.4.4 Discussion

Both sessile guilds contain a "dominant" (*Crella* sp. at Edithburgh and *Culicia* sp. at Rapid Bay) in the sense that one species is by far the most abundant (Whittaker 1965). Since abundance has been measured in terms of the utilization of a vital resource, the primary substratum, these two "dominant" species occupy niche space potentially occupied by the other species in the guilds.

As pointed out in Section 1.1 of the Introductory chapter many hard substrate communities in the marine environment contain a "competitive dominant" which is able to monopolize the

primary substratum in the absence of certain disturbance factors. Whether the two "dominant" species at Edithburgh and Rapid Bay fall into this category cannot be determined from the preceding descriptions of guild structure alone. This question is addressed in the following chapter of this thesis.

The sessile guilds at both sites were not characterized by continuous and drastic changes in the number of species, the list of species and the abundances of species. The guilds at Edithburgh and Rapid Bay were consistently dominated by *Crella* sp. and *Culicia* sp. respectively and no species which attained a mean percentage cover of at least 1% on one sample date completely disappeared from the sample quadrats for the two year period at either site. Most of these species at both sites showed minor fluctuations in mean percentage cover for the two year period (Figs. 2.9, 2.10, 2.11, 2.12).

In this respect both guilds were unlike the fouling communities studied by Sutherland (1974, 1975, 1978) and others (see Sutherland 1976, Sutherland and Karlson 1977) from which the present generalizations about fouling communities in temperate and subtropical localities originated. In these communities large fluctuations in the number of species and abundances of species occur frequently and catastrophic slough-offs from the substratum are a more or less annual event.

The community flux, calculated from arithmetic means and on the scale used by Sutherland (1975), ranged between .1 and .3 at both sites for the two year period. Community flux calculated from arithmetic means in the developing fouling commun-

ity at Beaufort that was not manipulated (Sutherland 1975) was greater than .5 in the majority of cases for a period of 2½ years. Comparison of community flux between the South Australian sessile guilds and Sutherland's fouling community is questionable because of differences in sample size and quadrat/plate area. In Sutherland's investigation arithmetic means were calculated from four plates of 232cm^2 in area compared to 16 quadrats of 600cm^2 in this investigation. Larger quadrat number could produce lower estimates of this parameter if exchange of space between species is not simultaneous and in the same direction in each quadrat. Similarly larger quadrat size could produce lower estimates if colonies or individuals of the same species are not acquiring or losing space simultaneously in each quadrat. However, Sutherland and Karlson (1977) maintain that the observed changes in the structure of the fouling community at Beaufort were not a function of spatial scale. If this is so, then the low values of community flux in the two South Australian guilds compared to those values for the fouling community at Beaufort support the proposition that the total amount of variation in the abundances of all species over time in the sessile guilds at Edithburgh and Rapid Bay is less than that in the fouling community at Beaufort.

Localized spatial changes can be averaged out over large areas (Spight 1974). The low values for community flux calculated from the arithmetic means from 16 quadrats compared to the mean of community flux calculated for the individual quadrats suggests that this is occurring at both sessile guilds in

this study. The mean of community flux, calculated for individual quadrats and using Sutherland's scale, ranged between .2 and .45 at both sites. Although the data for individual plates in Sutherland's work are not available community flux for individual plates would be greater than or equal to the values calculated from arithmetic means from four plates. Thus it is very likely that, on average, the turnover of the space resource in the South Australian sessile guilds is lower than that in the fouling community at Beaufort.

At both sites the standard deviations associated with the means of community flux calculated for individual quadrats (Fig. 2.13) are reasonably large and often greater than 50% of the mean value. This suggests that changes in community structure were not spatially uniform at either site which was expected considering the extreme unevenness in the distribution of species at each site.

In summary there is less change in the structure of the sessile guilds at Edithburgh and Rapid Bay over time than in the structure of the fouling community at Beaufort from which, among others, (see Sutherland 1976), generalizations about fouling communities have arisen. A similar observation has been made at another Australian pier at Portsea, Victoria (Harris 1978 unpublished). The explanations for this difference are discussed in Chapter 7.

Although the sessile guilds appear similar in terms of dynamics their structure is different in a quantitative sense when the identity of component species is ignored and even more

so in a qualitative sense when the identity of the species is taken into account.

The sessile guild at Rapid Bay is more diverse in terms of species number but less diverse in terms of species evenness than the sessile guild at Edithburgh. This is a rather curious fact in the light of observations made in hard substrate communities of the marine environment in other areas. In the rocky intertidal zones of the west coast of America and elsewhere a high level of dominance (low species evenness) is usually correlated with low species number and vice versa (Paine 1966, 1971, 1974; Dayton 1971, 1975; Menge 1976 and Lubchenco and Menge 1978). Studies of hard substrate communities on rocks and plates in subtidal zones suggest a similar correlation (e.g. Osman 1977, Sutherland 1975, Russ In press). However in both cases this pattern was observed either in communities containing many of the same species at different localities or as a result of experimental manipulation of the same community in one locality. Of the 64 species recorded at Edithburgh and Rapid Bay only 27, less than one half, were recorded at both sites (Table 2.1). Furthermore two phyletic groups had markedly different abundances at both sites. Sponges and bryozoans were far more abundant at Edithburth than at Rapid Bay (Fig. 2.8). Also the dominant species at each site is relatively rare at the other (Fig. 2.8 for *Culicia* sp. and Fig. 2.9 and Fig. 2.11 for *Crella* sp.)

Species from different taxonomic groups often exhibit characteristically different life history patterns (Jackson

1977a, 1977b, In press) thus from the outset it seemed unlikely that all the organizational processes at Edithburgh and Rapid Bay would be similar. Consideration of the difference in the structure of the two sessile guilds in combination with the results of Chapter 3 suggested that different experimental procedures were required at each site to investigate community organization. The details may be found in the introductory sections of Chapters 4, 5, and 6.

TABLE 2.1 Species in the sessile guilds at Edithburgh pier and Rapid Bay pier. A species presence in a guild is indicated by "X".

		Edithburgh	Rapid Bay
Sponges			
SP1	*Aplysilla rosea* Schulze	X	X
SP2	*Aplysilla sulphurea* Schulze	X	X
SP14	*Aplysilla* sp.	X	X
SP3	*Dysidea fragilis* Montagu	X	
SP30	*Crella* sp.	X	X
SP20	*Mycale* sp.	X	X
SP47	*Chondropsis* sp.	X	
SP13	*Callyspongia* sp.	X	X
SP49	*Lissodendoryx* sp.	X	X
SP50	*Tedania* sp.a	X	
SP51	*Tedania* sp.b	X	
SP18	*Ircinia* sp.	X	X
SP33	*Sycon* sp.		X
SP54	Mauve spiky sponge		X
SP46	Royal blue spiky sponge	X	X
SP5	Red encrusting sponge	X	X
SP55	Brown/maroon encrusting sponge	X	
SP36	Light grey/green encrusting sponge		X
SP4	Green encrusting sponge		X
SP8	Grey volcanoe sponge	X	X
SP56	Coral volcanoe sponge		X
SP7	Large orange sponge		X
SP57	Cream lumpy sponge	X	X
SP58	Slate-grey lumpy sponge	X	X
SP59	Red finger sponge		X
SP60	Light grey finger sponge		X
SP62	Mauve honeycombe sponge	X	
SP63	White tendril sponge		X
SP64	Gelatinous sponge		X
Solitary Tunicates			
T28	*Cnemidocarpa etheridgii* (Herdman)		X
T10	*Polycarpa pedunculata* Heller	X	
T40	*Ascidia thompsoni* Kott		X

TABLE 2.1 (continued)

		Edithburgh	Rapid Bay
Colonial Tunicates			
T11	*Botrylloides leachii* (Savigny)	X	X
T15	*Botrylloides nigrum* Herdman		X
T20	*Botrylloides* sp.		X
T13	*Botryllus schlosseri* (Pallas)		X
T5	*Podoclavella cylindrica* (Quoy and Gaimard)	X	X
T19	*Pycnoclavella diminuta* (Kott)		X
T34	*Clavelina baudinensis* Kott		X
T12	*Didemnum patulum* (Herdman)		X
T9	*Didemnum* sp.a	X	X
T18	*Didemnum* sp.b	X	X
T32	*Aplidium australiensis* (Kott)		X
T25	*Atapazoa fantasiana* (Kott)		X
T8	*Stolonica australis* Michaelsen		X
T37	*Polysyncraton orbiculum* Kott		X
T23	Chesnut encrusting tunicate		X
T39	Opaque orange encrusting tunicate		X
T38	Pink encrusting tunicate		X
Bryozoans			
B1	*Celleporaria fusca* (Busk)	X	X
B2	*Celleporaria valligera* Harmer	X	X
B3	*Celleporaria pigmentaria* (Waters)	X	X
B4	*Smittina raigii* (Audouin)	X	X
B5	*Cryptosula pallasiana* (Moll)	X	
B6	*Biflustra perfragillis* McGillivray	X	X
B7	Mustard encrusting bryozoan	X	X
Cnidarians			
J5	*Culicia* sp.	X	X
Serpulids			
TW3	*Galeolaria caespitosa* Savigny	X	X
TW4	*Galeolaria hystrix* Morch	X	X
TW2	*Filograma implexa* Berkley		X
Molluscs			
M18	*Chlamys asperrimus* (Lamarck)	X	X
Algae			
A14	*Zonaria augustata* Paperfuzz		X
A17	*Rodymenia australis* Harvey		X
A16	*Erythroclonium muelleri* Sander		X

TABLE 2.2. Sampling schedule for permanent quadrats at Rapid Bay and Edithburgh. An asterisk (*) indicates the samples which were processed. (See Section 2.4.2.2)

SAMPLE DATES

Edithburgh	Rapid Bay
16/12/75*	
20/01/76	
26/02/76	
14/03/76*	
17/04/76	
18/05/76	20/05/76
20/06/76*	14/06/76*
17/07/76	22/07/76
26/08/76	
25/09/76*	04/09/76*
30/10/76	15/10/76
06/12/76*	28/12/76*
11/01/77	29/01/77
08/02/77	
18/03/77*	29/03/77*
18/04/77	
14/05/77	06/05/77
11/06/77*	20/06/77*
20/08/77	30/08/77
26/09/77*	29/09/77*
22/10/77	
27/11/77	02/11/77
27/12/77*	04/12/77*
	20/01/78
	01/03/78*

TABLE 2.3 Summary of Mann-Whitney U-tests comparing the estimator of species evenness, $\hat{J}'$, between Edithburgh and Rapid Bay on the September 1976 and March 1977 sample dates. The P value is for a one tailed test.

Date	Estimator $\hat{J}'$ ±S.D. Edithburgh	Rapid Bay	Mann-Whitney U-test Statistics N1	N2	U	P
September 1976	.74 ±.23	.49 ±.20	9	9	11	<.01
March 1977	.76 ±.20	.39 ±.17	12	12	16	<.001

TABLE 2.4 Summary of Smirnov tests comparing the distributions of species abundances between Edithburgh and Rapid Bay.

ED: Edithburgh RD: Rapid Bay
%CO.: abundances expressed as a percentage of the occupied substratrum
%CT.: abundances expressed as a percentage of the total available substratum
dcf: maximum difference between the cumulative frequency distributions of species abundances at each site.

The P value is for a one tailed test. A .05 significance level was used.

Sample Date	Number of species in sample ED	RB	Smirnov Test Statistics %CO. dcf	P	%CT. dcf	P
June 1976	31	41	.32	.025	.28	>.05 ns
September 1976	31	37	.31	<.05	.34	<.05
December 1976	32	35	.25	>.10 ns	.22	>.10 ns
March 1977	30	36	.25	>.10 ns	.22	>.10 ns
June 1977	30	35	.34	<.05	.32	<.05
September 1977	30	40	.31	<.05	.30	<.05
December 1977	29	37	.30	>.10 ns	.26	>.10 ns

TABLE 2.5 Summary of the Mann-Whitney U-tests comparing the percentage of substratum occupied at Edithburgh with that at Rapid Bay for the seven sample dates common to both sites. The P value is for a one tailed test.

	Mann-Whitney U-test Statistics			
Date	N1	N2	U	P
June 1976	16	16	58	<.01
September 1976	16	16	43	<.001
December 1976	16	16	35	<.001
March 1977	16	16	21	<.001
June 1977	16	16	33	<.001
September 1977	16	16	37	<.001
December 1977	16	16	33.5	<.001

PHOTOGRAPH 2.1 Edithburgh pier

PHOTOGRAPH 2.2 Rapid Bay pier

PHOTOGRAPH 2.3 The Nikonos II underwater camera, the electronic flash and the tripod used to photograph the quadrats.

FIGURE 2.1 A. Map of the Gulf Region of South Australia showing the position of Edithburgh and Rapid Bay.

FIGURE 2.1 B. Edithburgh pier from above

FIGURE 2.1 C. Rapid Bay pier from above

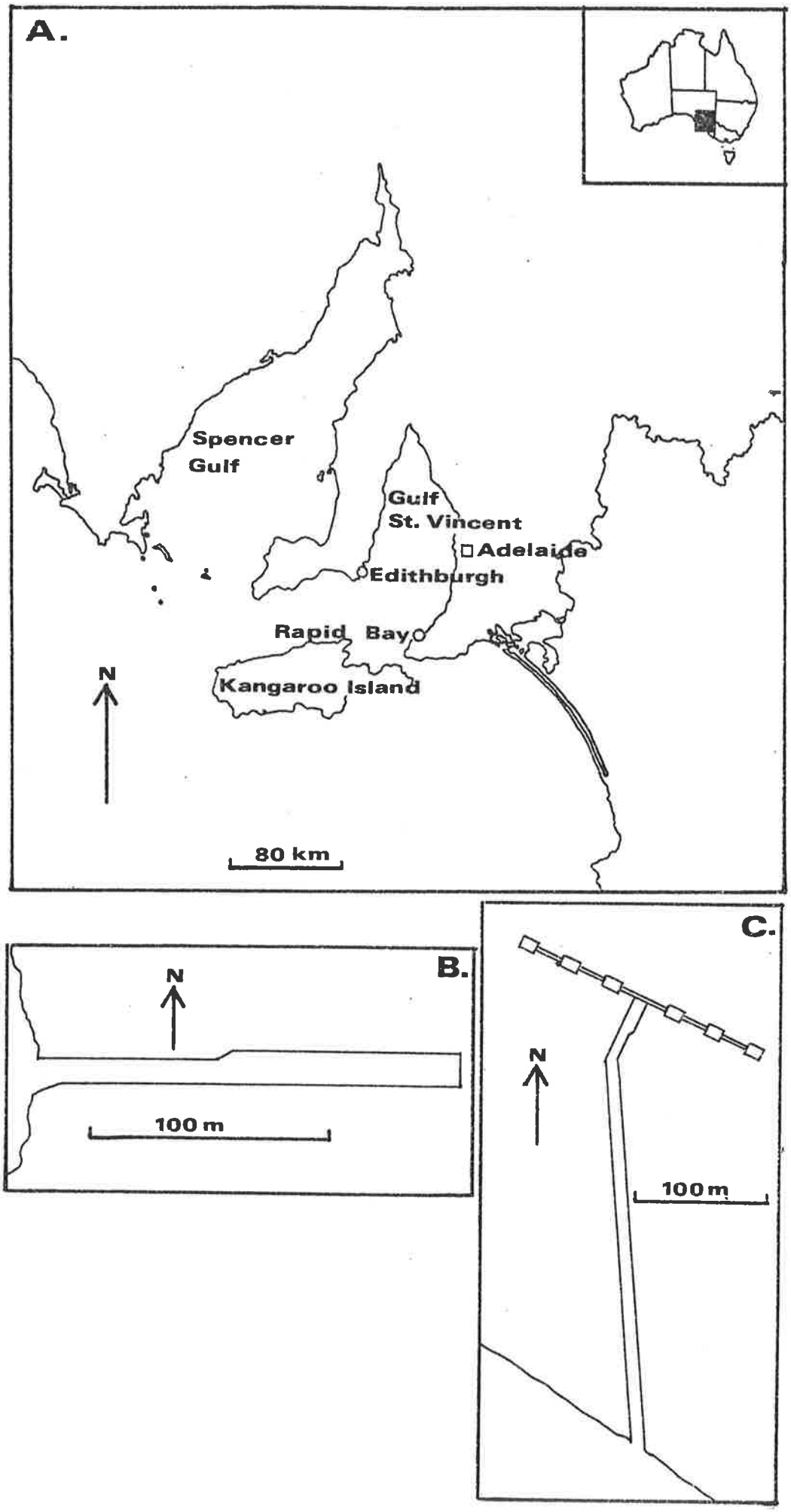

A.
Spencer
Gulf
Gulf
St. Vincent
Adelaide
Edithburgh
Rapid Bay
Kangaroo Island
N
80 km
B.
N
100 m
C.
N
100 m

FIGURE 2.2 The outer half of Edithburgh pier showing the position of the rows and columns of pilings used in the study.

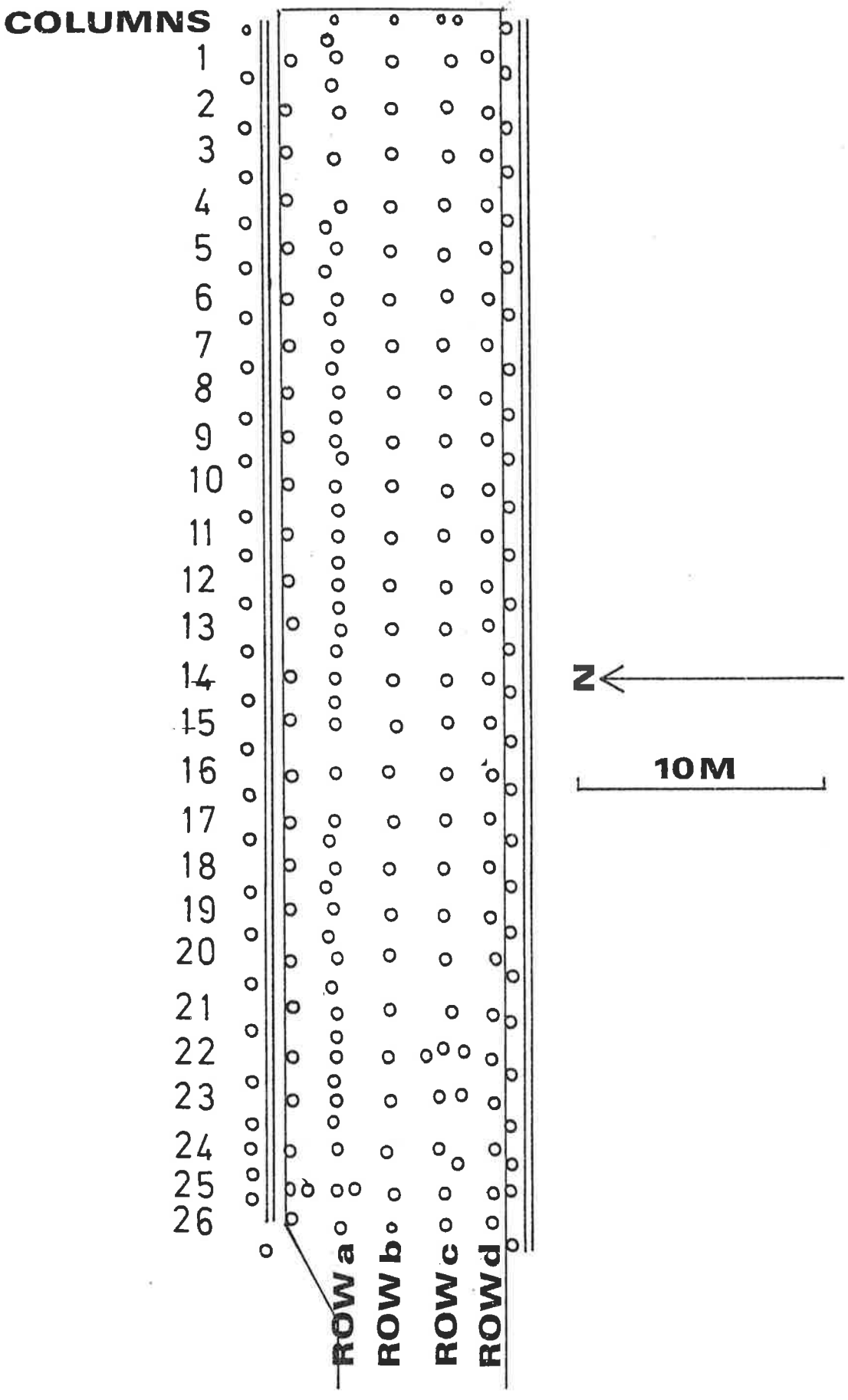

COLUMNS
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
ROW a
ROW b
ROW c
ROW d
N
10 M

FIGURE 2.3 The tee head section of Rapid Bay pier. The six central pilings of each dolphin are indicated by small rectangles.

Inset: Cross-section through a piling showing the position of the four faces. The orientation of the cross-section is the same as for the rest of the figure.

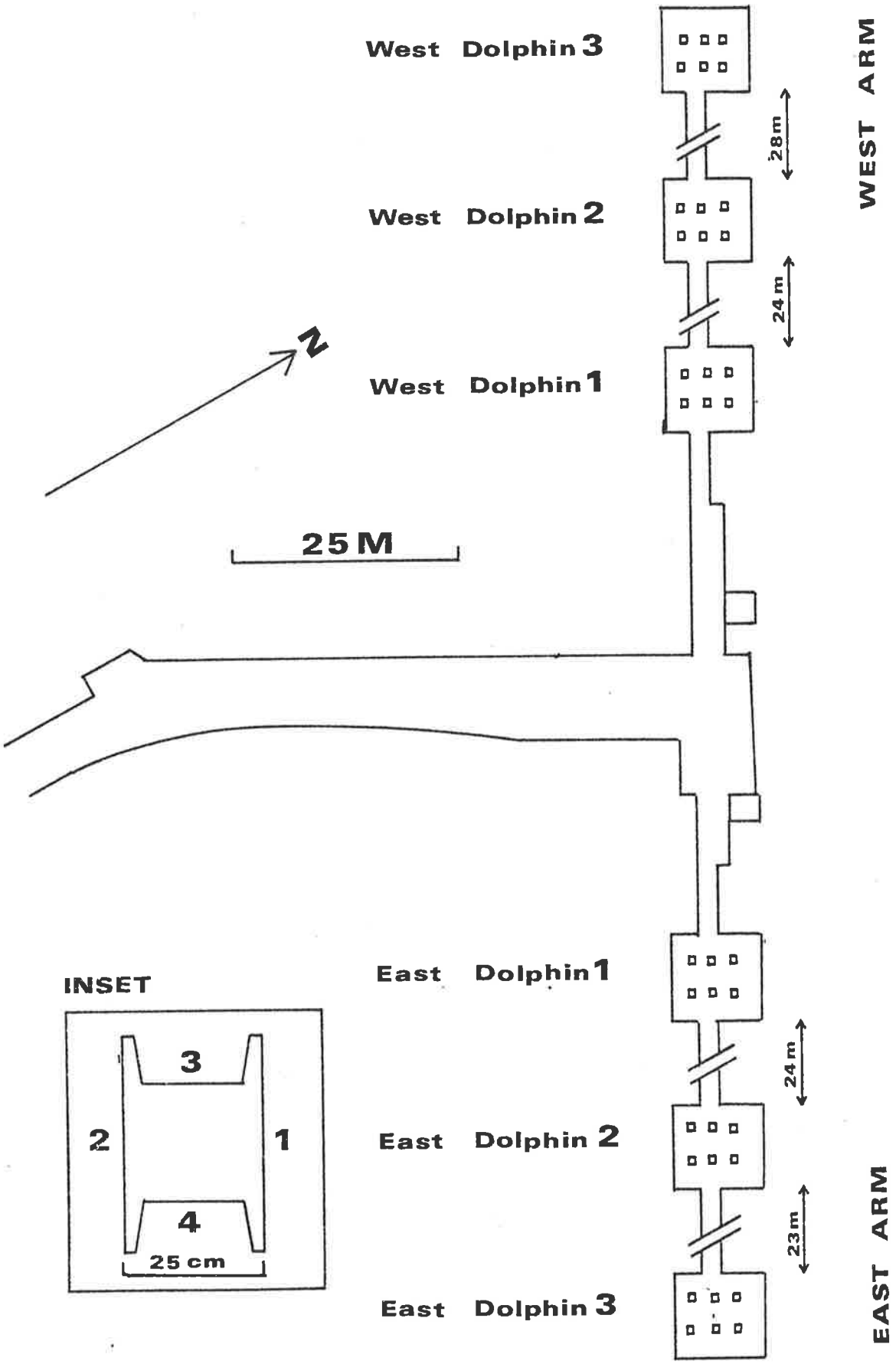

West Dolphin 3
West Dolphin 2
West Dolphin 1
WEST ARM
28m
24 m
N
25 M
East Dolphin 1
East Dolphin 2
East Dolphin 3
EAST ARM
24 m
23m
INSET
3
2
1
4
25 cm

FIGURE 2.4. A. S', the number of species recorded in the 16 quadrats, at Edithburgh and Rapid Bay.

B. J', species evenness calculated for the 16 quadrats, at Edithburgh and Rapid Bay.

Open circles (0) Edithburgh

Closed circles (●) Rapid Bay

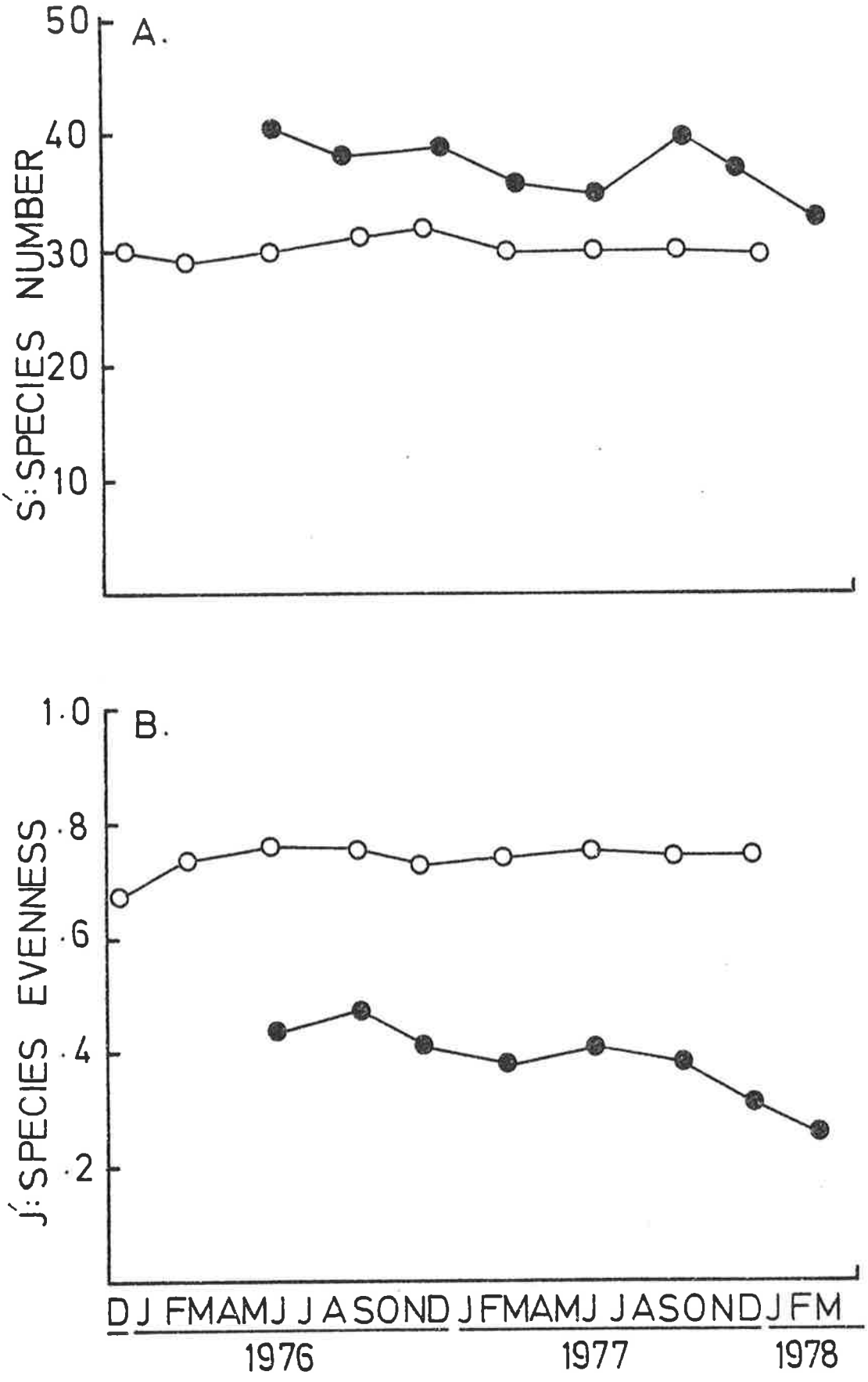

A.
50
40
30
20
10
Ś: SPECIES NUMBER
B.
1·0
·8
·6
·4
·2
J́: SPECIES EVENNESS
D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1976
1977
1978

FIGURE 2.5 Species number vs. quadrat number for Edithburgh and Rapid Bay on

A. September 1976

B. March 1977

Species evenness vs. quadrat number for Edithburgh and Rapid Bay on

C. September 1976

D. March 1977

Arrows indicate point at which curves become horizontal. Open circles (0) Edithburgh, solid circles (●) Rapid Bay

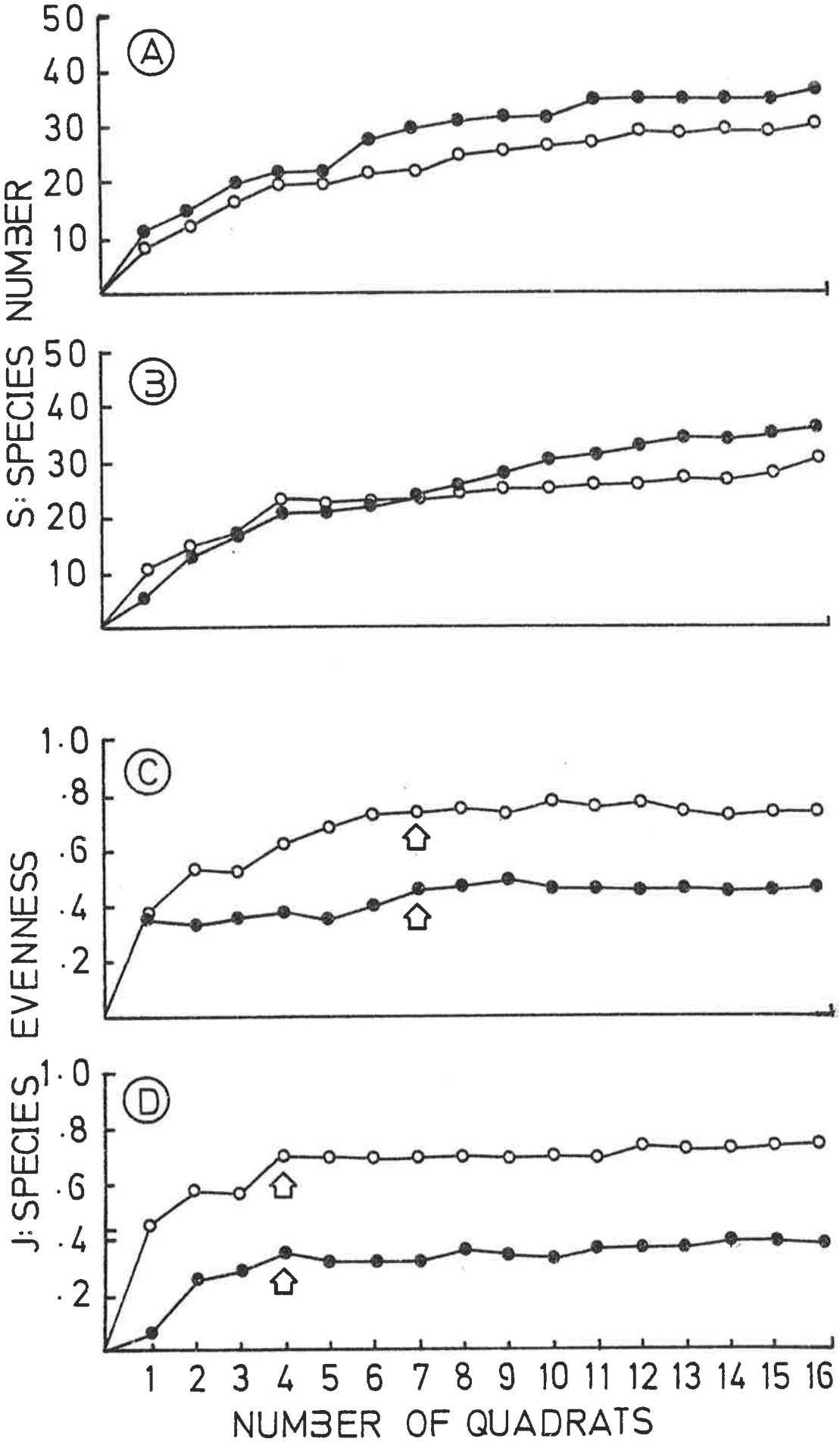

A
B
C
D
S: SPECIES NUMBER
J: SPECIES EVENNESS
50
40
30
20
10
1·0
·8
·6
·4
·2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
NUMBER OF QUADRATS

FIGURE 2.6 The distributions of species abundances at Rapid Bay and Edithburgh for the September 1976 and March 1977 sample dates. Numbers on the X-axis correspond to the lower limits of the 1% class intervals.

A. September 1976, abundances expressed as a percentage of the total available substratum

B. September 1976, abundances expressed as a percentage of the occupied substratum

C. March 1977, abundances expressed as a percentage of the total available substratum

D. March 1977, abundances expressed as a percentage of the occupied substratum

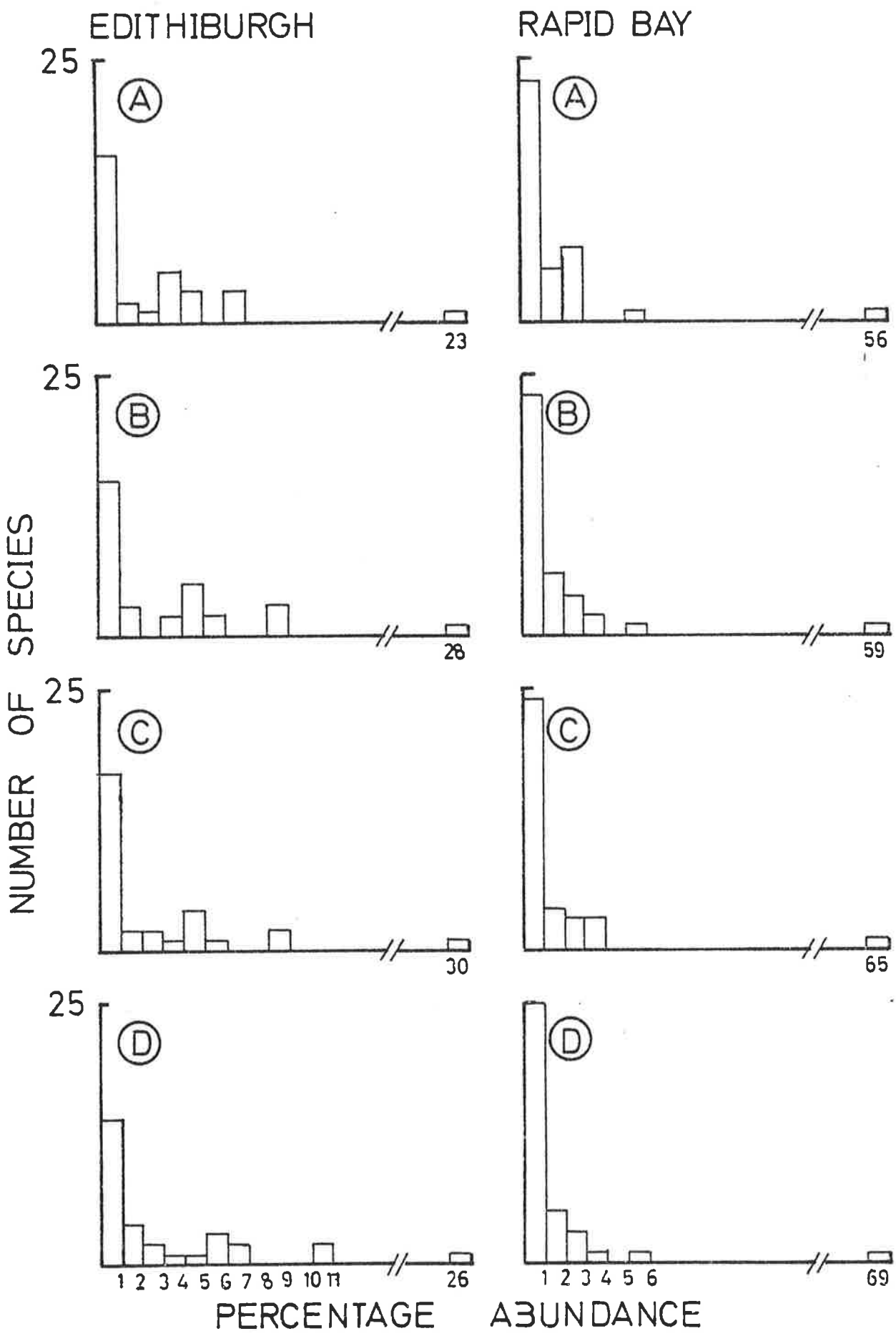

EDITHIBURGH
RAPID BAY
25
A
23
56
B
26
59
C
30
65
D
1 2 3 4 5 6 7 8 9 10 11
26
1 2 3 4 5 6
69
NUMBER OF SPECIES
PERCENTAGE ABUNDANCE

FIGURE 2.7 The percentage cover of all species present (total cover) at Edithburgh and Rapid Bay. Means are indicated by open cirlces (0) for Edithburgh and open squares (□) for Rapid Bay. Vertical lines are standard deviations.

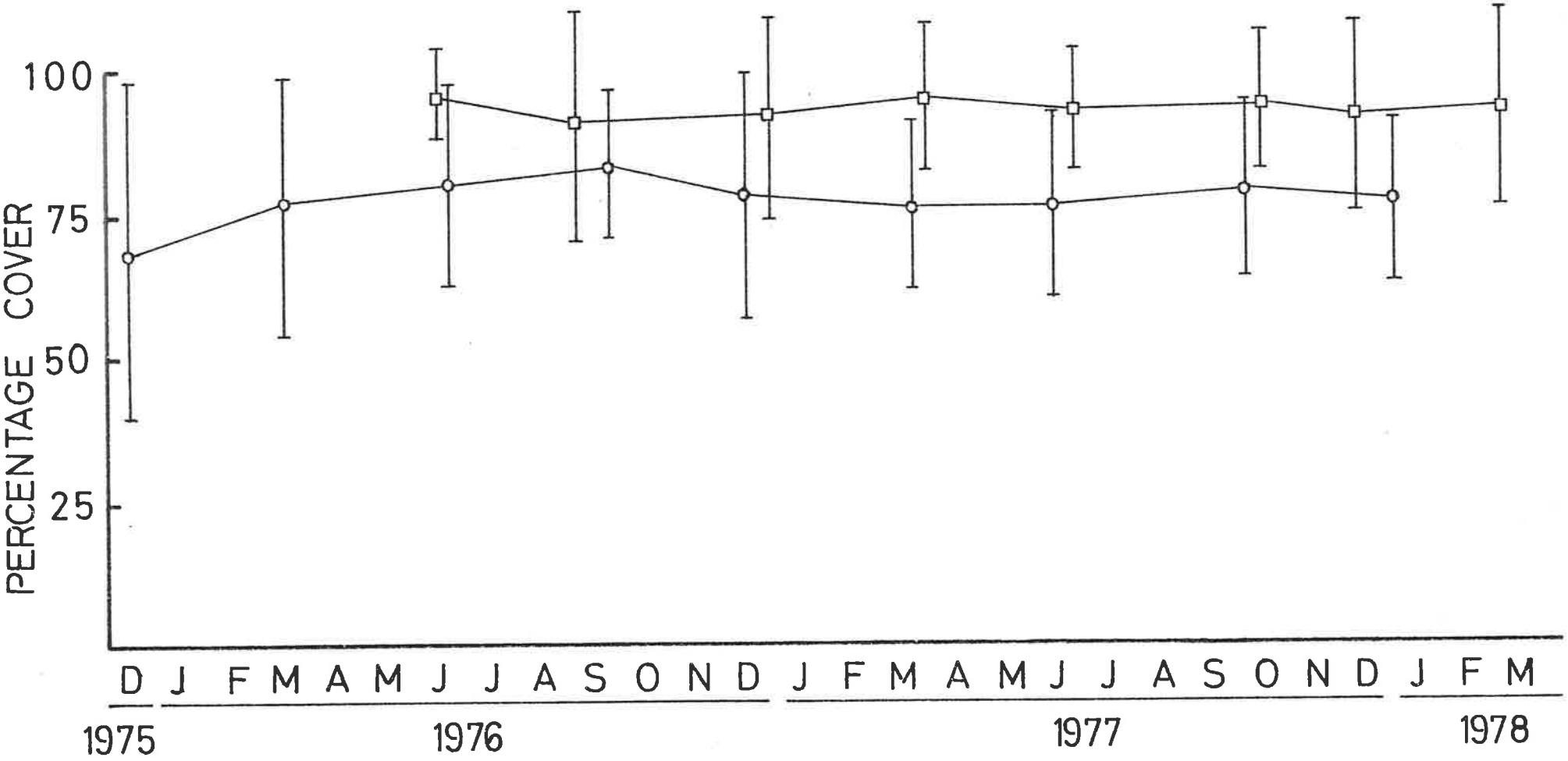

100
75
50
25
PERCENTAGE COVER
D J F M A M J J A S O N D J F M A M J J A S O N D J F M
1975
1976
1977
1978

FIGURE 2.8 The percentage cover of each of the four major phyletic groups at Edithburgh and Rapid Bay

Bar: mean

Line: standard deviation

Black: sponges

Spots: bryozoans

Open: tunicates

Stripes: cnidarians (*Culicia* sp.)

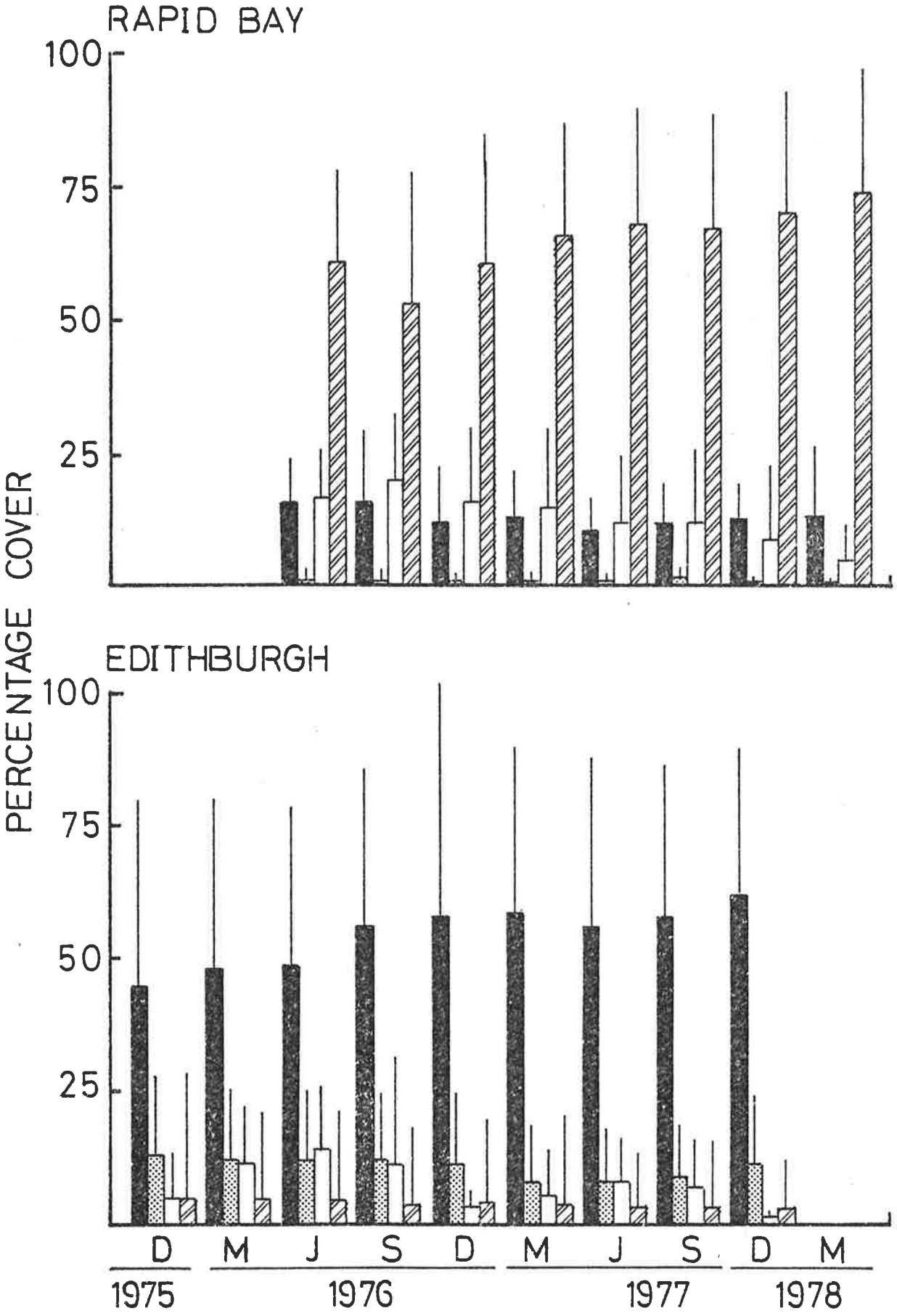

RAPID BAY
EDITHBURGH
PERCENTAGE COVER
100
75
50
25
D
M
J
S
D
M
J
S
D
M
1975
1976
1977
1978

FIGURE 2.9 Mean percentage cover (spot) and standard deviation (vertical line) for the eight sponge species at Edithburgh which attained a mean percentage cover of at least 1% on one sample date

SP1 *Aplysilla rosea*
SP30 *Crella* sp.
SP13 *Callyspongia* sp.
SP47 *Chondropsis* sp.
SP20 *Mycale* sp.
SP5 Red encrusting sponge
SP49 *Lissodendoryx* sp.
SP2 *Aplysilla sulphurea*

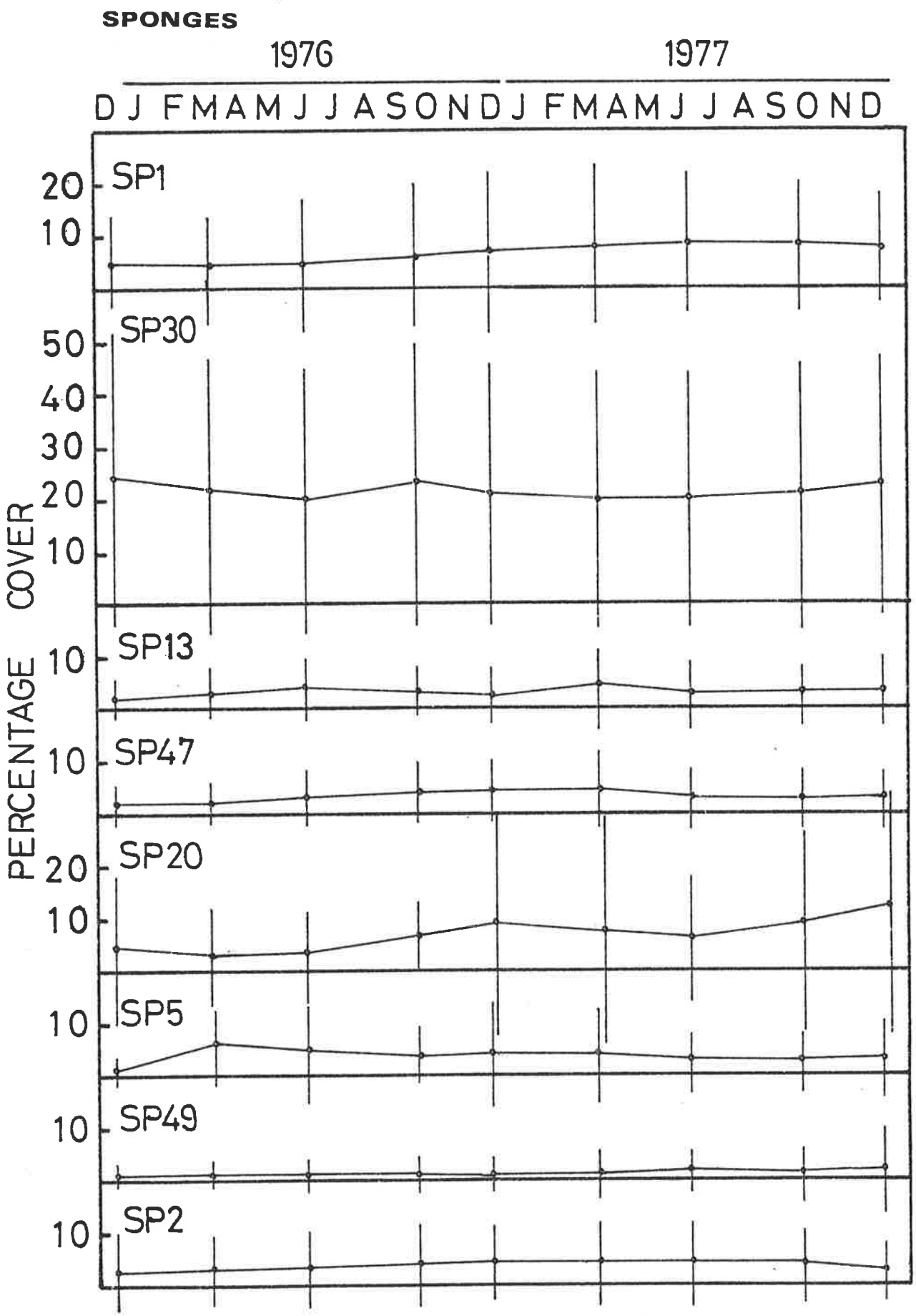

SPONGES
1976
1977
D J F M A M J J A S O N D J F M A M J J A S O N D
SP1
SP30
SP13
SP47
SP20
SP5
SP49
SP2
PERCENTAGE COVER
20
10
50
40
30
20
10
10
10
20
10
10
10
10

FIGURE 2.10 Mean percentage cover (spot) and standard deviation (vertical line) for the four bryozoan species, three tunicates species and *Culicia* sp. at Edithburgh which attained a mean percentage cover of at least 1% on one sample date

B1 *Celleporaria fusca*
B2 *Celleporaria valligera*
B7 Mustard encrusting bryozoan
B3 *Celleporaria pigmentaria*
T11 *Botrylloides leachii*
T18 *Didemnum* sp.b
T9 *Didemnum* sp.a
J5 *Culicia* sp.

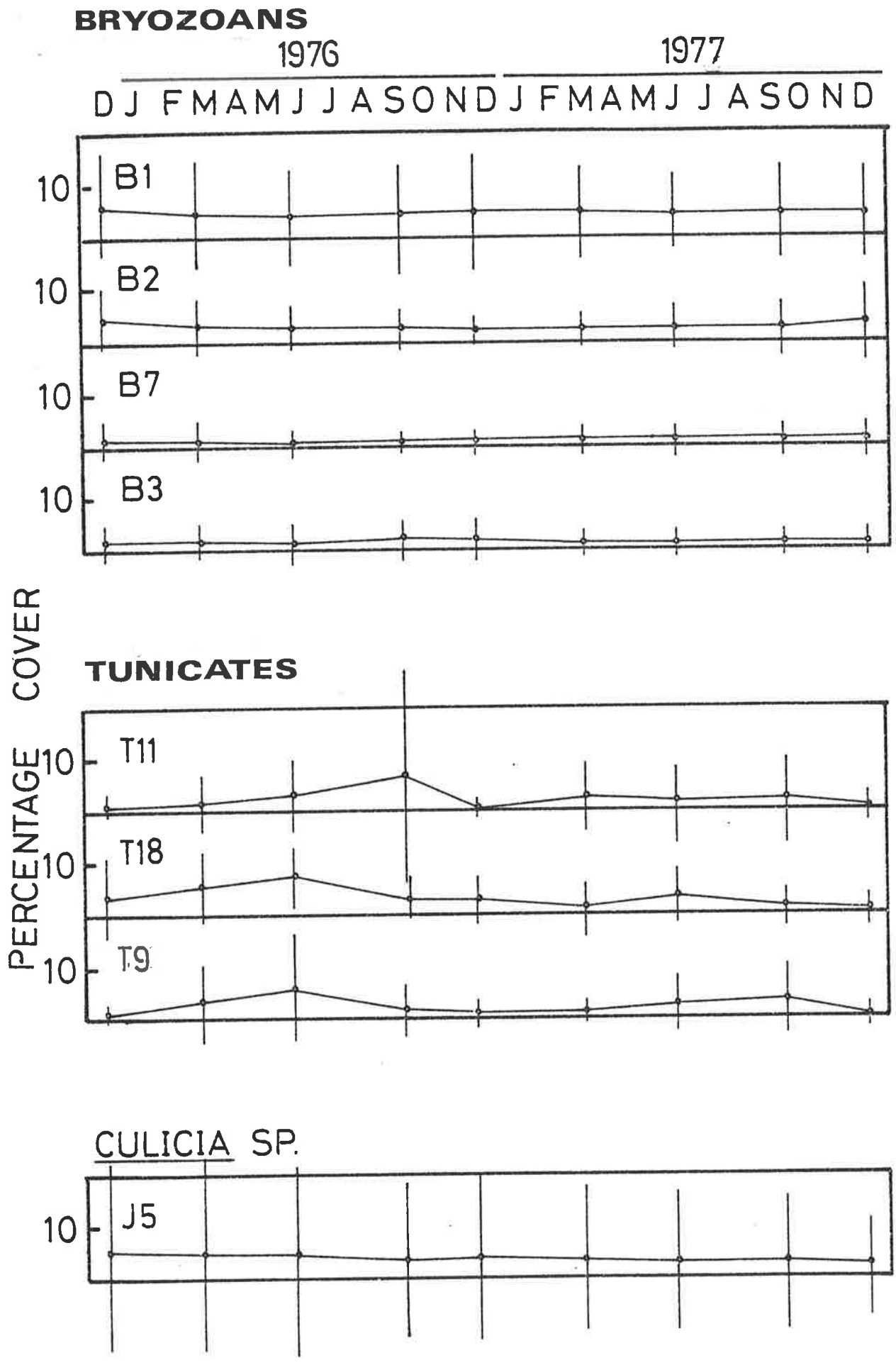

BRYOZOANS
1976
1977
D J F M A M J J A S O N D J F M A M J J A S O N D
B1
B2
B7
B3
10
PERCENTAGE COVER
TUNICATES
T11
T18
T9
CULICIA SP.
J5

FIGURE 2.11 Mean percentage cover (spot) and standard deviation (vertical line) for the five sponge species and *Culicia* sp. at Rapid Bay which attained a mean percentage cover of at least 1% on one sample date

SP1 *Aplysilla rosea*
SP30 *Crella* sp.
SP13 *Callyspongia* sp.
SP5 Red encrusting sponge
SP4 Green encrusting sponge
J5 *Culicia* sp.

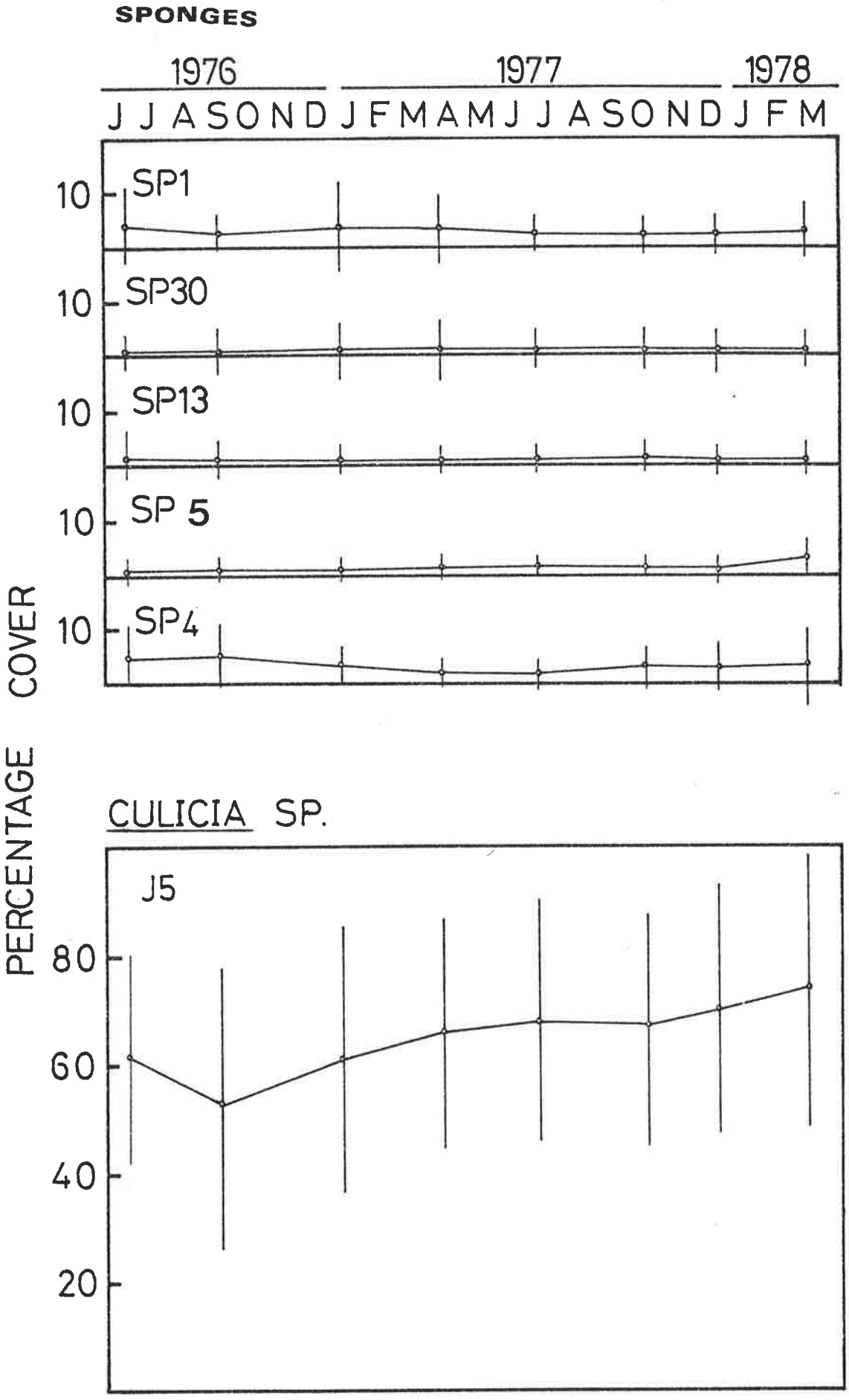

SPONGES
1976
1977
1978
J J A S O N D J F M A M J J A S O N D J F M
SP1
SP30
SP13
SP 5
SP4
10
10
10
10
10
PERCENTAGE COVER
CULICIA SP.
J5
80
60
40
20

FIGURE 2.12 Mean percentage cover (spot) and standard deviation (vertical line) for the ten tunicate species at Rapid Bay which attained a mean percentage cover of at least 1% on one sample date

T11 *Botrylloides leachii*
T9 *Didemnum* sp.a
T23 Chestnut encrusting tunicate
T32 *Aplidium australiensis*
T19 *Pycnoclavella diminuta*
T12 *Didemnum patulum*
T13 *Botryllus schlosseri*
T25 *Atapazoa fantasiana*
T40 *Ascidia thompsoni*
T28 *Cnemidocarpa etheridgii*

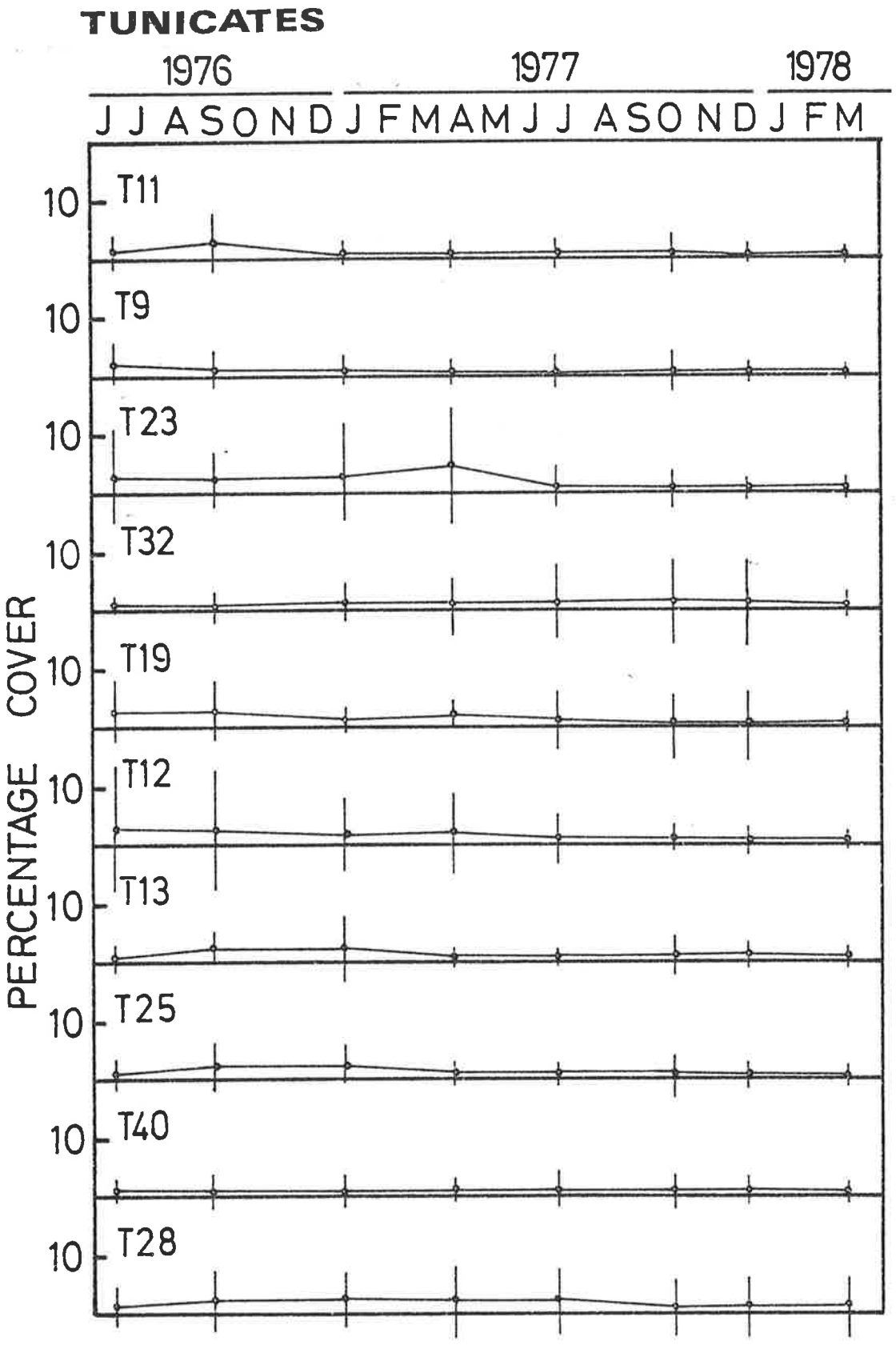
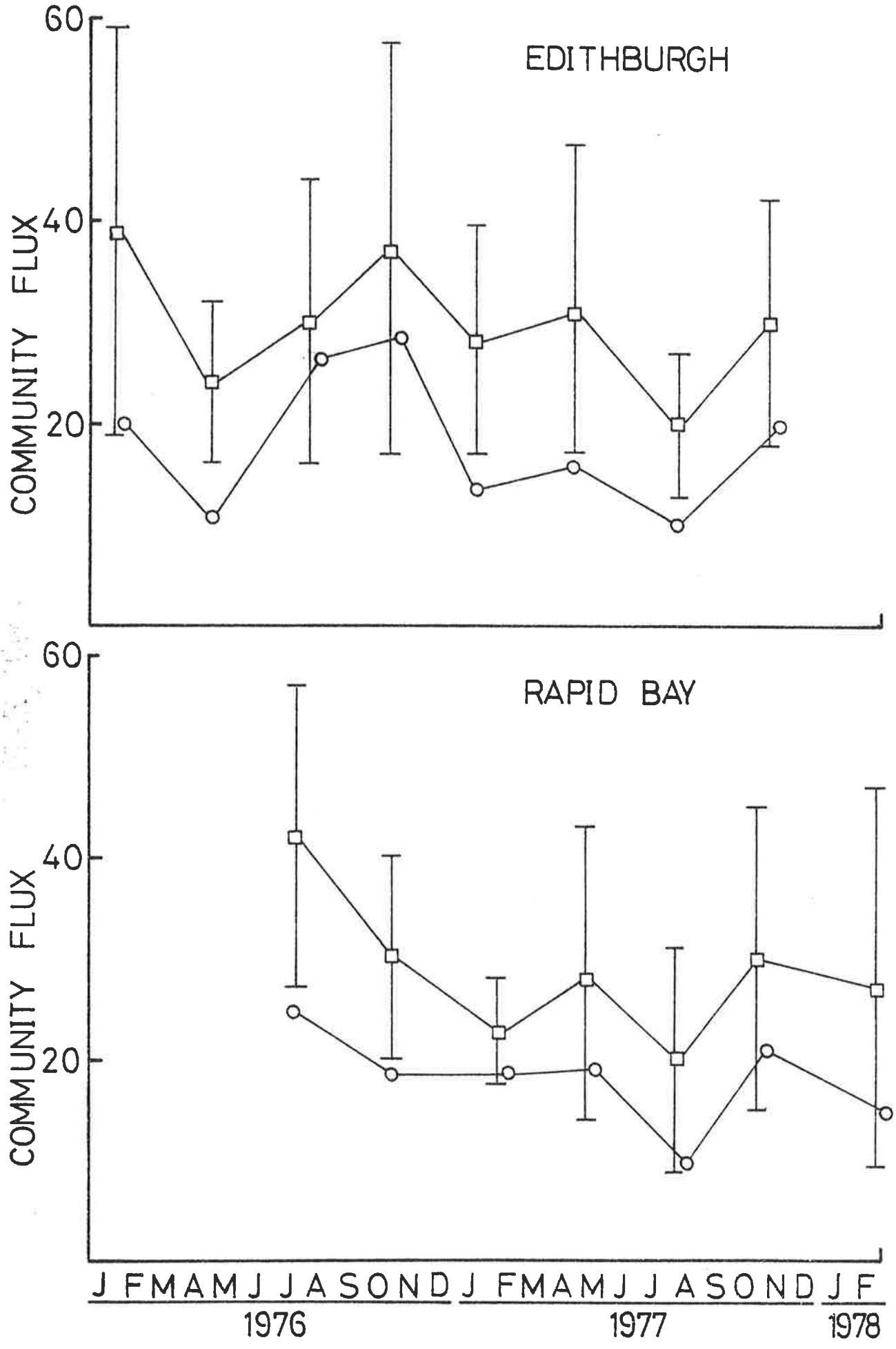

TUNICATES
1976
1977
1978
J J A S O N D J F M A M J J A S O N D J F M
PERCENTAGE COVER
10
T11
T9
T23
T32
T19
T12
T13
T25
T40
T28

FIGURE 2.13 Community flux calculated using the arithmetic means of percentage cover averaged over the 16 quadrats (open circles {0}) and the means of community flux calculated using individual quadrats (open squares {□}) at Edithburgh and Rapid Bay. Vertical lines are standard deviations. Both types of community flux have been calculated for standard 90-day intervals.


EDITHBURGH
RAPID BAY
COMMUNITY FLUX
60
40
20
J F M A M J J A S O N D J F M A M J J A S O N D J F
1976
1977
1978

3.0 COMPETITIVE INTERACTIONS IN THE SESSILE GUILDS

3.1 Introduction

Milne (1961) defines competition "as the endeavour of two (or more) animals to gain the same particular thing, or to gain the measure each wants from the supply of a thing when that supply is not sufficient for both (or all)." This endeavour is generally thought to take one or both of two generalized forms; "interference" and "exploitation" (Park 1954). Interference competition occurs when the utilization of the resource by the individuals or colonies of one species is detrimental to the existence of individuals and colonies of another species. Exploitative competition occurs when utilization of a resource by one species creates a resource shortage for the other. This endeavour has various direct and indirect results such as the death of an individual during a competitive encounter or a reduction in the reproductive potential of a given population due to the shortage of a vital resource.

In hard-substrate communities in the marine environment competition for attachment space and access to the water column takes place in a variety of ways. In situations where the space resource is nearly fully occupied organisms adjacent to each other may crowd, undercut and crush (Connell 1961b, Paine 1971, Dayton 1971), overgrow and smother (Dayton 1971, Stebbing 1973a, b, Paine 1976, Jackson 1977b, Osman 1977, Anger 1978, Russ In press), overshadow (Lang 1971, Dayton 1971) or poison (Bryan, 1973, Jackson and Buss 1975, Al-ogily and Knight Jones 1977) their neighbours. The ability for such competitive interfer-

ence, regardless of the mechanism, is thought to play in important role in the acquisition of the space resource (Paine 1966, Dayton 1971, Connell 1975, Jackson and Buss 1975, Buss and Jackson 1979). Additionally the efficiency with which a sessile species can exploit newly available free space by rapid vegetative growth (Goodbody 1965, Jackson 1977b, In press, Karlson 1978) and/or heavy larval recruitment (Jackson 1977b, In press, Sutherland 1974) is also considered important. Furthermore the longer lived a species and the better able it is to resist larval invasion and/or competitive interference from established organisms the better its chance of monopolizing the substratum (Sutherland 1975, 1978, Karlson 1978).

There is little difficulty in quantifying direct interference competition in fouling communities when the predominant mechanism is overgrowth and smothering. Instances of overgrowth can easily be recorded, even on one sample date, by careful examination of colony interfaces and/or removing live individuals and colonies to reveal the dead remains of other organisms. Such observations have been used to rank species in dominance hierarchies (Osman 1977, Russ In press, Buss and Jackson 1979). However, when alternative mechanisms for interference competition are used quantification is likely to prove more difficult since it would not always be clear if the acquisition of space by one species was at the expense of another unless successive observations could be made at the same site.

In assessing the overall competitive ability of a sessile species compared to others in the same community, its capacity

for exploitative competition will also be relevant. Estimates of growth rate and recruitment rate will indicate the potential of a species to exploit newly available free space and estimates of life-span will indicate how long the species would be likely to monopolize it provided it could resist invasion by other species.

The morphology of a species is considered to be a critical factor in the efficient utilization of primary substratum in different physical environments and under different competitive conditions (Jackson In press, Dahl 1973). For example some sessile species which are incapable of overgrowing and killing their neighbours are, nevertheless, capable of avoiding deleterious competitive interference by virtue of an arborescent or stoloniferous growth form (Osman 1977, Jackson 1977b). Thus growth form will also be relevant to a description of the competitive status of a species.

The aim of the chapter is to quantify, as far as possible, the competitive abilities of the species in both sessile guilds. In particular I seek insights into the competitive strategies of the "dominant" species and of the different phyletic groups.

3.2 Methods

3.2.1 Interference Competition

3.2.1.1 Overgrowth

Examination of successive transparencies of the permanent quadrats used in the sampling schedule of Section 2.4.2.1 revealed that a considerable amount of overgrowth was occuring at

both sites (for examples see Photographs 3.1, 3.2, 3.3, 3.4, 3.5, 3.6). There was no evidence of undercutting, direct crowding, crushing and overshadowing. There was also no obvious evidence of poisoning between organisms adjacent to each other. However this did not exclude the possibility that an organism being overgrown by another was not in part killed by the secretion of allelochemicals by its dominator as well as being smothered.

The amount of overgrowth occuring in each of the permanent quadrats used in the sampling schedule of Section 2.4.2.1 was calculated for each sampling interval at each site by measuring the amount of live tissue present in a quadrat which was covered in the following three months. It is expressed as a percentage of the total area of the quadrat and was calculated for a standard period of 90 days (Appendix IIa). The mean of the figures calculated for a given sample interval was viewed as an estimate of the amount of competitive interference occuring in the sessile guild for that period of time. The mean and standard deviation of overgrowth were plotted against time for all sample intervals at both sites. The overgrowth at Edithburgh was statistically compared to that at Rapid Bay on the six sample intervals common to both sites using a Mann-Whitney U-test. Further statistical comparison is detailed in Section 3.3.1.1.

3.2.1.2 Competitive Hierarchy

The interference competitive ability of a species at each site was assessed using a competitive hierarchy based on the

overgrowth records from the 16 permanent quadrats. For all pairwise interactions where overgrowth occured the winner was recorded. If the number of observations for a given species pair was equal to or exceeded five, the competitive relationship between the two species was assessed in the following manner. The null hypothesis was that the two species were equally likely to win a competitive encounter. The binomial test (Siegel 1956) was then used to test whether the observed outcomes of competitive interactions were consistent with this null hypothesis (0.05 significance level). If the null hypothesis was rejected, the species which won the majority of encounters was said to be competitively dominant; otherwise the pair of species were designated competitively equal.

This method had one major shortcoming. No attempt was made to measure the speed at which overgrowth occured between any two species thus the relative defensive capacities of individual species were not accounted for. Two species which are overgrown by the same set of species at different rates are obviously not competitively equivalent even if both are equally likely to overgrow each other. This aspect of the overgrowth interactions reported in the results section is considered in the discussion.

Lastly, whenever possible, it was noted if overgrowth always resulted in the death of the overgrown colony.

3.2.2 Exploitative Competition

Ideally as indicated in Section 3.1 estimates of growth rate, recruitment rate, lifespan and descriptions of form are

necessary to define the capacity of a species for exploitative competition.

Due to the scarcity of free space in both communities there were few opportunities in the transparencies of the permanent quadrats described in Section 2.4.2.1 to measure the growth rates of different species under optimal conditions. Furthermore measurement of the increase in area of most colonies was complicated by the fact that colonies of the same species often fused, occasionally divided, were often partially overgrown and were frequently not completely included in the transparency. For these reasons estimates of growth rate were not made by calculating increases in area over time of the colonies seen in the permanent quadrats. The following alternative was used.

At Edithburgh a large number of artificially cleared patches were made during the study period as detailed in Section 4.2.1.1. A variety of species invaded these patches through the vegetative extension of colonies adjacent to the patch and by larval recruitment. This provided an opportunity to measure the rate at which a colony was able to grow over unoccupied substratum. At Rapid Bay opportunities to make a similar measurement were presented by the clearance of large areas of *Culicia* sp. in the experimental quadrats described in Section 6.2.1.1.

The distance the leading edge of a colony travelled before it abutted another colony was measured. The rate of growth in mm/day was calculated by dividing this figure by the time taken to travel the distance. The growth rates of individual colonies are presented in Appendix IIb.

It is worth noting that the growth rate of a species calculated in this fashion is likely to be a function of colony size, season, locality and intrinsic differences between the individual colonies measured. I have made no attempt to identify the sources of the variation between independent measurements for one species because the sample size was too small (see Appendix IIb, Table 3.4 and 3.5). Therefore these estimates are crude and will probably blur the more subtle differences between species. However, in the absence of controlled field manipulations to produce more accurate estimates, they will serve to identify the grosser differences between certain species and phyla.

The recruitment rate (number of colonists/unit time/unit area) will be a function of the suitability of the substratum available to the larvae, the size of the population of reproducing adults, the number of young produced per adult, mortality factors prior to settlement and temporal (seasonal and between years) variation in reproductive patterns. Many newly settled colonies could not be detected, let alone identified, in transparencies until they reached a size of at least $9mm^2$. Additionally during dives fish were often observed grazing on newly settled colonies that were only $4mm^2$ in size (*Didemnum* sp. in particular). Thus it appears certain that many new recruits of various species were being removed before they could be detected in transparencies particularly as the intervals between successive transparencies were approximately three months long. For this reason I felt that recruitment rate measured in

transparencies could lead to variably biased estimates of the actual recruitment rate for different species and could be rather misleading if used as an indication of a species potential to acquire new space through the medium of dispersive larvae. This aspect of the species competitive ability was not accounted for.

Estimates of life span were made by examination of successive transparencies of permanent quadrats and from observations made during the periods spent working at both field sites. The figures listed in Table 3.4 and Table 3.5 in Section 3.3.2 are equal to the range of the life spans of colonies/individuals seen for that species during the time spent working at each site. This range does not include colonies/individuals which obviously died due to factors other than senescence.

A qualitative description of the morphology of each species is given using Jacksons' (In press) terminology as reproduced in Table 3.1

3.3 Results

3.3.1 Interference Competition

3.3.1.1 Overgrowth

The mean of overgrowth recorded in the 16 quadrats at Rapid Bay was always lower than the mean of overgrowth recorded in the 16 quadrats at Edithburgh in each sample interval common to both sites (Fig. 3.1). Overgrowth at Rapid Bay was significantly less (.05 probability level) than overgrowth at Edithburgh for each of the three sample intervals from September 1976 until June 1977 (Table 3.2). If the six sample inter-

vals common to both sites are treated as six independent samples giving six independent estimates of overgrowth in each sessile guild for the 18 month period in question (an assumption that may not be seriously in error as discussed in Section 2.4.2.3.4) then overgrowth at Rapid Bay was significantly less than at Edithburgh (Mann-Whitney U-test N1=N2=6, U=3, P= .008).

At both sites the standard deviations around the means are large (>50% of the means) indicating that there was considerable variability between quadrats in the amount of overgrowth that was occuring. Examination of the overgrowth data for individual quadrats also shows that the range in values between sample intervals for one quadrat was large in relation to the mean values (Appendix IIa). Overgrowth was not spatially or temporally uniform when measured on the scale of a 20cm x 30cm quadrat at either site.

3.3.1.2 Competitive Hierarchy

At Edithburgh there were 1089 possible pairwise interactions where overgrowth could occur but only 164 of these were observed. Of these only 56 involved five or more observations. These have been compiled into contact matrices for interactions within phyla (Figs. 3.2A , 3.3A, C) and between phyla (Figs. 3.4A,C, 3.5A, C, E). The left-hand number in each cell equals the number of wins for the species in that column. The right-hand number equals the number of wins for the species in that row. In each cell an arrow points towards the superior species or a cross indicates competitive equivalence. The species repre-

sented in these matrices include all those species in the sessile guild which attained a maximum mean percentage cover of at least 1% on one sample date in the sampling schedule outlined in Section 2.4.2.1. Omission of the rarer species was unavoidable but I consider it to be unimportant because they are likely to play only a minor role in the structure and organization of the sessile guild due to their exteremely low abundance.

There was not a clearly defined linear hierarchy between the sponge species (Fig. 3.2A). For example *Aplysilla rosea* was superior to *Crella* sp. and *Mycale* sp. but *Crella* sp. and *Mycale* sp. were equivalent. However the following generalizations can be made. The Red encrusting sponge (SP5) was inferior in six out of six pairwise comparisons indicating that it was a poor interference competitor in relation to the other sponge species. *Callyspongia* sp. and *Aplysilla rosea* were superior in four out of five and three out of five comparisons respectively. Both were equivalent in the remaining comparisons. *Mycale* sp. was superior once and equivalent twice in three comparisons. *Crella* sp., *Aplysilla sulphurea*, and *Chondropsis* sp. were superior in some of the comparisons in which each was involved and inferior in others. Even though all possible combinations between these sponges were not reported there is sufficient evidence to suggest the *Aplysilla rosea* and *Callyspongia* sp. were the best interference competitors in relation to the other common sponges. *Mycale* sp., *Crella* sp., *Aplysilla sulphurea* and *Chondropsis* sp. rank intermediately while the Red encrusting sponge (SP5) ranks lowest. *Lissodendoryx* sp. was

only involved in one pair-wise comparison with *Crella* sp. and scored equivalently. Its status is, therefore, uncertain but it is likely to be intermediate.

There was no clear circular set of competitive relationships (A superior to B superior to C superior to A) amongst these sponges (Fig. 3.2A) although the overall pattern of species interaction is netlike (see Buss 1976).

Only one pair-wise comparison was made between tunicates (Fig. 3.3A) and four pair-wise comparisons were made between bryozoans (Fig. 3.3C). In both cases there was insufficient evidence to detect competitive hierarchies of any sort between the common species within the phylum.

Tunicate species were superior to sponge species in nine out of ten comparisons (Fig. 3.4A) and superior to bryozoan species in six out of six comparisons (Fig. 3.5A). Sponges species were superior to bryozoan species in nine out of 13 comparisons and equivalent in four comparisons (Fig. 3.4C). Sponge and tunicate species were superior to *Culicia* sp.and *Galeolaria* spp. in all comparisons (Fig. 3.5C,E). These results indicate that tunicates are the best interference competitors in the sessile guild with sponges the next best and bryozoans, *Culicia* sp. and *Galeolaria* spp. the worst. The competitive relationship between bryozoans, *Culicia* sp. and *Galeolaria* spp. was not established. When substratum is in short supply tunicates will overgrow sponges and tunicates and sponges will overgrow bryozoans, *Galeolaria* spp. and *Culicia* sp.

It is noteworthy that a superior species does not always

overgrow an inferior species in every competitive encounter (Figs. 3.2A, 3.3C, 3.4A,C) thus the preceding statement must be viewed as a generalization rather than a description of an inevitable sequence of events.

Additionally it was noted that tunicates did not always smother the organisms they overgrew especially if the overgrowth occured two months or less prior to the senescence of the tunicate colony. On several occasions in the 16 permanent quadrats after a tunicate colony had sloughed off old sections of previously covered bryozoan and sponge colonies recommenced growth.

At Rapid Bay there were 2500 possible pair-wise interactions where overgrowth could occur but only 98 of these were observed. Of these only 14 involved five or more observations. Twelve of these have been compiled into a contact matrix (Fig. 3.6A) and the remaining two are referred to below.

The species represented in these 14 comparisons did not include all those species in the sessile guild which attained a maximum mean percentage cover of at least 1% on at least one sample date in the sampling schedule outlined in Section 2.4.2.1. Two solitary tunicates *Cnemidocarpa etheridgii* and *Ascidia thompsoni* and three colonial tunicates, *Aplidium australiensis*, *Didemnum patulum* and *Botryllus schlosseri* were omitted.

Only one within phylum interaction was observed often enough to be tested for significance. *Crella* sp. was dominant to the

Red encrusting sponge (SP5) which it overgrew in six out of six overgrowth interactions. No conclusions could be made about the competitive relationships of species within phyla at Rapid Bay.

Excluding *Culicia* sp.and *Galeolaria* spp. only one between phylum interaction was observed often enough to be tested for significance. In this case *Atapazoa fantasiana* was superior to the Green encrusting sponge (SP4) which it overgrew in seven out of seven overgrowth interactions. If all the observed pair-wise interactions that did not involve five or more observations are considered tunicates overgrew sponges, sponges overgrew bryozoans and tunicates overgrew bryozoans in 35 out of 36, four or of four and 22 out of 22 occasions respectively. Although these data are pooled from almost as many different species-pairs as individual observations it suggests that the competitive relationships between tunicates, sponges and bryozoans follow the same general pattern as observed at Edithburgh.

Culicia sp. was inferior to two sponge species and equivalent to one (Fig. 3.6A). *Culicia* sp. was also inferior to four tunicate species and one bryozoan species (Fig. 3.6A). Additionally in 16 and 19 other overgrowth encounters with sponges and tunicates respectively it was overgrown.

Galeolaria spp. were inferior to three tunicate species and one bryozoan species (Fig. 3.6A). In five and three other overgrowth encounters with sponge species and tunicate species respectively it was overgrown.

The preceding evidence indicates that *Culicia* sp. and *Galeolaria* spp. are poor interference competitors which are overgrown in the majority of competitive encounters, if not all in the case of *Galeolaria* spp. with the other species in the sessile guild at Rapid Bay. The competitive relationship between *Culicia* sp. and *Galeolaria* spp. could not be assessed from the data presented here.

In summary, when free substratum is in short supply at Rapid Bay tunicates will overgrow sponges and sponges and tunicates will overgrow bryozoans, *Culicia* sp. and *Galeolaria* spp.

3.3.2 Exploitative Competition

3.3.2.1 Growth Rate

Only those species listed in the previous section of the results were included in the following assessment of ability to exploit the primary substratum. Assessment of all species at both sites, apart from being impossible for the very rare species, would be pointless since the interference ability of the species not included in the previous section would not be defined. Additionally pair-wise comparisons of growth rates corresponding exactly to those pairwise comparisons reported for interference interactions were made for all species using a Mann-Whitney U-test. The results of these tests are reported in the text or have been compiled into contact matrices (Fig. 3.2B, 3.3B,D, 3.4B,D, 3.5B,D,F, 3.6B). In each cell an arrow points towards the species which had a significantly faster

growth rate than the other or a cross indicates that the growth rates were equivalent. A one tailed test and a .05 significance level were used.

At Edithburgh the growth rates of sponges varied significantly between species (Table 3.3). *Aplysilla rosea* had a significantly slower growth rate than other sponges in all five pairwise comparisons (Fig. 3.2B). *Callyspongia* had a significantly faster growth rate than *Aplysilla rosea* and *Aplysilla sulphurea* and a growth rate equivalent to *Crella* sp. and the Red encrusting sponge (SP5) (Fig. 3.2B). Both *Aplysilla rosea* and *Callyspongia* sp. ranked highly as interference competitors in relation to other sponges but did not have the correspondingly highest growth rates (Compare Fig. 3.2A and 3.2B and see Table 3.4). The growth rates of sponges in the remaining pairwise comparisons were equivalent (Fig. 3.2B) despite the fact that *Mycale* sp. had a mean growth rate considerably higher than the others (Table 3.4). The Red encrusting sponge (SP5) had a significantly higher growth rate than *Aplysilla sulphurea* to which it was competitively equivalent (compare Fig. 3.2A and 3.2B). Obviously amongst the sponge species considered here a faster growth rate is not necessarily correlated with superior interference capacity or vice-versa.

The growth rates of tunicates and bryozoans respectively also varied significantly between species at Edithburgh (Table 3.3). As can be seen from a comparison of Fig. 3.3A and Fig. 3.3C with Fig. 3.3B and Fig. 3.3D respectively faster growth rate was not necessarily correlated with superior interference

ability for within phylum comparisons of tunicates and bryozoans.

Tunicates had significantly faster growth rates than sponges in four out of ten comparisons and faster growth rates than bryozoans in six out of six comparisons (Fig. 3.4B, 3.5B). Sponges had faster growth rates than bryozoans in 12 out of 13 comparisons (Fig. 3.4C). Tunicates and sponges had equivalent growth rates in six out of ten occasions (Fig. 3.4B) and on the one occasion when a sponge did not grow significantly faster than a bryozoan the growth rates were equivalent (Fig. 3.4B). These comparisons indicate that in the sessile guild at Edithburgh the common sponge and tunicate species are able to exploit newly available free space by vegetative growth more rapidly than do the bryozoan species. This generalization is supported by the fact that mean growth rates of all sponge and tunicate species are greater in every instance than the mean growth rates of bryozoans (Table 3.4). Although no one tunicate species had a significantly greater growth rate than all other sponge species to which it was compared all tunicate species had higher mean growth rates than all sponge species except *Mycale* sp. (Table 3.4). This suggests, as do the pairwise comparisons of growth rates between sponge and tunicate species in Figure 3.4B, that the common colonial tunicate species in the sessile guild at Edithburgh are, on average, able to exploit newly available free space by vegetative growth as well as, if not better than, the common sponge species.

Culicia sp. had a significantly slower growth rate than both *Callyspongia* sp. and *Didemnum* sp. a (Fig. 3.5D and 3.5F). All sponge and tunicate species had larger mean growth rates than the mean growth rate for *Culicia* sp. with the exception of the sponge *Aplysilla rosea* (Table 3.4). This evidence suggests that *Culicia* sp. was unable to exploit free space by vegetative growth in the sessile guild at Edithburgh as rapidly as the common sponge and tunicate species.

Although a direct measurement of the growth rate of *Galeolaria* spp. was not made it can be safely assumed due to its solitary life form, deterministic growth pattern, and extremely small size that its capacity to exploit newly available free space by vegetative growth was far less than any other colonial species in the sessile guild with the possible exception of *Podoclavella cylindrica*. For this reason its growth rate has been taken as zero in Table 3.4 and Table 3.5.

At Rapid Bay the growth rate of tunicates varied significantly between species (Table 3.3). The growth rates of sponges did not differ significantly between species (Table 3.3) and the growth rates of the two bryozoan species were equivalent (Mann-Whitney U-test N1=N2=3, U=3, P=.35).

It is worth noting that *Crella* sp. was superior to the Red encrusting sponge (SP5) in terms of overgrowth (Section 3.3.1.2) despite the fact that they had equivalent growth rates. (Table 3.3). This was also the case at Edithburgh (Figs.3.2A,B).

Since no overgrowth interaction between tunicate species was observed often enough to assess statistically at Rapid Bay

(Section 3.3.1.2) I felt a comparison of the growth rates of these species would not contribute significantly to understanding the competitive relationships between the more common species at Rapid Bay.

Excluding comparisons involving *Galeolaria* spp. only one interphyletic comparison in the section on interference competition was reported which did not involve *Culicia* sp. In this case the Green encrusting sponge (SP4) had a greater growth rate than the colonial tunicate *Atapazoa fantasiana* (see Table 3.5 Mann-Whitney U-test, N1=6, N2=5, U=2, $P<.05$) although the latter was superior to the Green encrusting sponge (SP4) in terms of overgrowth (Section 3.3.1.2). However the range in mean growth rates of the sponge species and tunicate species listed in Table 3.5 overlap considerably suggesting that there was no clear cut difference in the abilities of these two phyletic groups to exploit newly available free space by vegetative growth in this sessile guild.

The mean growth rates of the two bryozoan species did not over lap with the range in mean growth rates of the sponges and tunicates species listed in Table 3.5. This suggests that they were unable to exploit newly available free space as rapidly as the sponge and tunicate species.

At Rapid Bay *Culicia* sp. had a significantly faster growth rate than all of the eight species to which it was compared (Fig. 3.6B). It was, however, inferior to all these species in terms of overgrowth except the Green encrusting sponge (SP4) to which

it was equivalent (Fig. 3.6A,B). Additionally the mean growth rate of *Culicia* sp. was greater than the mean growth rates of all other species included in the analysis of competitive ability (Table 3.5). Thus the evidence suggests that *Culicia* sp. was able to exploit newly available free space by vegetative growth more rapidly than the other more common species in the sessile guild at Rapid Bay.

For the same reasons listed earlier the ability of *Galeolaria* spp. to exploit newly available free space by vegetative growth was assumed to be far less than that of the common colonial species in the sessile guild at Rapid Bay.

Five of the nine species common to both sessile guilds and included in the previous analysis had equivalent growth rates at both sites (Table 3.6). The Red encrusting sponge (SP5), *Botrylloides leachii* and *Didemnum* sp.a had significantly higher growth rates at Edithburgh while *Culicia* sp. had a significantly higher growth rate at Rapid Bay. Although the mean growth rate of *Crella* sp. at Edithburgh was at least double that at Rapid Bay the Mann-Whitney U-test did not indicate there was a significant difference. The very small sample size at Rapid Bay (mean growth rate was calculated from only two figures) is worthwhile considering in relation to this outcome. Despite this the comparison in Table 3.6 shows that some species may not be able to exploit free space by vegetative growth at the same rates in different localities.

3.3.2.2 Lifespan

The majority of species which were considered at both sites had relatively long life-spans (greater than one year; see Tables 3.4 and 3.5). Three colonial tunicates at Edithburgh and four colonial tunicates at Rapid Bay were the only annuals with a maximum colony life-span of ten months. Colonies of most species included in this analysis lived far longer than the time period of the sampling schedules in Section 2.4.2.1 thus their life-spans cannot be accurately estimated. They are recorded as having life-spans greater than a certain known minimum (Table 3.4 and 3.5).

Certain easily identifiable colonies of *Mycale* sp., *Crella* sp., *Celleporaria fusca*, *Celleporaria valligera* and *Culicia* sp. have monopolized areas of pilings at both sites from June 1975 until June 1979 indicating that these species at least have life spans of more than four years.

3.3.2.3 Growth Form

Most species which were considered in this section had sheet-like growth forms (Tables 3.4 and 3.5). Since these species were the common species the greater part of the occupied substratum at both sites was covered by low, essentially two-dimensional, encrustations.

At Edithburgh a greater number of species included in the list had growth forms which produced vertical growth (mounds and vines see Tables 3.4 and 3.5). Thus the sessile guild at this site would be expected to have a larger three-dimensional

component than the sessile guild at Rapid Bay. Visual impressions while diving support this proposition.

All of the sponges reported here, with the exception of *Callyspongia* sp. have been observed to produce flat encrustations through vegetative growth that are considerably thinner, vertically, than the parent colonies. These encrustations are usually produced when free space is made available next to a colony and the side of the colony adjacent to the free space is damaged and torn in the process. These encrustations thicken and take on the typical growth form of the colony after they have grown over the newly formed free space. Many of the growth rate estimations made for sponges involved these encrustations and casual observations suggest that they grew very much faster than the thickened portions of the colonies.

Two species of bryozoans, *Celleporaria fusca* and *Celleporaria valligera* had variable growth forms. Both species begin growth as small flattened discs and at some time commence frontal budding (see Banta 1972) which produces vertical fronds (see Frontispiece and Photograph 3.6). Massive dome shaped colonies up to 50cm in diameter can be produced by this budding process. Casual observations suggest that vertical growth commences only when the substratum becomes crowded and colonies of other species begin to abutt the bryozoan colonies.

3.4 Discussion

Although a greater proportion of the substratum was occupied at Rapid Bay than at Edithburgh (Section 2.4.3.3) the

amount of overgrowth was less at Rapid Bay. Thus it appears, superficially, that competition for space was less in a situation where it was in shorter supply. However this proposition is based on the assumption that space is competed for only by the process of competitive interference. Since many species in both sessile guilds could exploit available substratum by the vegetative extension of established colonies this assumption may not be correct.

As explained in Section 2.4.2.3.4 the mean of community flux calculated for individual permanent quadrats (i.e. space turnover expressed as a percentage of quadrat area/90 days) is an estimate of the total amount of space acquired plus the total amount of space given up by individual organisms over time. Obviously a proportion of the space turnover will be due to the overgrowth of one organism by another. Although the mean of overgrowth calculated for individual permanent quadrats is also expressed as a percentage of quadrat area/90 days it is an estimate of the total amount of substratum exchanged between organisms over time. Thus two units of community flux calculated for individual permanent quadrats are approximately equivalent to one unit of overgrowth.

If this fact is taken into account the means of community flux for individual quadrats (Fig. 2.13 Section 2.4.3.4) can be compared to the means of overgrowth (Fig. 3.1 Section 3.3.1.1). Visual inspection of these two figures suggests that approximately one half or less of the space turnover at Edithburgh and ap-

proximately one quarter or less of the space turnover at Rapid Bay was due to overgrowth.

The total amount of space occupied at each site showed little variation during each sample interval (Fig. 2.7 Section 2.4.2.3.3) compared to the amount of space turnover each sample interval (Fig. 2.13 Section 2.4.3.4). Thus approximately half of the space turnover was due to organisms loosing space and half was due to organisms acquiring space. Obviously exactly one half of the space turnover due to overgrowth must be due to organisms loosing space and the other half due to organisms acquiring space. Thus approximately one half of the space turnover not due to overgrowth (i.e. a quarter or more) at both sites must have been due to established organisms and new recruits acquiring space by vegetative growth. The remaining proportion of the space turnover was due to established organisms giving up space due to senescence, physical disturbance or predation.

Clearly competition for space in both sessile guilds involved exploitation by vegetative growth as well as interference in the form of overgrowth interactions. The importance of vegetative growth in the structure and dynamics of the sessile guild at Edithburgh is evaluated more fully in Chapter 4. Further discussion of the role of vegetative growth in the organization of both sessile guilds may be found in Chapter 7.

Despite the preceding considerations the reason why the amount of overgrowth at Rapid Bay was less than that at Edithburgh is still not obvious. One likely explanation is that a

larger proportion of the substratum at Rapid Bay than at Edithburgh is occupied by organisms which rarely overgrow others but are capable of retarding or inhibiting completely overgrowth by organisms adjacent to them. The following discussion about the competitive status of the "dominant" species in each sessile guild suggests that *Culicia* sp. may be such an organism. However no definite conclusion can be made without further experimentation.

Neither of the "dominant" species in each sessile guild was the dominant competitor in terms of overgrowth. At Edithburgh the sponge *Crella* sp. was competitively inferior to three, equivalent to four and superior to four of the species to which it was compared. At Rapid Bay the stony coral *Culicia* sp. was competitively inferior to all except one of the species to which it was compared.

However both species showed several other characteristics which together partly explain how they maintain high abundances. Firstly, both species were able to exploit bare substratum by vegetative growth very well. *Crella* sp. had a growth rate that was significantly lower than another species only once in the comparisons made at Edithburgh and *Culicia* sp. had a significantly faster growth rate than all other species to which it was compared at Rapid Bay. Secondly, both species had long life-spans. Thirdly, as the following evidence suggests, *Crella* sp. and *Culicia* sp. inhibited overgrowth and larval invasion.

The ability to monopolize space is a function of resistance to overgrowth (Karlson 1978) and to larval invasion (Karlson 1978,

Sutherland 1974, 1975, 1978) as well as growth rate and life-span. Although both *Crella* sp. and *Culicia* sp. were often overgrown by other species I rarely saw an entire colony of *Crella* sp. being overwhelmed at Edithburgh and I never saw an entire colony of *Culicia* sp. being overwhelmed at Rapid Bay. In the cases where a colony of *Crella* sp. was completely overgrown the colony was small and always covered less than $100cm^2$ of the substratum. The greatest proportion of the substrate occupied by *Crella* sp. was covered by very large colonies which were equal to or greater than $2,500cm^2$ in area. At Rapid Bay all pilings (including some wooden ones outside of the study area) had a virtually unbroken cover of the skeletal remains of *Culicia* sp. and the live sections were never isolated from each other. At Rapid Bay visual impressions suggested that the sessile guild consisted of a more or less continuous background of *Culicia* sp. upon which were superimposed discontinuous patches of other species. Inspection of successive transparencies of the permanent quadrats suggested that species grew over *Crella* sp. and *Culicia* sp. much more slowly than over bare substratum. Additionally a large number of stand offs where the edges of two adjacent colonies cease growth on contact were observed between each of these species and other competitively superior sponge and tunicate species at both sites. Thus despite the fact that both species could be overgrown the preceding observations suggest that both had the ability to retard and in some instances completely inhibit overgrowth. Whether these two species are

able to retard overgrowth better than any of the other sponge or tunicate species requires further investigation.

During the study period I never observed a bryozoan or a *Galeolaria* spp. settled on top of a live colony of sponge or *Culicia* sp. in any quadrat at either site. However both bryozoans and *Galeolaria* spp. colonized bare substratum in high numbers at both sites (for Edithburgh see Section 4.3.1.2 and for Rapid Bay see Section 5.3.2). Tunicate and sponge species were occasionally observed settled on top of live colonies of *Crella* sp. and *Culicia* sp. but casual appraisal of the transparencies of the permanent quadrats suggested that they colonized bare substratum more heavily. These observations suggest that both species were resisting larval invasion.

In summary all of the preceding evidence suggests that *Crella* sp. and *Culicia* sp. maintain high abundance in the sessile guilds at Edithburgh and Rapid Bay respectively not because of superior overgrowth ability but as a result, at least in part, of the combined effect of rapid vegetative growth, long life span and the ability to inhibit overgrowth and larval settlement. Karlson (1978) has suggested that the colonial hydroid *Hydractinia echinata* Fleming has attained high abundance on pier pilings at Beaufort for similar reasons.

Consideration of the competitive status of the common sponge species at Edithburgh (Fig. 3.2A,B and Table 3.4) does not clearly indicate why *Crella* sp. is the most abundant of those sponges. *Crella* sp. ranks intermediately as an interference competitor and its growth rate is equivalent to most of the sponges to

which it was compared. Although it may be longer lived than most of the other common sponges (Table 3.4) it is noteworthy that the sponge *Mycale* sp. which has an equivalent growth rate and overgrowth capacity as *Crella* sp. (Fig. 3.2A,B) may be as long lived. However it is approximately half as abundant as *Crella* sp. (Fig. 2.9 Section 2.4.3.3). One possible explanation for this is that *Mycale* sp. is more prone to mechanical dislodgment by wave action than *Crella* sp. When I was creating patches within colonies of these two species as described in Section 4.2.2.1 a great deal more care was needed to avoid dislodging the *Mycale* sp. colonies than the *Crella* sp. colonies. The latter appeared to have a denser structure and adhered more firmly to the pilings.

It is likely that the competitive relationships between sponges in the sessile guild at Edithburgh were even more complicated than indicated by the results of the overgrowth interactions due, for example, to the existence of specific mechanisms which allow survival during overgrowth (i.e. "co-operative phenomena" see Section 1.1). On two occasions when I removed *Crella* sp. colonies at Edithburgh there were live portions of the Red encrusting sponge (SP5) underneath. This suggests that the Red encrusting sponge was not smothered easily. Additionally some areas of the pilings at Edithburgh were covered with densely interwoven masses of *Chondropsis* sp. and the Red encrusting sponge (SP5). When I broke these masses up by hand I found live portions of sponge at lower levels.

Furthermore although overgrowth interactions between sponges occured frequently in the 16 permanent quadrats at Edithburgh competitive stand offs were also observed. According to Burton (1949) Sara (1970) and Ayling (1978) competitive stand offs are very characteristic of sponge assemblages. An adequate explanation for the numbers and abundances of sponge species in the sessile guild at Edithburgh will obviously require a more thorough investigation into their competitive mechanisms and life histories than is presented here.

Nevertheless consideration of the competitive status of the different phyletic groups at each site does provide insights into the reasons for their various abundances.

Although the colonial tunicates were the best interference competitors at each site they were not the most abundant group at each site (Fig. 2.8 Section 2.4.3.3).

At Edithburgh these species were able to exploit free space by vegetative growth as or more rapidly than other phyletic groups. However, due to their short annual life-spans, they were unable to hold it for more than approximately ten months. Although sponges were frequently overgrown by tunicates and did not have as rapid growth rates they had much longer life-spans. This fact in combination with the observation that sponges were not always killed by the tunicates which overgrew them is the most likely explanation for the fact that sponges are more abundant than tunicates in the sessile guild at Edithburgh (Fig. 2.8 Section 2.4.3.3).

At Rapid Bay sponges and tunicates had very similar abundances (Fig. 2.8 Section 2.4.3.3). At this site these phyletic groups were able to exploit free space at equivalent rates but not all tunicate species were annuals. Of the 17 species of colonial tunicates recorded at Rapid Bay (Table 2.1 Section 2.3) inspection of successive transparencies of permanent and experimental quadrats indicated that only eight had life-spans of less than one year. These were *Botrylloides leachii*, *Botrylloides nigrum*, *Botrylloides* sp., *Botryllus schlosseri*, *Podoclavella cylindrica*, *Didemnum* sp.a, *Didemnum* sp.b, *Atapazoa fantasiana* and *Pycnoclavella diminuta*. This is likely to be part of the explanation for the similarity of the abundances of tunicates and sponges at Rapid Bay.

Bryozoans were inferior interference competitors and were unable to exploit newly available free space as rapidly as sponges and tunicates at both sites. I would expect them to be the least abundant phyletic group with the exception of *Galeolaria* spp. in both sessile guilds. This is clearly the case at Rapid Bay (Fig. 2.8 Section 2.4.3.3). However at Edithburgh they are at least as abundant as tunicates for the period of the sampling schedule (Fig. 2.8 Section 2.4.3.3). The longer life-spans of bryozoans compared to colonial tunicates at this site must be partly responsible.

Since the recruitment rates of the species in both guilds have not been accounted for in this chapter it is possible that bryozoans may be able to exploit free space by vagile larvae as well if not better than the other phyletic groups. This would

explain why they are more abundant at Edithburgh than at Rapid Bay where free substratum is in shorter supply. It would also explain why they are more abundant than might be expected at Edithburgh on the basis of the results presented in this chapter.

Galeolaria spp. were also inferior interference competitors at both sites and were unable to exploit newly available free space be vegetative growth. As expected from this result they were very rare in both sessile guilds (<<1%) see Appendices Ia and Ib). However as was suggested for bryozoans these species may be able to exploit free space by vagile larvae as well if not better than many other species in both sessile guilds.

The role that larval recruitment plays in the competitive repertoire of bryozoans and *Galeolaria* spp. and also in the structure of both sessile guilds is considered further in Chapters 4 and 5.

In this chapter I have treated growth rate and overgrowth ability as independant aspects of competitive ability. However growth rate is often positively correlated with overgrowth ability in fouling communities containing both colonial and solitary forms (Osman 1977, Jackson 1977b). The relative overgrowth abilities and growth rates of the three major phyletic groups, sponges, tunicates and bryozoans, at Edithburgh certainly showed this correlation. However the competitive relationships between sponge species at Edithburgh and between *Culicia* sp. and other species at Rapid Bay indicate that superior overgrowth ability is not necessarily correlated with a faster growth rate. Thus

overgrowth ability is likely to be a function of other characteristics as well as rapid growth rate.

At Edithburgh the two sponges which were the best overgrowers, *Aplysilla rosea* and *Callyspongia* sp. in relation to other sponges did not have encrusting growth forms. The edges of the colonies of both these species were usually elevated above those of potential sponge competitors. Correspondingly, colonies of the Red encrusting sponge (SP5) which was the inferior sponge competitor were much thinner than the colonies of all the other sponge species. The edges of the colonies of this sponge were usually lower than those of any potential sponge competitor. These observations suggest that greater colony height may be an advantage in overgrowth interactions between these sponges. Similar observations have been made for plants in marine communities (Dayton 1971) and terrestrial communities (Horn 1974) and for corals (Lang 1970).

Observations at Rapid Bay also suggest that greater colony height may be an advantage in overgrowth interactions. Inspection of successive transparencies of permanent quadrats indicated that *Culicia* sp. was lower than any organism which overgrew it. This was partly a result of the fact that the latter were actually growing on dead portions of *Culicia* sp. skeleton which were continuous with the live portions. Although these observations are suggestive I cannot determine from the results if the other species at Rapid Bay would have overgrown *Culicia* sp. less frequently if they had not been slightly elevated in respect to it. However, the following observations suggest that the in-

ability of *Culicia* sp. to overgrow other species was not a result of its low elevation. Close examination of *Culicia* sp. colonies in the field showed that this species grows vegetatively by extending a runner of soft tissue on the end of which a polyp develops. I have seldom seen such runners extending across the surface of other colonies even when *Culicia* sp. has been elevated in relation to a potential competitor due to irregularities in the substratum. One possible explanation for its inability to overgrow most of the species at Rapid Bay despite its rapid growth rate is that the calcareous cups and the runners of soft tissue do not adhere well to soft substrates such as sponge or colonial tunicate surfaces. This species is found on the hard tests of some solitary tunicates and over laying *Galeolaria* spp. tubes and bryozoan skeletons. The results of the experiments in Chapter 5 suggest that the latter two types of organisms were not alive during overgrowth.

The importance of colony morphology in competitive interactions was also illustrated by the observations suggesting that some sponge species and two bryozoan species modify their growth forms in response to localized changes in competitive conditions. The sponges produced thin encrustations when growing into newly available free space and the bryozoans produced upright fronds in response, apparently, to nearby colonies which might overgrow them. Ayling (1978) and R. Harris (pers. comm.) have also observed sponges extending thin encrustations over newly available free space in a subtidal sponge community on rock faces off the New Zealand coast line and on the pilings of Portsea

pier in Victoria respectively. Ayling (1978) suggests that this phenomena allows damaged sponge species to regain rapidly lost space in habitats which are exposed to moderate but localized disturbance. Experimental confirmation of my own observations seems worthwhile in view of the potential usefulness of such species for testing the adaptive significance of morphology in fouling communities (see Jackson In press).

TABLE 3.1 Six basic growth forms of colonial animals taken from Table 1 in Jackson (In press)

Growth form	Definition
Runners	Linear or branching forms lying parallel to the substratum; more or less continuously encrusting
Sheets	Two-dimensional encrustations more or less completely attached to the substratum
Mounds	Regular or irregular massive encrustations with vertical as well as lateral growth; usually attached to substratum along most of basal area
Plates	Flattened, foliose forms more or less parallel to the substratum and projecting into the water column from a limited zone of basal attachment
Vines	Linear or irregularly branching erect, semi-erect, or climbing forms, with one or more restricted zones of attachment to the substratum
Trees	Erect, usually regularly branching forms, with a restricted zone of basal attachment to the substratum

TABLE 3.2 Summary of Mann-Whitney U-tests comparing overgrowth at Edithburgh with overgrowth at Rapid Bay for the six sample intervals common to the sample schedules at each site
N1=N2=16

	Mann-Whitney U-test Statistics	
Sample Interval	U	P
June 1976-September 1976	120	0.2<P<0.3 ns
September 1976-December 1976	57	<.01
December 1976-March 1977	81	<.05
March 1977-June 1977	34	<.001
June 1977-September 1977	99	0.1<P<0.2 ns
September 1977-December 1977	93	0.05<P<0.1 ns

TABLE 3.3 Summary of Kruskal Wallis one-way ANOV comparing the growth rates of different species within phyletic groups at Edithburgh and Rapid Bay

		Kruskal-Wallis one-way ANOV Statistics		
Site	Phyletic Group	H	d.f.	P
Edithburgh	Sponges	21.37	7	.001< P<.01
Edithburgh	Tunicates	6.903	2	.02<P<.05
Edithburgh	Bryozoans	12.542	5	.02<P<.05
Rapid Bay	Sponges	4.34	3	.2<P<.3
Rapid Bay	Tunicates	12.1859	4	.01<P<.02

TABLE 3.4 Growth rate, life span and growth form for selected species at Edithburgh. See Section 3.3.2.1 for the rationale for selection.
N: Sample size from which growth rate has been estimated

	Species	Growth rate $\bar{x}$(S.D.)mm/day	N	Life span years	Growth form
Sponges					
SP1	*Aplysilla rosea*	0.28(0.13)	9	2-2.5	Mound
SP2	*Aplysilla sulphurea*	0.49(0.02)	2	2-2.5	Mound
SP30	*Crella* sp.	0.66(0.30)	13	>4	Sheet
SP20	*Mycale* sp.	1.18(0.73)	8	>4	Sheet
SP13	*Callyspongia* sp.	0.68(0.12)	3	>2.5	Vine
SP47	*Chondropsis* sp.	0.61(0.21)	4	>2.5	Sheet
SP49	*Lissodendoryx* sp.	0.63(0.12)	2	>2.5	Low Mound
SP5	Red encrusting sponge	0.67(0.14)	8	>2.5	Sheet
Tunicates					
T11	*Botrylloides leachii*	1.11(0.53)	6	0.8	Sheet
T9	*Didemnum* sp.a	0.90(0.45)	6	0.8	Sheet
T18	*Didemnum* sp.b	1.45(0.46)	6	0.8	Sheet
Bryozoans					
B1	*Celleporaria fusca*	0.17(0.06)	7	>4	Sheet/Mound
B2	*Celleporaria valligera*	0.11(0.05)	11	>4	Sheet/Mound
B3	*Celleporaria pigmentaria*	0.14(0.06)	8	>2.5	Sheet
B4	*Smittina raigii*	0.18(0.07)	9	1.5-2.0	Sheet
B6	*Biflustra perfragillis*	0.18(0.09)	8	1.5-2.0	Sheet
B7	Mustard encrusting bryozoan	0.08(0.05)	6	>2.5	Sheet
Other					
J5	*Culicia* sp.	0.3(0.11)	3	>4	Sheet
TW3/4	*Galeolaria* spp.	0.0(See Section 3.3.2.1)		>1	Solitary

TABLE 3.5 Growth rate, life span and growth form for selected species at Rapid Bay. See Section 3.3.2.1 for the rationale for selection

N: Sample size from which growth rate has been estimated

	Species	Growth rate $\bar{x}$(S.D.)mm/day	N	Life span years	Growth form
Sponges					
SP1	*Aplysilla rosea*	0.21(0.16)	4	2-2.5	Mound
SP30	*Crella* sp.	0.27(0.04)	2	>4	Sheet
SP13	*Callyspongia* sp.	0.46(0.14)	2	>2.5	Vine
SP5	Red encrusting sponge	0.40(0.17)	4	>2.5	Sheet
SP4	Green encrusting sponge	0.47(0.11)	6	>2.5	Sheet
Tunicates					
T11	*Botrylloides leachii*	0.44(0.16)	6	0.8	Sheet
T9	*Didemnum* sp.a	0.51(0.21)	4	0.8	Sheet
T25	*Atapazoa fantasiana*	0.21(0.07)	5	0.8	Sheet
T19	*Pycnoclavella diminuta*	0.61(0.21)	9	0.8	Sheet
T23	Chestnut encrusting tunicate	0.55(0.21)	4	>1	Sheet
Bryozoans					
B6	*Biflustra perfragillis*	0.16(0.07)	3	1.5-2.0	Sheet
B7	Mustard encrusting bryozoan	0.12(0.04)	3	>2.5	Sheet
Other					
J5	*Culicia* sp.	1.04(0.39)	9	>4	Sheet
TW3/4	*Galeolaria* spp.	0.0(See Section 3.3.2.1)		>1	Solitary

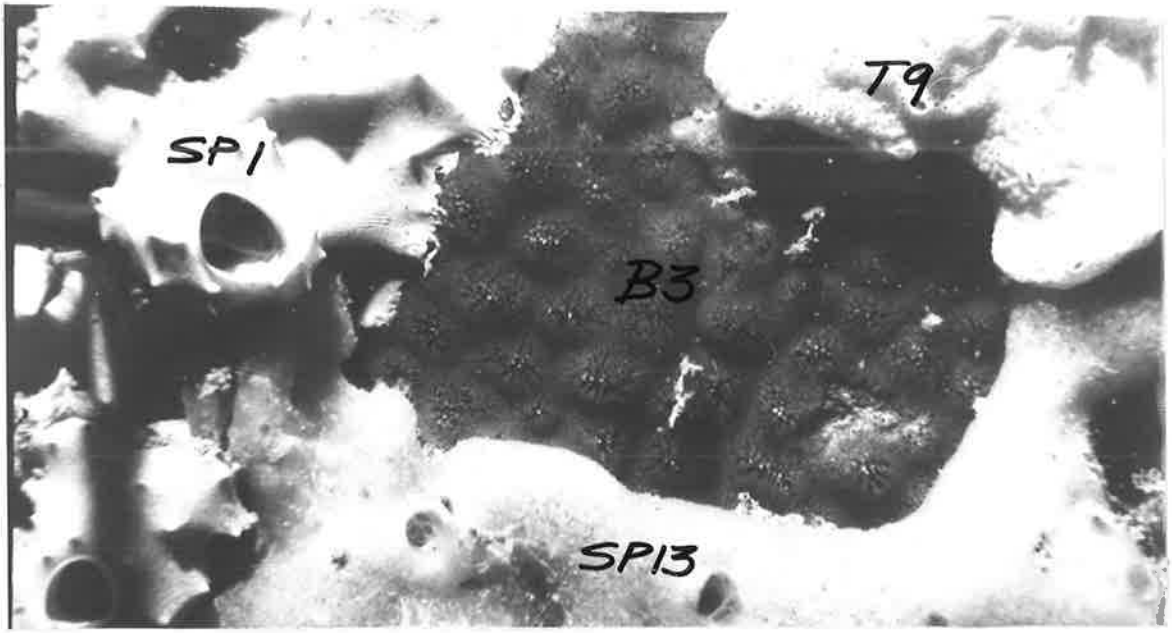
TABLE 3.6 Summary of Mann-Whitney U-tests comparing growth rates of species between Edithburgh (ED) and Rapid Bay (RB)

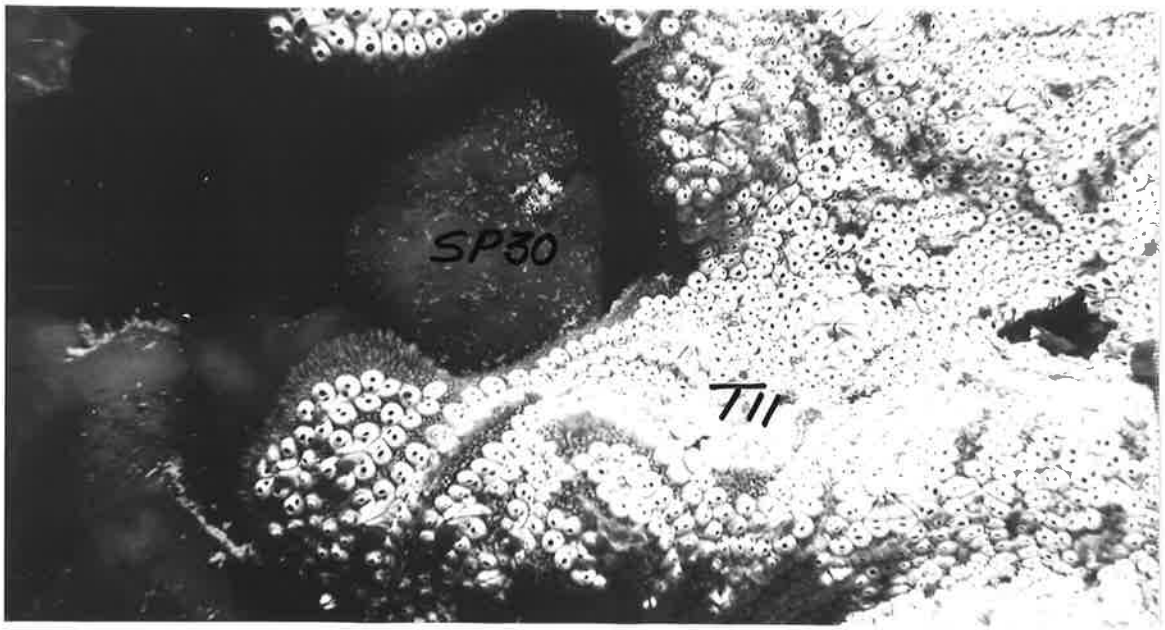
Species		Sample Size ED	Sample Size RB	Mann-Whitney U-test Statistics U	Mann-Whitney U-test Statistics P
SP1	*Aplysilla rosea*	9	4	11.5	>.05
SP30	*Crella* sp.	13	2	16.5	>.05
SP13	*Callyspongia* sp.	3	2	1.5	>.05
SP5	Red encrusting sponge	8	4	3.5	.024
Tunicates					
T11	*Botrylloides leachii*	4	4	3.0	.008
T9	*Didemnum* sp.a	6	6	3.0	.033
Bryozoa					
B6	*Biflustra perfragillis*	8	3	11.0	>.05
B7	Mustard encrusting bryozoan	6	3	3.5	>.05
Other					
J5	*Culicia* sp.	9	3	0	<.05

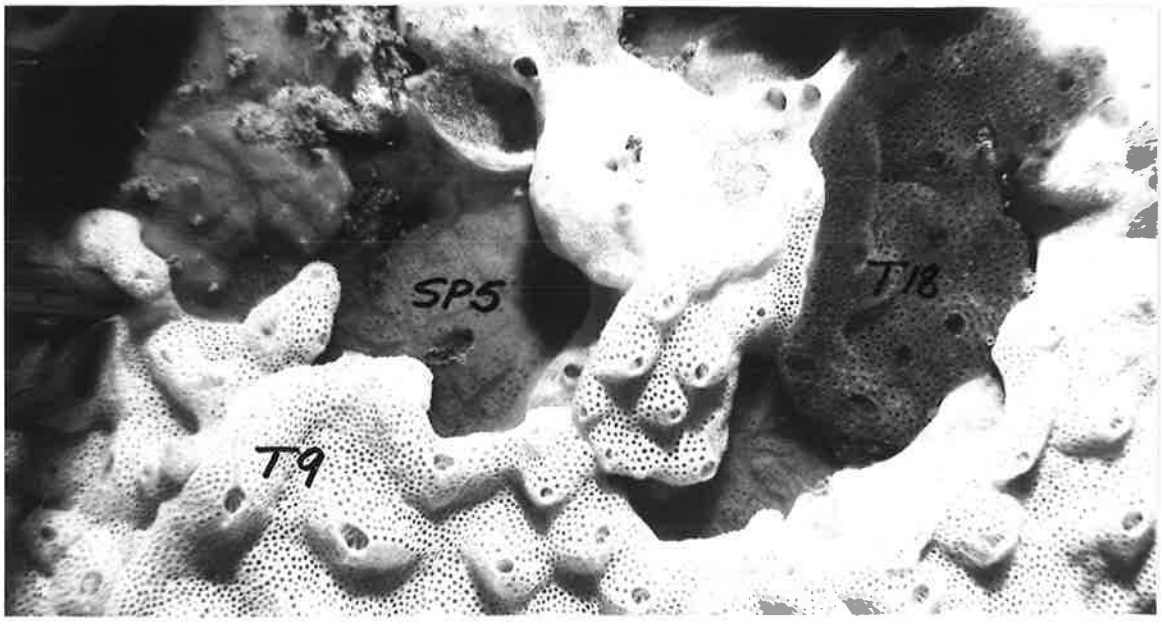
PHOTOGRAPH 3.1 The sponges *Aplysilla rosea* (SP1) and *Callyspongia* sp. (SP13) and the colonial tunicate *Didemnum* sp.a (T9) overgrowing the bryozoan *Celleporaria pigmentaria* (B3) at Edithburgh

PHOTOGRAPH 3.2 The colonial tunicate *Botrylloides leachii* (T 11) overgrowing the sponge *Crella* sp. (SP30) at Edithburgh

PHOTOGRAPH 3.3 The colonial tunicates *Didemnum* sp.a (T9) and *Didemnum* sp.b (T18) overgrowing the Red encrusting sponge (SP5) at Edithburgh


T9
SP1
B3
SP13

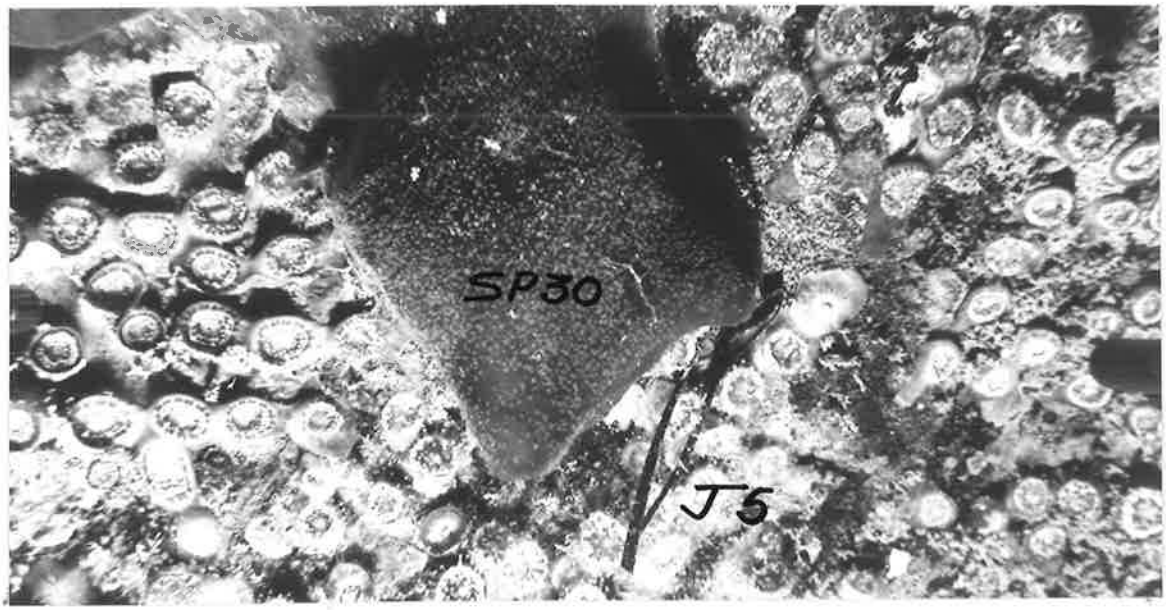

SP30
T11

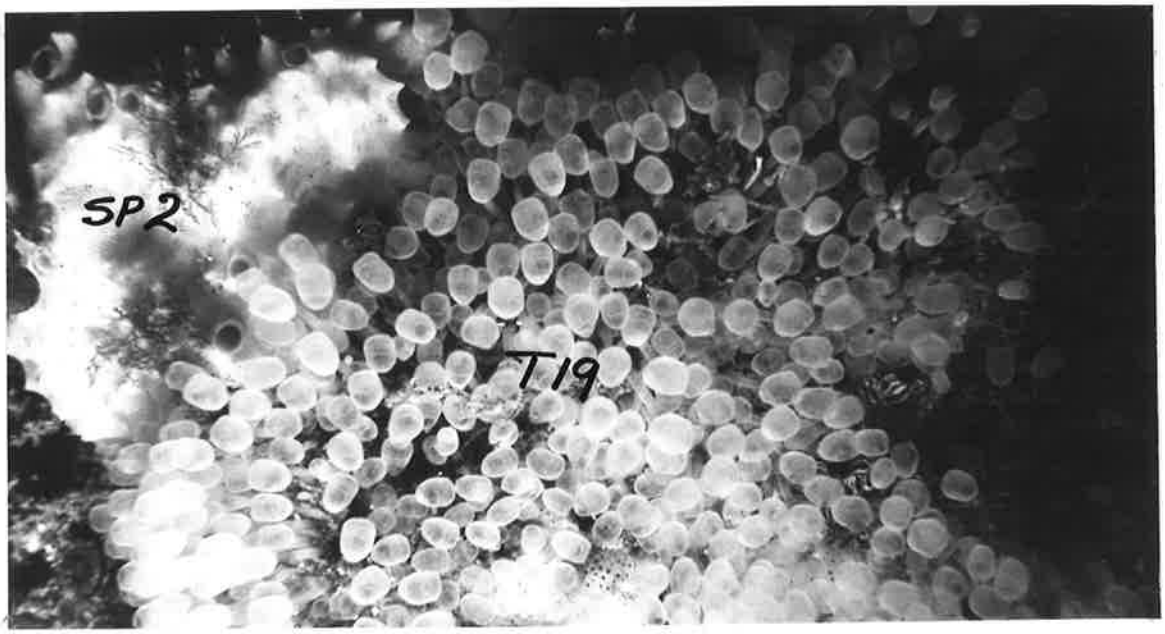

SP5
T18
T9

PHOTOGRAPH 3.4 The sponge *Crella* sp. (SP30) overgrowing the stony coral *Culicia* sp. (J5) at Rapid Bay

PHOTOGRAPH 3.5 The colonial tunicate *Pycnoclavella diminuta* (T19) overgrowing the sponge *Aplysilla sulphurea* (SP2) at Rapid Bay

PHOTOGRAPH 3.6 The colonial tunicate *Botrylloides leachii* (T 11) overgrowing thebryozoan *Celleporaria fusca* (B 1) at Rapid Bay


SP30
J5


SP2
T19

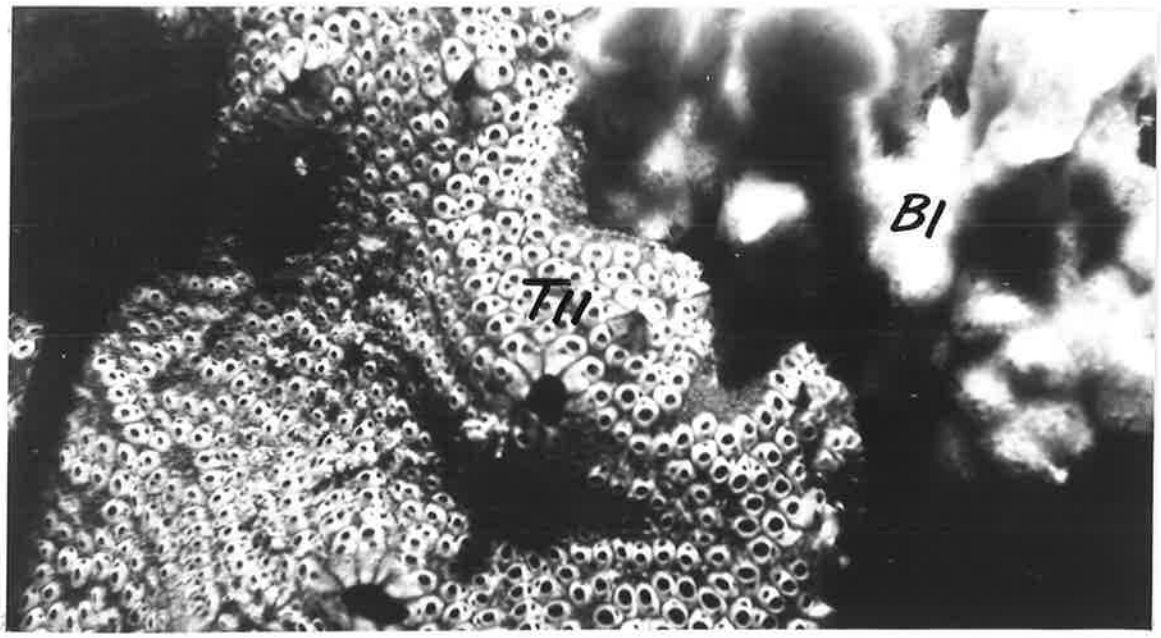

B1
T11

FIGURE 3.1 The means and standard deviations of overgrowth (percentage of quadrat/90 days) recorded in the 16 permanent quadrats at Edithburgh and Rapid Bay for all sample intervals

Edithburgh: open circles (O)

Rapid Bay: closed circles (●)

Vertical lines are standard deviations

Points on the graph are positioned in the centre of each sample interval.

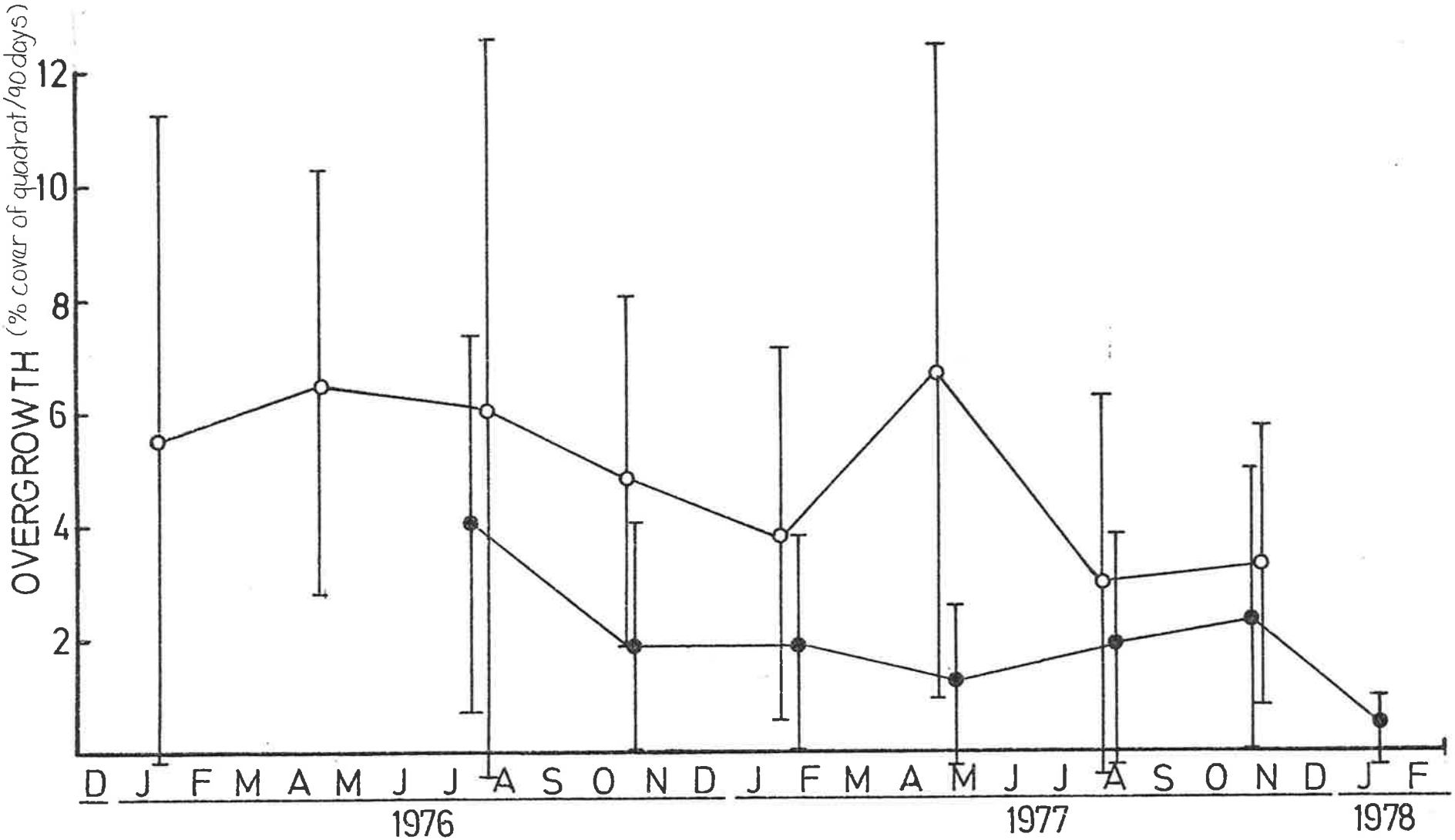

OVERGROWTH (% cover of quadrat/90 days)
12
10
8
6
4
2
D J F M A M J J A S O N D J F M A M J J A S O N D J F
1976
1977
1978

FIGURE 3.2 A. Contact matrix for overgrowth interactions between sponge species at Edithburgh. In each cell an arrow points towards the superior species or a cross (X) indicates competitive equivalence. See Section 3.3.1.2 for further details.

B. Contact matrix for pair-wise comparisons of growth rates between sponge species at Edithburgh. In each cell an arrow points towards the species which had a significantly faster growth rate than the other or a cross (X) indicates that the growth rates were equivalent.
See Section 3.3.2.1 for further details

SP1 *Aplysilla rosea*
SP2 *Aplysilla sulphurea*
SP30 *Crella* sp.
SP20 *Mycale* sp.
SP13 *Callyspongia* sp.
SP47 *Chondropsis* sp.
SP49 *Lissodendoryx* sp.
SP5 Red encrusting sponge

Ⓐ SPONGES OVERGROWTH

SP2	SP30	SP20	SP13	SP47	SP49	SP5	
	12 → 27	2 x 7	2 x 6	0 → 10		0 → 7	SP1
	4 x 4		6 ↑ 1			0 → 10	SP2
		3 x 8	10 ↑ 3	7 → 21	4 x 5	1 → 30	SP30
						1 → 7	SP20
						0 → 9	SP13
						3 → 24	SP47
							SP49

Ⓑ SPONGES GROWTH RATES

SP2	SP30	SP20	SP13	SP47	SP49	SP5	
	↑	↑	↑	↑		↑	SP1
	x		↑			x	SP2
		x	x	x	x	x	SP30
				x		x	SP20
						x	SP13
						x	SP47
							SP49

FIGURE 3.3 A. Contact matrix for overgrowth interactions between tunicate species at Edithburgh

B. Contact matrix for pair-wise comparisons of growth rates between tunicate species at Edithburgh

C. Contact matrix for overgrowth interactions between bryozoan species at Edithburgh

D. Contact matrix for pair-wise comparisons of growth rates between bryozoan species at Edithburgh

See captions to Figures 3.2 A. and 3.2 B. for further details

T11 *Boytrylloides leachii*

T9 *Didemnum* sp.a

T18 *Didemnum* sp.b

B1 *Celleporaria fusca*

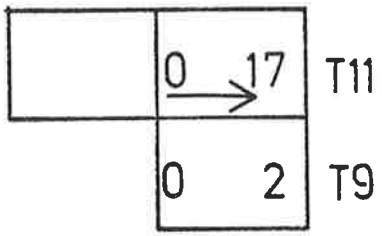
B2 *Celleporaria valligera*

B3 *Celleporaria pigmentaria*

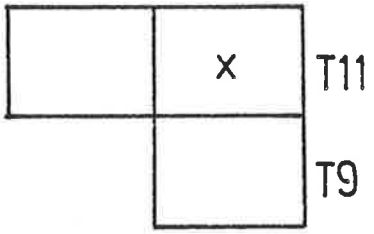
B4 *Smittina raigii*

B7 Mustard encrusting bryozoan

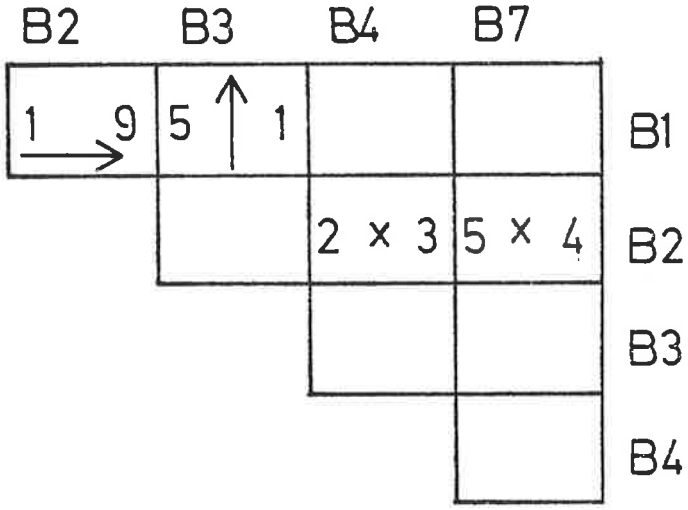
Ⓐ TUNICATES OVERGROWTH



③ TUNICATES GROWTH RATE



Ⓒ BRYOZOANS OVERGROWTH



Ⓓ BRYOZOANS GROWTH RATE

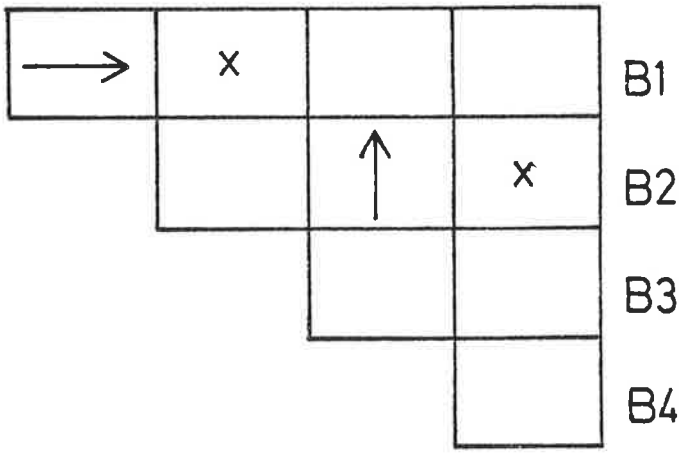


FIGURE 3.4 A. Contact matrix for overgrowth interactions between tunicate species and sponge species at Edithburgh

B. Contact matrix for pair-wise comparisons of growth rates between tunicate species and sponge species at Edithburgh

C. Contact matrix for overgrowth interactions between sponge species and bryozoan species at Edithburgh

D. Contact matrix for pair-wise comparisons of growth rates between sponge species and bryozoan species

See captions to Figures 3.2 A. and 3.2 B. for further details

T11 *Boytrylloides leachii*

T9 *Didemnum* sp.a

T18 *Didemnum* sp.b

SP1 *Aplysilla rosea*

SP30 *Crella* sp.

SP20 *Mycale* sp.

SP13 *Callyspongia* sp.

SP47 *Chondropsis* sp.

SP5 Red encrusting sponge

B1 *Celleporaria fusca*

B2 *Celleporaria valligera*

B3 *Celleporaria pigmentaria*

B4 *Smittina raigii*

TUNICATES VS. SPONGES

(A) OVERGROWTH

T11	T9	T18
	12 ↑ 0	17 ↑ 3
5 ↑ 0	11 ↑ 0	2 × 3
	6 ↑ 0	19 ↑ 1
7 ↑ 0	6 ↑ 0	9 ↑ 0

(B) GROWTH RATE

T11	T9	T18	
	×	↑	SP30
×	×	×	SP20
	×	↑	SP47
↑	×	↑	SP5

SPONGES VS. BRYOZOANS

(C) OVERGROWTH

SP1	SP30	SP20	SP13	SP47	SP5	
4 × 1	14 ↑ 4	9 × 3			7 × 2	B1
9 ↑ 1	13 ↑ 1	14 ↑ 2	7 ↑ 0	8 × 2	6 ↑ 1	B2
	5 ↑ 0		6 ↑ 0			B3
	14 ↑ 0					B4

(D) GROWTH RATE

SP1	SP30	SP20	SP13	SP47	SP5	
×	↑	↑			↑	B1
↑	↑	↑	↑	↑	↑	B2
	↑		↑			B3
	↑					B4

FIGURE 3.5 A. Contact matrix for overgrowth interactions between tunicate species and bryozoan species at Edithburgh

B. Contact matrix for pair-wise comparisons of growth rates between tunicate species and bryozoan species at Edithburgh

C. Contact matrix for overgrowth interactions between a sponge species and *Culicia* sp. and between a sponge species and *Galeolaria* spp. at Edithburgh

D. Contact matrix for pair-wise comparisons of growth rates between a sponge species and *Culicia* sp. and between sponge species and *Galeolaria* spp. at Edithburgh

E. Contact matrix for overgrowth interactions between a tunicate species and *Culicia* sp. and between a tunicate species and *Galeolaria* spp. at Edithburgh

F. Contact matrix for pair-wise comparisons of growth rates between a tunicate species and *Culicia* sp. and between a tunicate species and *Galeolaria* spp. at Edithburgh

See captions to Figures 3.2 A. and 3.2 B. for further details

T11	*Botrylloides leachii*
T9	*Didemnum* sp.a
T18	*Didemnum* sp.b
SP1	*Aplysilla rosea*
SP20	*Mycale* sp.
SP13	*Callyspongia* sp.
B1	*Celleporaria fusca*
B2	*Celleporaria valligera*
B6	*Biflustra perfragillis*
B7	Mustard encrusting bryozoan
J5	*Culicia* sp.
TW3/4	*Galeolaria* spp.

TUNICATES VS. BRYOZOANS

Ⓐ OVERGROWTH

T11	T9	T18
9 ↑ 0	7 ↑ 0	
12 ↑ 0	10 ↑ 0	
9 ↑ 0		
		5 ↑ 0

Ⓑ GROWTH RATE

T11	T9	T18	
↑	↑		B1
↑	↑		B2
↑			B6
↑		↑	B7

SPONGES VS. CULICIA SP. AND GALEOLARIA SPP.

Ⓒ OVERGROWTH

SP1	SP20	SP13
		6 ↑ 0
5 ↑ 0	7 ↑ 0	13 ↑ 0

Ⓓ GROWTH RATE

SP1	SP20	SP13	
		↑	J5
↑	↑	↑	TW3/4

TUNICATES VS. CULICIA SP. AND GALEOLARIA SPP.

Ⓔ OVERGROWTH

T11	T9
20 ↑ 0	
	7 ↑ 0

Ⓕ GROWTH RATE

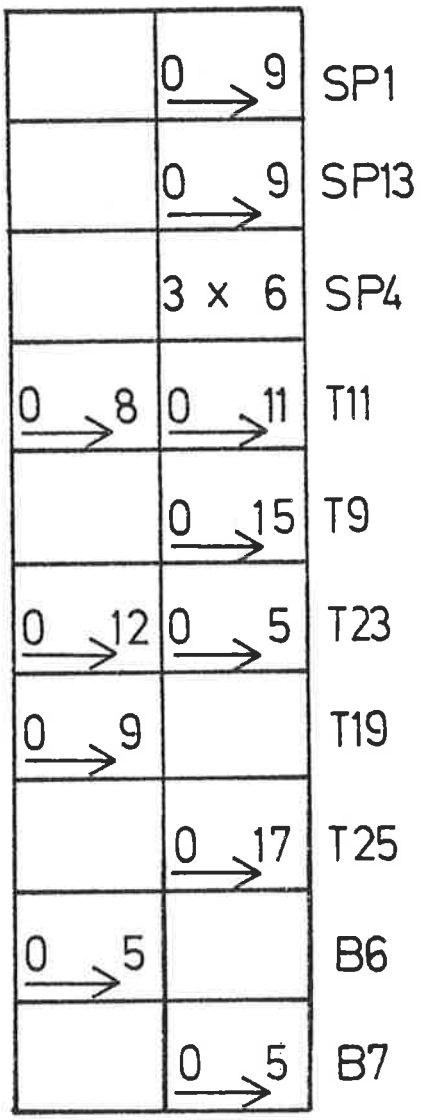
T11	T9	
↑		J5
	↑	TW3/4

FIGURE 3.6 A. Contact matrix for overgrowth interactions at Rapid Bay
See caption to Figure 3.2 A. for further details

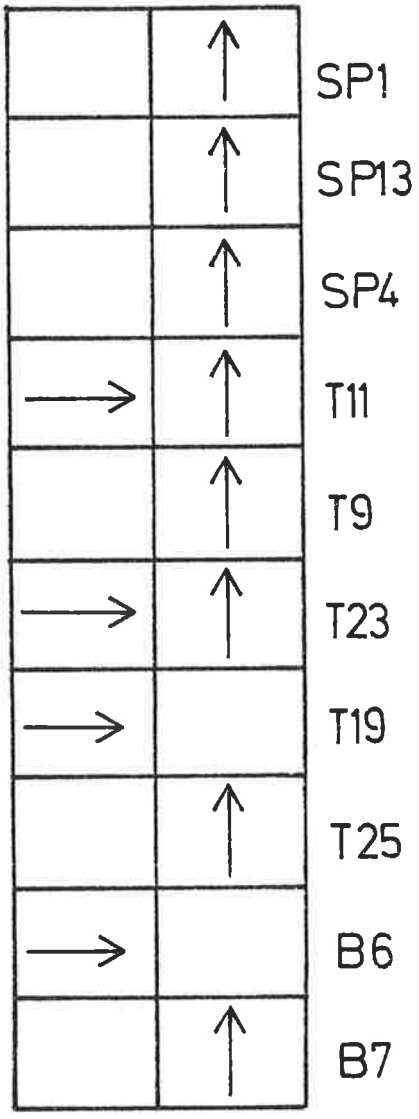
B. Contact matrix for pair-wise comparisons of growth rates at Rapid Bay
See caption to Figure 3.2 B. for further details

SP1	*Aplysilla rosea*
SP13	*Callyspongia* sp.
SP4	Green encrusting sponge
T11	*Botrylloides leachii*
T9	*Didemnum* sp.a
T23	Chestnut encrusting tunicate
T19	*Pycnoclavella diminuta*
T25	*Atapazoa fantasiana*
B6	*Biflustra perfragillis*
B7	Mustard encrusting bryozoan
TW3/4	*Galeolaria* spp.
J5	*Culicia* sp.

Ⓐ OVERGROWTH



Ⓑ GROWTH RATES



4.0 THE REOCCUPATION OF PATCHES OF BARE SUBSTRATUM IN THE SESSILE GUILD AT EDITHBURGH

4.1 Introduction

Patchiness is a common attribute of natural communities in which space is limited (Whittaker and Levin, 1977). However the exact definition of a patch will depend upon the characteristics of the community under consideration. In generalized terms a patch is a bounded but connected discontinuity in a homogenous reference background (Levin and Paine 1974). In hard substrate communities in marine environments patches may begin as unoccupied holes or breaks in sessile fauna and flora covering a two-dimensional surface (Dayton 1971, 1975, Paine 1966, 1971, 1977, Grant 1977, Karlson 1978). The reference background of sessile organisms may consist of a monoculture (Paine 1966, 1971) or a mixture of species (Grant 1977, Karlson 1978). Alternatively a patch may be seen as an isolated piece of substratum surrounded by areas unsuitable for occupation (habitat island) (Osman 1977, 1978, Jackson 1977a). In either case the communities can be viewed as spatial and temporal mosaics of small interrelated systems (Levin and Paine 1974). Although patchiness is not confined to marine communities on hard substrata (for other examples see Dayton 1975, Whittaker and Levin 1977, Connell 1978), many investigations of the phenomenon leading to explanations for community structure have been undertaken in this environment.

Much of the work in rocky intertidal systems has concentrated on the processes responsible for the formation of patches of bare

substratum. Localized distrubance in the form of wave driven logs, wave shock and/or the foraging activity of certain predators creates holes in the sessile communities covering the rocks (Dayton 1971, 1975, Paine 1966, 1971, Grant 1977). Theoretical formulations relating the sizes and ages of such patches to different degrees of disturbance (Levin and Paine 1974, 1975) are based on the patterns found in these communities. However, it is clear from these models that an explanation for patterns of species abundances based on the dynamics of patches also requires a knowledge of events within patches.

As pointed out in Section 1.1 the reoccupation of patches in the rocky intertidal usually ends when one or more "competitive dominants" exclude the early occupants of a patch through various methods of competitive interference (Paine 1977). It follows that if the level of disturbance in a given locality decreases the abundance of these competitive dominants will rise and the number of species co-existing in the locality will decrease. This has been confirmed in several experimental investigations (Paine 1966, 1971, 1974).

The concept of patchiness has also been used in investigations of the organization of sessile communities in the subtidal (Osman 1977, Sutherland 1974, 1975, 1978 Sutherland and Karlson 1977). In particular Sutherland (1974) proposed that it was appropriate to view the fouling communities on the pier pilings at Beaufort, North Carolina as being composed of a mosaic of smaller patches with differing species composition and develop-

mental history.

In a series of investigations at this locality Sutherland (1974, 1975, 1976, 1978) and Sutherland and Karlson (1977) used small ceramic tiles (232cm^2 in area) to simulate the natural patches of bare substratum which were frequently formed on the pilings either by the grazing of the urchin *Arbacia punctulata* (Lamarck) or the senescence of adult organisms. These studies showed that the identity and abundance of the species which invaded these plates depended largely on which larvae were in the plankton when the plates were first submerged (Sutherland 1974). Moreover the species which initially invaded the plates inhibited further colonization resulting in a "stable point." "Multiple stable points" are localized patches of different species composition, within the same habitat, which persist for some period of time without changing (Sutherland 1974). Thus the relative abundances of different species on the pier pilings at any given time was a function of the relative abundances of different larvae in the plankton during the initial formation of all those patches which make up the spatial mosaic of the community.

Unoccupied substratum was available in both the sessile guilds under investigation in this thesis (Section 2.4.3). However a significantly greater proportion of the substratum was occupied at Rapid Bay than at Edithburgh (Section 2.4.3). Inspection of Figure 2.7 in Section 2.4.3 shows that approximately one quarter and one fifteenth of the substratum was unoccupied at Edithburgh and Rapid Bay respectively during the two year period of the non-destructive census. Additionally, examination

of transparencies of the permanent quadrats and casual observations in the field indicated that patches of bare substratum at Edithburgh ranged in size from one square centimetre to one square metre, whereas at Rapid Bay patches of bare substratum were comparatively small (less than $25cm^2$). In most cases they were simply the dead skeletal remains of *Culicia* sp.

These observations suggested that the factors influencing the reoccupation of patches of bare substratum at Edithburgh would be of considerable significance to the overall structure of the sessile guild while those at Rapid Bay would have less significance. Accordingly I decided that it was only worthwhile to investigate the process of patch reoccupation in the sessile guild at Edithburgh. I used a different experimental approach to investigate potentially important factors in the organization of the sessile guild at Rapid Bay (see Sections 5.1 and 6.1).

The reoccupation of bare substratum was investigated in the sessile guild at Edithburgh using artificially cleared patches on the pilings. In view of the following evidence artificial plates were not used because it could not be assumed that the organisms surrounding the patches at Edithburgh had no effect on the events taking place within the patches. Firstly it appeared likely that patches of bare substratum would be partially reoccupied by the vegetative growth of adjacent colonies. Casual observations before the experiment was set up suggested that most of the colonial species in the sessile guild at Edithburgh were capable of rapid vegetative growth onto unoccupied substratum.

It has since been reported that patches of bare substratum in a number of sessile communities are partly reoccupied by vegetative growth (e.g. epifauna of cryptic habitats in coral reefs: Jackson 1977a; epibiota of old pier pilings: Karlson 1978, Harris 1978; sponge communities on rocks: Ayling 1978). Secondly adult organisms surrounding settlement plates have been found to influence the recruitment of species onto the plates (Goodbody 1961, Sutherland and Karlson 1973). In addition to these considerations it may also be inappropriate to use small and isolated substrata to simulate patches on a large piece of substratum because different species may settle preferentially on different sized substrata (Jackson 1977a).

Two field experiments were carried out. The first was designed to assess the importance of larval availability in the reoccupation of bare patches; the second was designed to demonstrate the effect of initial size and position of a patch on its reoccupation. The results of both experiments are used to indicate the extent to which some factors influence the identity and abundance of species found in individual patches, and further to identify some of the factors which are important in the organization of the sessile guild at Edithburgh.

4.2 Methods

4.2.1 Experiment I

4.2.1.1 Experimental Design and Field Methods

Twenty artificial patches 20cm x 30cm were created on the pilings within the circumscribed study area. The position of

each patch was chosen using the method described in Section 2.4.2.1. The sessile organisms were removed using a knife and a chisel and the newly exposed wood was scrubbed vigorously with a stiff brush to ensure complete removal of particles of live tissue. Each patch was then outlined with orange nylon rope nailed to the piling. The 20 patches were divided into four groups of five patches each. Each group was created at a different time as follows: 26/2/76 February group, 18/5/76 May group, 26/8/76 August group, 6/12/76 December group. Each patch was photographed at approximately monthly intervals for one year after initial formation. The experimental design and sampling schedule is summarized in Table 4.1. The choice of patch size was based on experimental convenience and the observation that patches between 500cm^2 and 700cm^2 in area did occur naturally on the pilings.

TABLE 4.1 Experimental design and sampling schedule for Experiment I.
CL: date of initial clearance of patch
X: photograph taken of patch

	1976											1977									
Month	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N
Interval in days	18-	34-	31-	33-	27-	40-	30-	35	-	36-		36-	28-	28-	31-	26-	28	-	70-	37-	26-	26
February group	CL	X	X	X	X	X	X	X	X			X	X	X								
May group				CL	X	X	X	X	X			X	X	X	X	X	X					
August group							CL	X	X			X	X	X	X	X	X	X	X			
December group											CL	X	X	X	X	X	X	X	X	X	X	X

4.2.1.2 Calculations and Analysis

4.2.1.2.1 Percentage Cover

The percentage cover due to the vegetative growth of colonies adjacent to the patches and due to the growth of new recruits on the patches was calculated for each species on each sample date for each patch.

For each of the four groups of patches the mean and standard deviation of percentage cover were plotted against time for

1) All species present (Total cover)
2) Total cover due to the vegetative growth of colonies adjacent to the patches
3) Total cover due to the growth of new recruits on the patches
4) The vegetative growth of colonies adjacent to the patches for each of the three following phyletic groups: sponges, tunicates and bryozoans
5) The growth of new recruits on the patches for each of the three following phyletic groups: sponges, tunicates and bryozoans.

Additionally for each of the four groups of patches the mean and standard deviation of the percentage cover for each species was plotted on the sample dates approximating as nearly as possible to three, six, nine and 12 months after the initial clearance of the patch.

Statistical tests are detailed as necessary in Section 4.3.1.1.

4.2.1.2.2 Colonization Rate

The number of new recruits on any patch was measured by counting the number of colonies or individuals present in a patch which were not present on the preceding sample date. This was done by comparison and inspection of successive transparencies of a given patch. As was pointed out in Section 3.2.2. many newly settled colonies could not be detected, let alone identified, in transparencies until they reached a size of at least 9 mm^2. Also many new recruits may be removed by predators before they are detected. However although these factors could lead to variously biased estimates of the actual recruitment rate for different species they should not seriously affect the detection of temporal differences in the seasonal peaks of larval abundance of different species or phyletic groups.

Colonization rate was expressed as the number of new recruits/600cm^2/30 days. For each of the four groups of patches the mean and standard deviation of the colonization rate for each species was calculated for each sample interval. (see Appendix IIIa) Additionally the mean and standard deviation of colonization rate for each of the following phyletic groups, sponges, tunicates, bryozoans and *Galeolaria* spp. were plotted against time for each group of patches.

4.2.1.2.3 Interference Competition

The amount of overgrowth occuring in each patch was calculated for each sample interval using the method described in Section 3.2.1.1. It is expressed as a percentage of the ini-

tial total area of a patch and was calculated for a standard period of 90 days. Thus it is expressed in the same units as overgrowth in the undisturbed guild was expressed (see Section 3.2.1.1).

For each of the four groups of patches the mean and standard deviation of overgrowth was plotted against time.

A competitive hierarchy based on the overgrowth records from all of the twenty patches was also constructed. The methods described in Section 3.2.1.2 were used. The results are depicted in a contact matrix which was described and explained in Section 3.3.1.2.

4.2.2 Experiment II

4.2.2.1 Experimental Design and Field Methods

Forty-seven patches were cleared at the same time, 20/4/77, using the method described for Experiment I. The patches were divided into two groups. In one group all patches were completely surrounded by *Mycale* sp., in the other group all patches were completely surrounded by *Crella* sp. Each group was made up of patches of three different sizes: 10cm x 10cm, 25cm x 25cm, 50cm x 50cm. Each patch was photographed at approximately monthly intervals for 11 months after initial formation. The experimental design, replicate number, and sampling schedule is summarized in Table 4.2.

All patches were cleared in positions such that at least 20cm of sponge tissue bounded them on all sides. Sponge colonies were selected at random within the study area. To mark a patch's

starting size a nail was driven into each of the four corners. The replicate numbers for the largest patches, 50cm x 50cm, were small because there were few colonies of either species of sponges exceeding the patch size. Casual observations made in the first experiment suggested that the growth rate (distance travelled by the growing edge of an isolated colony in a given time) of *Mycale* sp. was approximately twice that of *Crella* sp.

TABLE 4.2 Experimental design and sampling schedule for Experiment II

CL: date of initial clearance of patch

X: photograph taken of patch

		Year	1977								1978		
		Month	A	M	J	J	A	S	O	N	D	J	F	M
		Interval in days	26-28			-70	-37	-26	-26	-30	-31	-28	-27	
Patch size	No. of patches	Surrounding species												
10cm x 10cm	10	*Mycale* sp.	CL	X		X		X	X	X	X	X	X	X
25cm x 25cm	10	*Mycale* sp.	CL	X		X		X	X	X	X	X	X	X
50cm x 50cm	4	*Mycale* sp.	CL	X		X		X	X	X	X	X	X	X
10cm x 10cm	10	*Crella* sp.	CL	X		X		X	X	X	X	X	X	X
25cm x 25cm	10	*Crella* sp.	CL	X		X		X	X	X	X	X	X	X
50cm x 50cm	3	*Crella* sp.	CL	X		X		X	X	X	X	X	X	X

4.2.2.2 Calculations and Analysis

The mean and standard deviation of percentage cover due to the vegetative growth of the sponge colonies adjacent to the

patches was calculated on each sample date for each of the six groups of patches. These data were plotted against time and are presented in Figure 4.8 in Section 4.3.2.

Additionally a power curve with the equation $y=ax^b$, where y=percentage cover due to vegetative growth of the sponge colonies and x=time in days, was fitted to the mean values for percentage cover in each group of patches. The coefficients of determination (r^2) for these curves (Appendix IIIb) show that they fit the data well. This curve was then fitted to the data for each individual patch and the time in days for the patch to be half covered by the vegetative growth of the surrounding sponge was read from the curve in each case (Appendix IIIb). This value was taken as a measure of the rate at which a patch is occupied by the vegetative growth of the surrounding sponge.

Clearly the nature of these data precludes parametric analyses (see Appendix IIIb). A suitable non parametric two-way analysis of variance was not available, and therefore I proceeded directly to pairwise comparisons between treatments. A Mann-Whitney U-test (Siegel 1956) was used to compare the rate of occupation of

1) 10cm x 10cm patches surrounded by *Mycale* sp. and 10cm x 10cm patches surrounded by *Crella* sp.
2) As above for 25cm x 25cm sized patches
3) As above for 50cm x 50cm sized patches
4) 10cm x 10cm and 25cm x 25cm patches surrounded by *Mycale* sp.

5) 10cm x 10cm and 50cm x 50cm patches surrounded by *Mycale* sp.

6) 25cm x 25cm and 50cm x 50cm sized patches surrounded by *Mycale* sp.

7) 10cm x 10cm and 25cm x 25cm sized patches surrounded by *Crella* sp.

8) 10cm x 10cm and 50cm x 50cm sized patches surrounded by *Crella* sp.

9) 25cm x 25cm and 50cm x 50cm sized patches surrounded by *Crella* sp.

The results of these tests are summarized in Table 4.4.

Additionally for each of the six groups of patches the mean and standard deviation of percentage cover due to the growth of new recruits on the patches were calculated for each species at each sample date (Appendix IIIc). These quantities are presented in Table 4.5 for the four following phyletic groups: sponges, tunicates, bryozoans and *Galeolaria* spp., 161 days and 329 days after the initial clearance of the patches for each of the six groups of patches.

4.3 Results

4.3.1 Experiment I

4.3.1.1 Percentage Cover

Species reoccupied patches by vegetative growth of established colonies and by colonization from the plankton (Fig. 4.1). In

all four groups the average percentage of space covered by vegetative growth was greater than that covered by growth of colonists on all sample dates (Fig. 4.1). After one year space covered by vegetative growth was at least three times as great as that occupied by colonists except in the February group (Table 4.3). There was no significant heterogeneity between groups for the percentage of space covered by vegetative growth, growth of colonists or total growth after one year (see Table 4.3). There was, however, a significant difference between the percentage of space occupied by vegetative growth and that occupied by growth of colonists after one year (Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) on pooled data from the four groups, sample size=20, $T=-6, P<.005$).

Sponges covered the greatest proportion of reoccupied space at all times after initial clearance of patches in all groups (Figs. 4.2 and 4.3). Additionally they invaded patches almost exclusively by vegetative growth of established colonies except in the February group where approximately 1/3 of the area covered by sponges was due to growth of colonists (Fig. 4.2). Tunicates and bryozoans represented a much smaller proportion of the reoccupied space in all groups (Figs. 4.2 and 4.3). Bryozoans invaded patches almost exclusively through colonization in all groups while tunicates invaded patches both by colonization and vegetative growth of established colonies (Fig. 4.3).

Sponges showed a steady increase in average percentage cover in all groups during the one year period to a maximum of between

45% and 60% in the last 60 days (Fig. 4.2). Bryozoans showed a similar steady increase in mean percentage cover in all groups for the first seven months (Fig. 4.3). This increase continued in the February and December groups to maxima of 9.25% and 11.6% at the end of one year. In the May and August groups the mean percentage cover of bryozoans decreased from maxima of 4.77% and 7.38% to 3.92% and 3.83% respectively by the end of the year. Peaks in percentage cover of tunicates occurred during the July-Aug.-Sept. periods of the two years spanned by the experiment (Fig. 4.3). As pointed out in Section 2.4.3 the four species of colonial tunicates, *Podoclavella cylindrica, Botrylloides leachii, Didemnum* sp.a and *Didemnum* sp.b, in the sessile guild at Edithburgh are annuals. Colonies of these species settle in Summer, reach a maximum size during July, August and September and reproduce and die off during Octo ber and November of each year. The sum of the means of percentage cover for the four species not belonging to the three major phyla in this community did not exceed 1% at any time except in the February group. In this group a maximum of 3.6% was reached in the first four months, falling to 1.5% at the end of one year.

These results show that in this sessile guild bare patches of the size used in the experiment were reoccupied mainly by the vegetative growth of sponge colonies adjacent to them. Colonizing bryozoans, tunicates and sponges plus the vegetative growth of tunicates contributed to this process of reoccupation but made up only a small proportion of the total cover.

The mean percentage cover for individual species three, six nine and 12 months after initial clearance of patches (Fig. 4.4) shows that no one species occupied a high percentage of space in one group and not in another. *Mycale* sp. and *Crella* sp. were the commonest species in all groups by the end of the one year period. *Crella* sp. was the "dominant" species in the sessile guild at Edithburgh (Section 2.4.4). It occupied between 20% and 25% of the substratum for the two year period of the non-destructive census (Fig. 2.9, Section 2.4.3). *Mycale* sp. together with *Aplysilla rosea* was the second commonest species in the sessile guild at Edithburgh (Section 2.4.3). These two species each occupied between 7% and 12% of the substratum during the two year period of the non-destructive census (Fig. 2.9, Section 2.4.3). As pointed out in Section 3.4 both *Crella* sp. and *Mycale* sp. formed large sheet-like colonies on the pilings. Additionally both species were long-lived and had rapid growth rates (Table 3.4 Section 3.3.2).

The large standard deviations for percentage cover show that there is considerable variability in species composition and abundance within groups. For example one patch in the August group was completely covered by *Crella* sp. six months after clearance. In the same group 70% of another patch was covered by *Mycale* sp. at the end of the one year period. Casual observations up to two years after initial clearance of these patches revealed that these particular patch compositions persisted. *Crella* sp. was never seen in the *Mycale* sp. patch.

4.3.1.2 Colonization

Evidence for seasonality in larval abundances can be found in the colonization records for the four groups (Fig. 4.5). Peaks in the colonization curves for sponges, tunicates, bryozoans and *Galeolaria* spp. occurred during the Dec.-Jan.-Feb.-March period of 1976-1977. These peaks are most pronounced in August and December groups despite the fact that the mean percentage of bare space available for colonization in the May group in the middle of this period was 8% more than that for the August group. There was no indication in the data for individual species of a different seasonal trend (Appendix IIIa).

Sponges showed an overall decrease in colonization rate for the two year period spanned by the experiment (Fig. 4.5). Inspection of Appendix IIIa suggests that this was mainly due to a differences between years in larval availability for *Aplysilla rosea*, *Mycale* sp., *Crella* sp., and the Red encrusting sponge (SP5). *Chlamys asperrimus* did not colonize any patch and *Culicia* sp. colonized one patch in the February group on all sample dates and one patch in the December group on one sample date (Appendix IIIa). The patch in the February group had previously been occupied by *Culicia* sp. and was also bounded on all sides by it. It is possible that the polyps of this species appearing in the patch should not have been recorded as colonists since colonies of this species have been observed to extend a runner of soft tissue on the end of which develops a polyp. Unfortunately this was not realized during the course of the experiment and this patch was not examined closely in the field.

No evidence of these runners can be distinguished in the transparencies. In either case the appearance of this species within a patch appears to be correlated with the presence of an adult colony adjacent to the patch or previous occupancy of the piling substratum by this species.

The large standard deviations on the colonization curves for the four phyletic groups in Fig. 4.5 and the large standard deviations of the means of the colonization rates for individual species (Appendix IIIa) indicate that there was considerable variability in the number of colonists belonging to different species and phyletic groups between patches within groups. Differences in the percentage of bare substratum between patches would account for some of this variation. Inspection of successive transparencies of the permanent quadrats described in Section 2.4.2.1 and of the patches in Experiment I and II of this chapter suggested that neither bryozoans nor *Galeolaria* spp. were able to settle on top of live tissue. Colonists of these two groups always appeared on bare substratum or the non-living skeletal structures on remains of other organisms. Sponges and tunicates were occasionally observed to settle on live tissue in these quadrats and patches. However casual appraisal of the transparencies suggested strongly that bare wood was the much preferred substratum. In addition to this some species appeared to settle aggregatively. For example in the February group 19 colonies of *Didemnum* sp. settled on one patch in the first month compared to 2, 2, 1 and 0 colonies in the other four patches. Overall 181 colonies of this species settled in this

patch for the rest of the experimental period compared to three in another patch in the same group which showed the same percentage of bare substratum for the corresponding sample dates.

4.3.1.3 Interference Competition

Partial and total overgrowth of colonies was observed in all groups (Fig. 4.6). The large standard deviations indicate considerable variability in the total amount of overgrowth between patches within groups. Rates of overgrowth in any patch depend largely on the juxtaposition of species of different overgrowth capacity. The preceding results demonstrated that there was considerable variation in the species composition of different patches. For the February group average overgrowth reaches a maximum at the end of the one year period when average total percentage cover is 70%. For the May, August and December groups average overgrowth reaches a maximum six to seven months after patch clearance. The average total percentage covers at this time were 38%, 76% and 50% respectively. After this overgrowth decreases. There does not appear to be a clear relationship between maximum overgrowth and total percentage cover from these results. This is most likely due to the extreme variability of species composition between patches.

It is also noteworthy that only for the February and December groups does the mean abundance of overgrowth lie above the range of mean overgrowth values calculated from overgrowth records in the permanent quadrats (compare Fig. 4.6 with Fig. 3.1). The maximum mean overgrowth values of the May and August groups lie

well within the range. Therefore there was no convincing evidence that competitive interference became more intense during the reoccupation of patches than it was in the sessile guild as a whole.

Species interactions where overgrowth occured were observed for 98 different pairs of species. However only 42 of these pairwise interactions were observed five or more times. These 42 pairwise interactions have been compiled into a contact matrix (Fig. 4.7).

Tunicate species were dominant to bryozoan species and *Galeolaria* spp. in all cases. They were either dominant to sponge species (three cases) or equivalent (five cases). Sponge species were also dominant to *Galeolaria* spp. in all cases and they were either dominant (seven cases) or equivalent (three cases) to bryozoan species.

These results suggest that tunicate species will usually overgrow sponge species, bryozoan species and *Galeolaria* spp. and sponge species will usually overgrow bryozoans and *Galeolaria* spp. when bare substratum is in short supply. This conclusion is also in good agreement with the competitive hierarchy constructed from the overgrowth records from the permanent quadrats at Edithburgh (Section 3.3.1.2.).

Complete exclusion of bryozoans by sponge did occur in one patch. Eighteen colonies of bryozoans (four different species) were overgrown in the first six months after clearance resulting in a patch monopolized completely by one colony of *Crella* sp. Partial overgrowth of colonizing bryozoans and *Galeolaria* spp.

occured in the majority of patches (note the fall in percentage cover for bryozoans in the May and August groups in Fig. 4.3). However the one-year period of observation was not long enough to observe complete exclusion.

4.3.2 Experiment II

Small patches were reoccupied by the vegetative growth of surrounding sponge more rapidly than large patches (Fig. 4.8 and Table 4.4). Additionally patches of the same size were reoccupied more rapidly by *Mycale* sp. than by *Crella* sp. (Fig. 4.8 and Table 4.4).

No colonists were observed in the 10cm x 10cm and 25cm x 25cm sized patches surrounded by *Mycale* sp. (Table 4.5 and Appendix IIIc). Bryozoans and *Galeolaria* spp. did colonize the 50cm x 50cm sized patches surrounded by *Mycale* sp. (Table 4.5). However inspection of successive transparencies indicated that they were overgrown completely by the end of the experimental period (also see Table 4.5, Appendix IIIc). Similarly the bryozoans which colonized the 10cm x 10cm sized patches surrounded by *Crella* sp. were overgrown by the end of the experimental period (Table 4.5 and Appendix IIIc). The mean percentage cover for colonizing tunicates, sponges and bryozoans increased over the experimental period in the 25cm x 25cm and 50cm x 50cm sized patches surrounded by *Crella* sp. (Table 4.5). Even so inspection of successive transparencies of these patches indicated that the vegetative extension of the surrounding *Crella* sp. colony grew over some of these colonists. After an initial increase the mean percentage cover of *Galeolaria* spp. decreased in these

two groups of patches (Table 4.5 and Appendix IIIc). Inspection of successive transparencies indicated that this occured because individuals were overgrown, the colonization rate of the group decreased and established individuals, which were not overgrown, had reached maximum size and could not acquire space by vegetative growth.

These results demonstrate that patch size and the growth rate of the species surrounding a patch can influence within patch events in the sessile guild at Edithburgh. In particular they indicate that species which invade patches using dispersive larvae will be much less abundant in small patches and patches surrounded by fast growing species than in large patches and patches surrounded by slow growing species. However, in the case of poor competitors such as the bryozoans and *Galeolaria* spp., this difference in abundance will eventually decrease as they are overgrown by sponges and/or tunicates.

Although the conclusions made from this experiment were derived from observations of patches surrounded by one or the other of the sponges, *Mycale* sp. and *Crella* sp., I think that it will also apply to most patches found within the sessile guild at Edithburgh for the following reasons. Firstly, well over half of the occupied substratum at Edithburgh is covered by sponges (Fig. 2.4, 2.5 in Section 2.4.3.3) and each species is capable of vegetative growth (Table 3.4 Section 3.3.2.1 and casual observations). Thus most patches formed in the sessile guild will be bordered by sponges which will invade them by vegetative growth. Secondly, all the common sponge species are

capable of overgrowing bryozoans and *Galeolaria* spp. (Fig. 3.4c, 3.5c, Section 3.3.1.2; Fig. 4.7, Section 4.3.1.3).

4.3.3 Summary of Results

The results of Experiment I and Experiment II show that the following four attributes of patches will influence the identity and abundance of species in them.

1. Position in space.

This will determine which species can reoccupy a patch by vegetative growth of adult colonies. Additionally the distribution of colonists in space is not uniform for some species.

2. Age.

The abundance of species occupying patches changes over time. Given the probable competitive relationships between tunicates, sponges, bryozoans and *Galeolaria* spp. a bare patch formed in this community will eventually be monopolized by sponges and/or tunicates. Bryozoans and *Galeolaria* spp. will be overgrown and excluded.

3. Time of clearance.

Seasonal and between-year variations in larval availability will partially determine the colonization rate of individual species and phyletic groups onto patches.

4. Initial size of patch.

This will partially determine the proportion of a patch occupied by the vegetative growth of colonies adjacent to the patch compared to that occupied by colonists. Colonists will occupy a greater proportion of the substratum in large patches than in small ones.

4.4 Discussion

4.4.1 Reoccupation of Patches and Models of Succession

The model for classical succession proposes that certain species will invade newly available free space first (Odum 1969, Horn 1974, Connell and Slatyer 1977). These "early successional" species grow and mature quickly, have high reproductive rates, disperse widely and are poor interference competitors (Horn 1974). These characteristics enable such species to invade free space quickly and to reproduce before being competitively excluded by "late successional" species which are long-lived, have low reproductive rates and are good interference competitors (Horn 1974). Additionally, the "early successional" species modify the local environment such that it becomes more suitable for the recruitment of the "late successional" species (Odum 1969, Horn 1974, Connell and Slatyer 1977).

At Edithburgh pier certain species repeatedly colonized some patches very heavily (Section 4.3.1.2). The mechanism responsible for this could not be determined from the experiments. If it was an example of active aggregative settlement rather than habitat selection or spatially variable settlement due to poor dispersal of larvae from nearby adults, then these colonists could be thought of as preparing the substratum for later arrivals (Anger 1978). However, since the later arrivals were the same species it would not provide evidence for the occurrence of classical succession. There was no evidence in any patch that the vegetative growth of established colonies into a patch

was facilitated in any way by those species already present. Additionally, no one species or group of species always invaded patches first. Instead the results show that the identity of species first invading a patch will be determined mainly by temporal and spatial heterogeneity in the distribution of planktonic larvae and the identity of the colonial species capable of vegetative growth next to the patch rather than the age of the patch. Succession in the classical sense was not observed.

Two alternative models for succession presented by Connell and Slatyer (1977) propose that both late and early successional species may invade newly available bare space simultaneously although the latter type are likely to do so in greater numbers. Once these early occupants are established they may either inhibit completely further invasion by any species ("inhibition model") or only inhibit further invasion by the early successional species which cannot tolerate reduced levels of resources ("tolerance model").

In the marine subtidal the pattern of species replacements on newly submerged artificial plates has been found to conform to either one or the other model at a particular locality. At Beaufort, North Carolina, the pattern conforms to the inhibition model (Sutherland 1974, 1975, 1978). The species which initially colonized the plates inhibited further colonization. This resulted in the formation of multiple stable points (see Section 4.1). At other localities the pattern conforms to the tolerance model (e.g. Osman 1977, Jackson 1977a, Anger 1978, Russ In press).

In these cases many initial colonists could not inhibit further colonization and were often overgrown by later colonists.

As pointed out in Section 4.3.1.2 bryozoans and *Galeolaria* spp. never settled on live tissue. Hence, as the percentage of bare substratum in a patch decreased, these species would be less able to invade by larval recruitment. Tunicates and sponges were observed to settle on live tissue but bare wood appeared to be the preferred substratum (Section 4.3.1.2) therefore the same reasoning applies to these species. These observations are in good agreement with the inhibition model. However, since the greatest percentage of space in patches was occupied by the vegetative growth of established colonies these observations alone are not adequate to determine which of the two models, if either, best fits the observed patterns of patch reoccupation.

Any species occupying a patch will resist further invasion by the vegetative growth of adjacent colonies only if the adjacent species is competitively inferior. Thus the early occupants of a patch may or may not inhibit further invasion depending on the identity of the species within and immediately surrounding the patch. Bryozoan species and *Galeolaria* spp. did not, in most cases, inhibit the invasion of sponges and tunicates; thus the patterns of reoccupation in some patches conformed to the tolerance model. On the other hand, tunicate species and certain sponge species often did inhibit the invasion of other sponge species (see Fig. 4.7); thus the patterns of reoccupation in other patches conformed to the inhibition model.

Both patterns of patch reoccupation often lead to multiple stable points (see Section 4.1). However, it is patch position, not larval availability that will determine which species will monopolize a patch. The two most common points are those which are completely monopolized by either *Mycale* sp. or *Crella* sp. Other stable points exist. These are usually no greater than 400 cm^2 in area and are simply areas that have been occupied by one colony of sponge. Larger areas up to 2,500cm^2 may be occupied by *Botrylloides leachii*, but these monopolies are short-lived (5-6 months) compared to sponge monopolies (between 1 and 5 years). Events within patches were directional only in the sense that colonizing bryozoans and *Galeolaria* spp. would in most cases eventually be overgrown by some species of sponge or tunicate.

The observation that bryozoan species and *Galeolaria* spp., the most common colonists of patches, were so often overgrown by sponges and tunicates supports the early successional and late successional roles proposed for small colonial or solitary species and large colonial species respectively in space-limited communities in the marine environment (Jackson, 1977b, In press). However the species in this sessile guild do not all fit neatly into the classification system which lists characteristics typical of early and late successional types (Horn 1974). A major characteristic is ability in interference competition; early successional types are poor interference competitors and late successional types are good interference competitors (Horn 1974). However, the best interference competitors in this sessile guild, the colonial tunicates, had some of the characteristics of early

successional species. These are a short life span (less than 11 months) and very rapid growth to maturity (Table 3.4, Section 3.3.2). A patch occupied by sponges which are much longer lived than the tunicates (Table 3.4, Section 3.3.2) will not always resist invasion by tunicates. Additionally tunicates did not always completely kill the species they grew over, particularly if overgrowth occured within two months of the senescence of the tunicate colony (Section 3.4). Also, two of the bryozoan species, *Celleporaria valligera* and *Celleporaria fusca,* had very long life spans (over four years see Table 3.4, Section 3.3.2) which is usually taken to be a characteristic of late successional species. Yet they are very poor interference competitors (Section 3.3.1 and Table 4.7, Section 4.3.1.3) and in most patches did not resist overgrowth by sponges or tunicates.

4.4.2 Sessile Guild Structure

As pointed out in Section 4.1 naturally cleared patches in the sessile guild at Edithburgh ranged in size from approximately one square centimetre to one square metre. However, the patches of bare substratum that were observed in or adjacent to the permanent quadrats (Section 2.4.2.1) were never larger than two thousand square centimetres during the two year period of the non-destructive census. Thus it can be assumed that most of the bare substratum in the sessile guild occured in patches that were smaller than the largest patches in Experiment II. Accordingly the results of Experiment I and Experiment II demonstrate that most of the free space available in the sessile guild at Edithburgh during this period would have been reoccupied by

the vegetative growth of established sponge colonies. Larval recruitment would have played a relatively minor role in the reoccupation of bare substratum.

In many benthic communities most of the substratum which is cleared by physical and/or biological disturbances is reoccupied by larval recruits (Sutherland 1976). Established sessile organisms have little direct influence on the fate of newly available free space in such communities. This was clearly not the case for the sessile guild at Edithburgh, where the established guild had considerable influence over the fate of newly cleared substratum because of the rapid vegetative growth of colonies next to bare patches. Members of the guild may have had other influences, e.g. by consuming approaching larvae or by releasing short-lived larvae which settle very near to the parent colonies or individuals, but they were not measured. Casual observations suggest that such influences were minor compared to that due to vegetative growth.

However, it should be noted that it is not only because some species possess great capacity for vegetative growth that the extension of neighbouring colonies is an important mode of reoccupation of cleared space. An additional necessary condition is that the frequency of disturbance is appropriate. The results of Experiment II indicated that the proportion of a patch occupied by larval recruits will increase as the patch size increases. Additionally the results of Experiments I and II indicate that, after an initial peak, there is a decrease in the proportion of a patch occupied by bryozoans and *Galeolaria* spp. which invade

patches by dispersive larvae. Thus, increases in the frequency of patch formation and in the size of patches would have two related effects. Firstly, larval availability would have a greater effect on the structure of the sessile guild. Secondly, bryozoans and *Galeolaria* spp. would be more abundant and sponges less abundant than presently observed. Thus, despite the presence of many species which are capable of vegetative growth, the established sessile guild would have much less influence over the fate of newly cleared substratum if disturbance levels were to increase dramatically.

It is easy to envisage such an increase. Casual observations in the field suggest that the asteroids *Patiriella brevispina* H.L. Clark, *Tosia australis* Gray and *Petticia vernicina* (Lamarck) (see Section 6.3.2.5), wave turbulence and the senescence of old colonies are responsible for the formation of bare patches of substratum. Thus an increase in the numbers of asteroids, the frequency of rough weather and/or the number of senescing colonies could lead to higher levels of disturbance. An increase in the number of senescing colonies could be brought about by an increase in the proportion of the substratum occupied by short-lived species. Most of the species in the sessile guild at Edithburgh are long-lived and most of the substratum is covered by perennials (Table 3.4, Section 3.3.2.2 and Section 2.4.3.3).

In summary, the established sessile guild at Edithburgh strongly influences the fate of newly cleared substratum through the vegetative growth of established colonies. This situation is not only a result of many species in the guild being capable

of rapid vegetative growth but also a result of the prevailing levels of disturbance. These levels are determined by factors external to the guild (weather and predators) and by characteristics of its component species, especially longevity. If any of these factors changed such that the levels of disturbance increased the established sessile guild would have less influence over the fate of newly cleared substratum and larval colonization would play a more important role in the structure of the guild.

TABLE 4.3 The means and standard deviations (parenthesis) of the percentage cover due to total growth, vegetative growth and the growth of colonists one year after initial patch clearnace for the four groups in Experiment I. A summary of the results of a Kruskal-Wallis one-way ANOV comparing the percentage of space covered between the four groups of patches for each of these three is included. For the May and December groups sample size=5; for the February and August groups sample size=4; ns: not significant at the .05 significance level.

	Time of Clearance				Kruskal-Wallis Statistic	
	February	May	August	December	H	P
Total growth	71.23(20.55)	63.60(33.27)	86.33(16.64)	62.60(25.38)	5.31	>0.05 ns
Vegetative growth	45.06 (15.39)	54.86(41.02)	79.80(21.28)	47.39(37.55)	3.12	>0.05 ns
Growth of Colonists	26.17 (20.68)	8.74 (8.31)	6.50 (7.48)	15.20(12.94)	5.60	>0.05 ns

TABLE 4.4 Summary of results of Mann-Whitney U-tests comparing rates of patch occupation by surrounding sponge between groups of patches in Experiment II. In each case the first named group was overgrown more rapidly than the second.

N1: sample size of first named group

N2: sample size of second named group

The P values are for a one tailed test

Groups of patches compared	Mann-Whitney U-test Statistics N1	N2	U	P
Mycale sp. 10cm x 10cm vs. *Crella* sp. 10cm x 10cm	10	10	1	<.01
Mycale sp. 25cm x 25cm vs. *Crella* sp. 25cm x 25cm	10	10	3	<.01
Mycale sp. 50cm x 50cm vs. *Crella* sp. 50cm x 50cm	4	3	0	.028
Mycale sp. 10cm x 10cm vs. *Mycale* sp. 25cm x 25cm	10	10	10	<.01
Mycale sp. 10cm x 10cm vs. *Mycale* sp. 50cm x 50cm	10	4	0	<.01
Mycale sp. 25cm x 25cm vs. *Mycale* sp. 50cm x 50cm	10	4	7	<.05
Crella sp. 10cm x 10cm vs. *Crella* sp. 25cm x 25cm	10	10	10	<.01
Crella sp. 10cm x 10cm vs. *Crella* sp. 50cm x 50cm	10	3	0	<.01
Crella sp. 25cm x 25cm vs. *Crella* sp. 50cm x 50cm	10	3	3	<.05

TABLE 4.5 The means and standard deviations (parenthesis) of percentage cover due to the growth of colonists belonging to each of the following phyletic groups: Sponges, Tunicates, Bryozoans and *Galeolaria* spp. in the six groups of patches in Experiment II. Only the values 161 days after patch clearance (20/09/77) and 329 days after patch clearance (24/03/78) are given.

Surrounding species	Patch size	Sample size	Percentage cover after 161 days				Percentage cover after 329 days			
			Sponges	Tunicates	Bryozoans	*Galeolaria* spp.	Sponges	Tunicates	Bryozoans	*Galeolaria* spp.
Crella sp.	10cm x 10cm	10	0.0	0.0	0.54 (1.48)	0.0	0.0	0.0	0.0	0.0
Crella sp.	25cm x 25cm	10	0.11 (0.36)	0.15 (0.42)	1.29 (1.47)	0.06 (0.08)	1.00 (3.07)	2.16 (5.43)	3.94 (5.42)	0.0
Crella sp.	50cm x 50cm	4	0.0	0.0	0.85 (0.31)	0.09 (0.14)	7.73 (6.70)	0.48 (0.47)	6.37 (1.56)	0.01 (0.01)
Mycale sp.	10cm x 10cm	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mycale sp.	25cm x 25cm	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mycale sp.	50cm x 50cm	3	0.0	0.0	0.15 (0.20)	0.04 (0.04)	0.0	0.0	0.0	0.0

FIGURE 4.1 Change in percentage cover after initial patch clearance. Graphs show mean and standard deviation (vertical line) of total cover (X), percentage cover due to vegetative growth (■), and percentage cover due to growth of new recruits (⬮) for all four groups in Experiment I on all sample dates

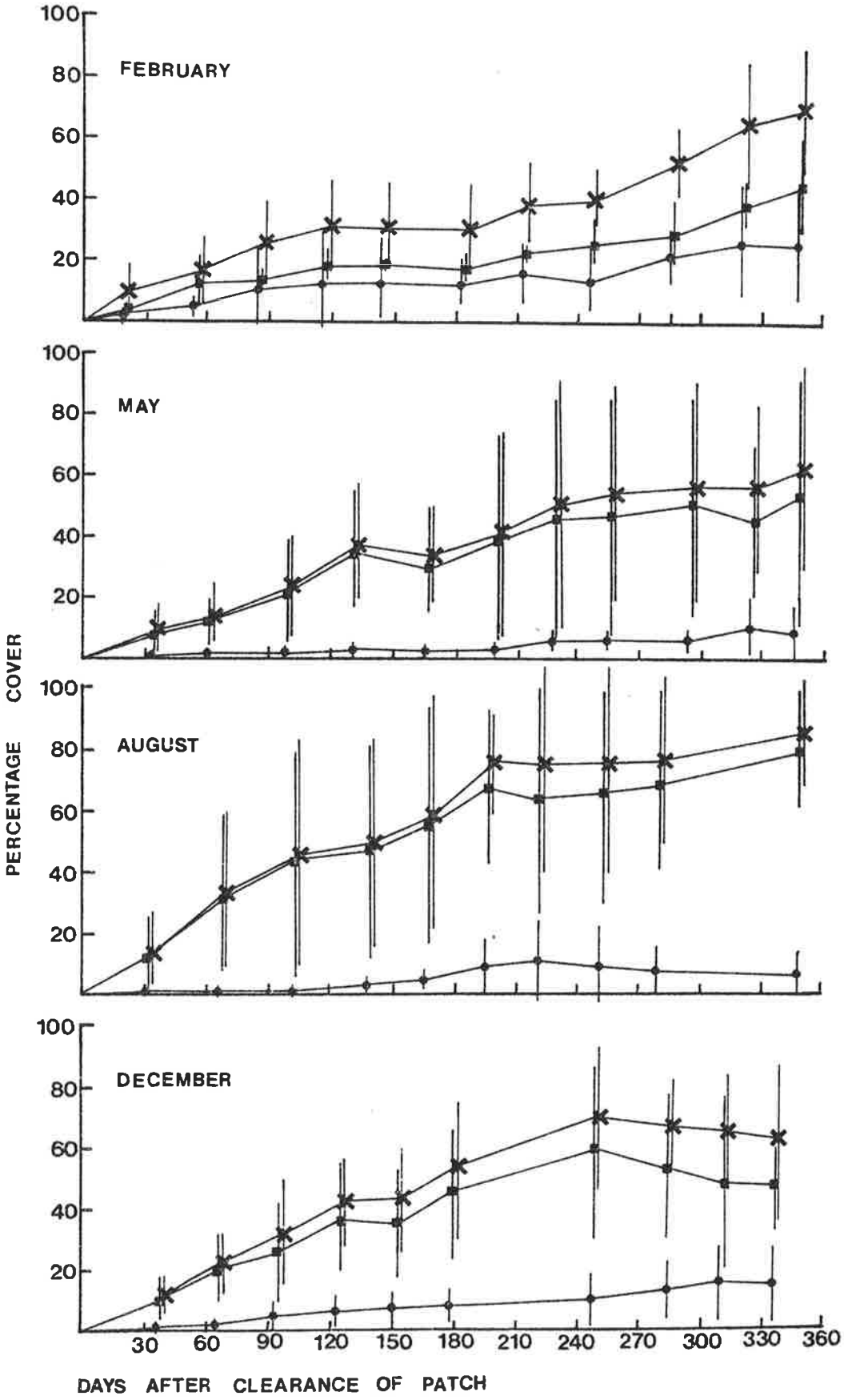

FEBRUARY
MAY
AUGUST
DECEMBER
100
80
60
40
20
PERCENTAGE COVER
30
60
90
120
150
180
210
240
270
300
330
360
DAYS AFTER CLEARANCE OF PATCH

FIGURE 4.2 The growth of new recruits and vegetative growth for sponges after initial patch clearance. Bar diagrams show mean (bar) and standard deviation (line) of percentage cover due to vegetative growth (solid bars) and due to growth of new recruits (open bars) for all four groups in Experiment I on all sample dates. Month of patch clearance indicated by *, last sample taken indicated by (●).

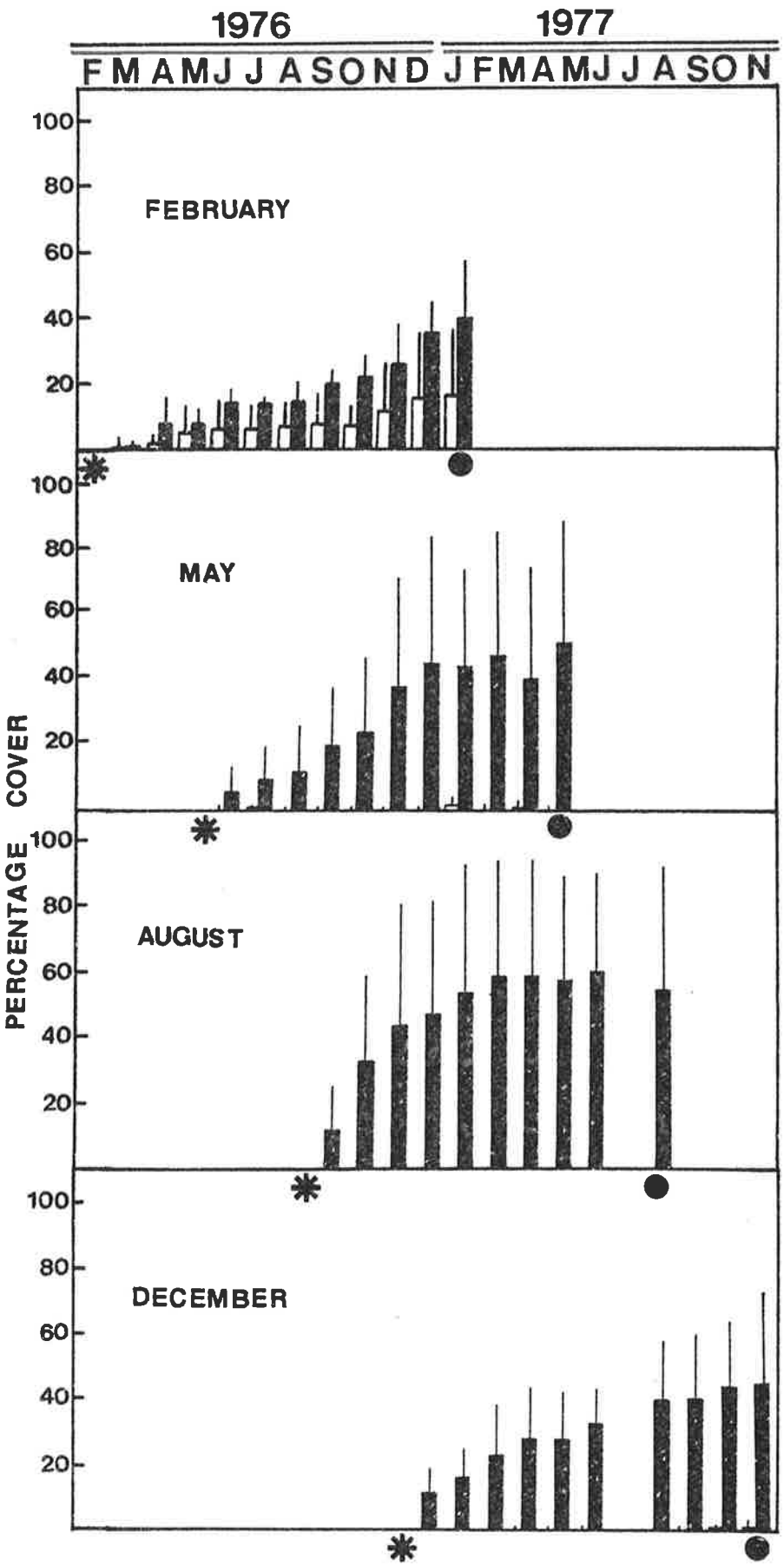

1976
1977
F M A M J J A S O N D J F M A M J J A S O N
PERCENTAGE COVER
100
80
60
40
20
FEBRUARY
MAY
AUGUST
DECEMBER

FIGURE 4.3 The growth of new recruits and vegetative growth for bryozoans (top four diagrams) and tunicates (lower four diagrams) after initial patch clearance for all four groups in Experiment I on all sample dates. For meaning of symbols see caption to Figure 4.2.

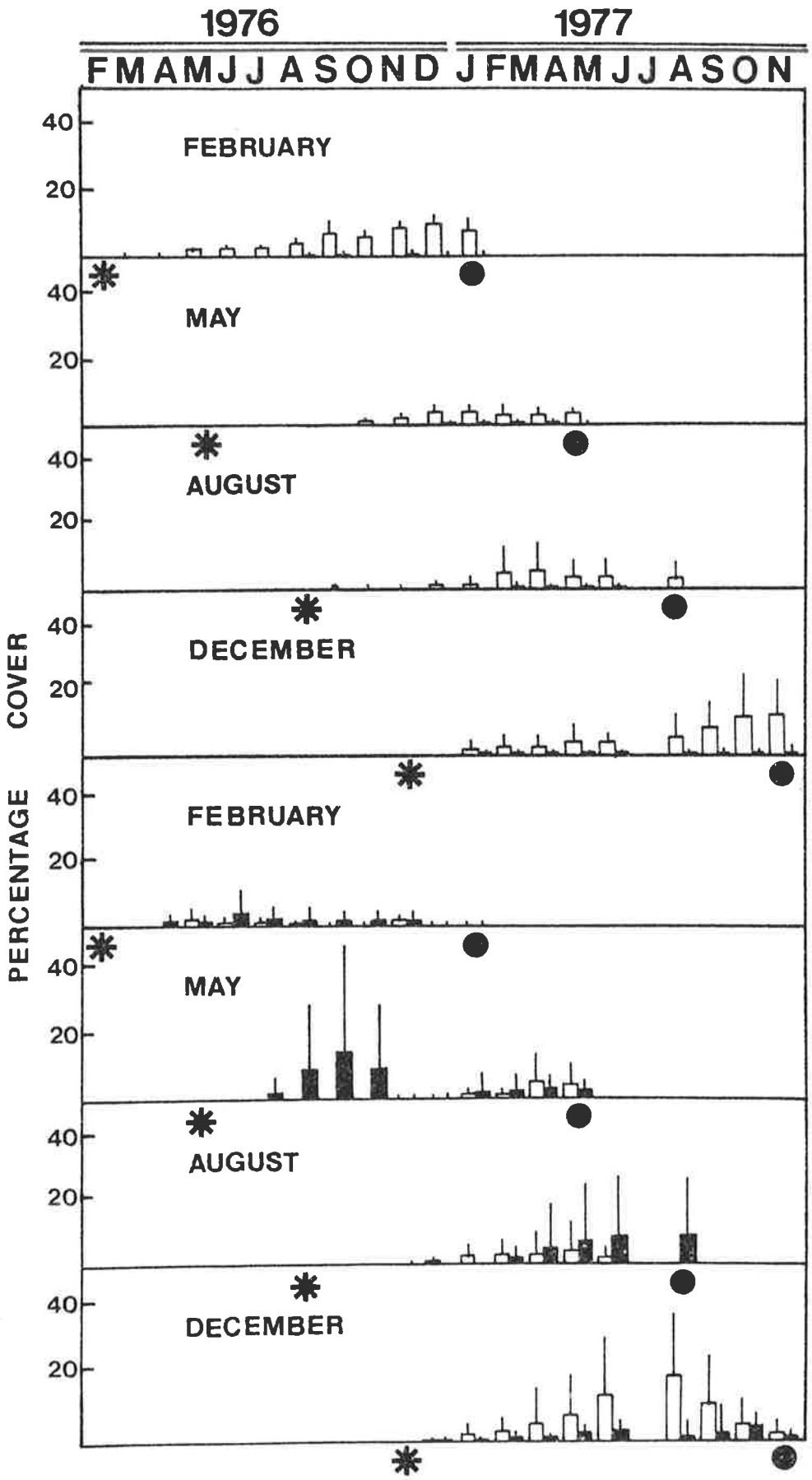

1976
1977
F M A M J J A S O N D J F M A M J J A S O N
PERCENTAGE COVER
40
20
FEBRUARY
MAY
AUGUST
DECEMBER
FEBRUARY
MAY
AUGUST
DECEMBER

FIGURE 4.4 Bar diagrams showing the mean (bar) and standard deviation (line) of percentage cover for individual species on sample dates corresponding as nearly as possible to 3, 6, 9, and 12 months after initial patch clearance in all four groups in Experiment I. Species code numbers (see Table 2.1) are given on the X-axis.

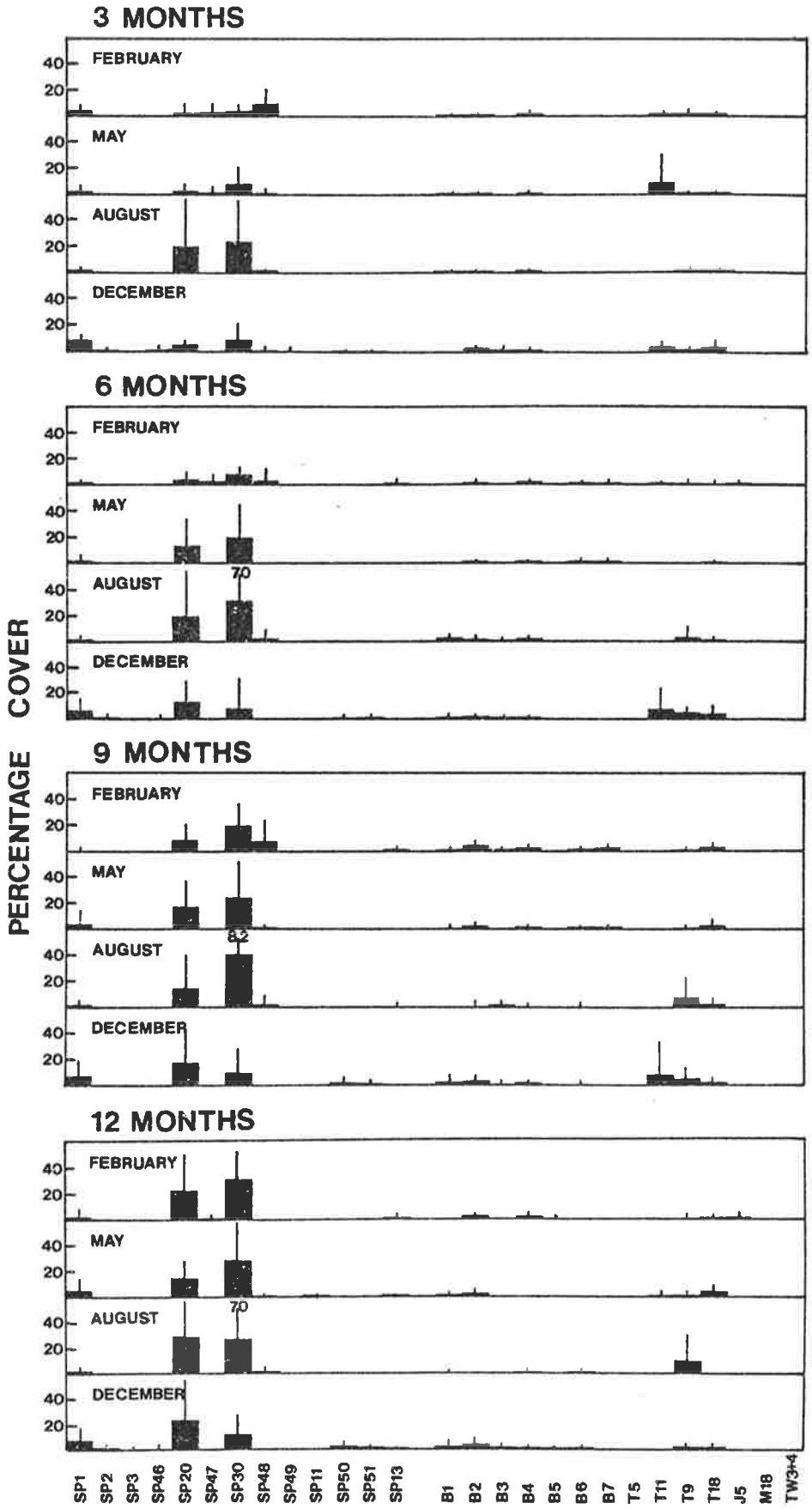

3 MONTHS
6 MONTHS
9 MONTHS
12 MONTHS
FEBRUARY
MAY
AUGUST
DECEMBER
PERCENTAGE COVER
40
20
70
82
70
SP1
SP2
SP3
SP46
SP20
SP47
SP30
SP48
SP49
SP11
SP50
SP51
SP13
B1
B2
B3
B4
B5
B6
B7
T5
T11
T9
T18
J5
M18
TW3+4

FIGURE 4.5 Colonization rates for major groups. Bar diagrams show mean (bar) and standard deviation (line) of the number of colonists/600cm^2/30 days recorded each sample interval in all four groups in Experiment I on all sample intervals. Sponges, solid bar; bryozoans, spotted bar; tunicates, open bar; *Galeolaria* spp., striped bar. Month of patch clearance indicated by *, last sample indicated by ●.

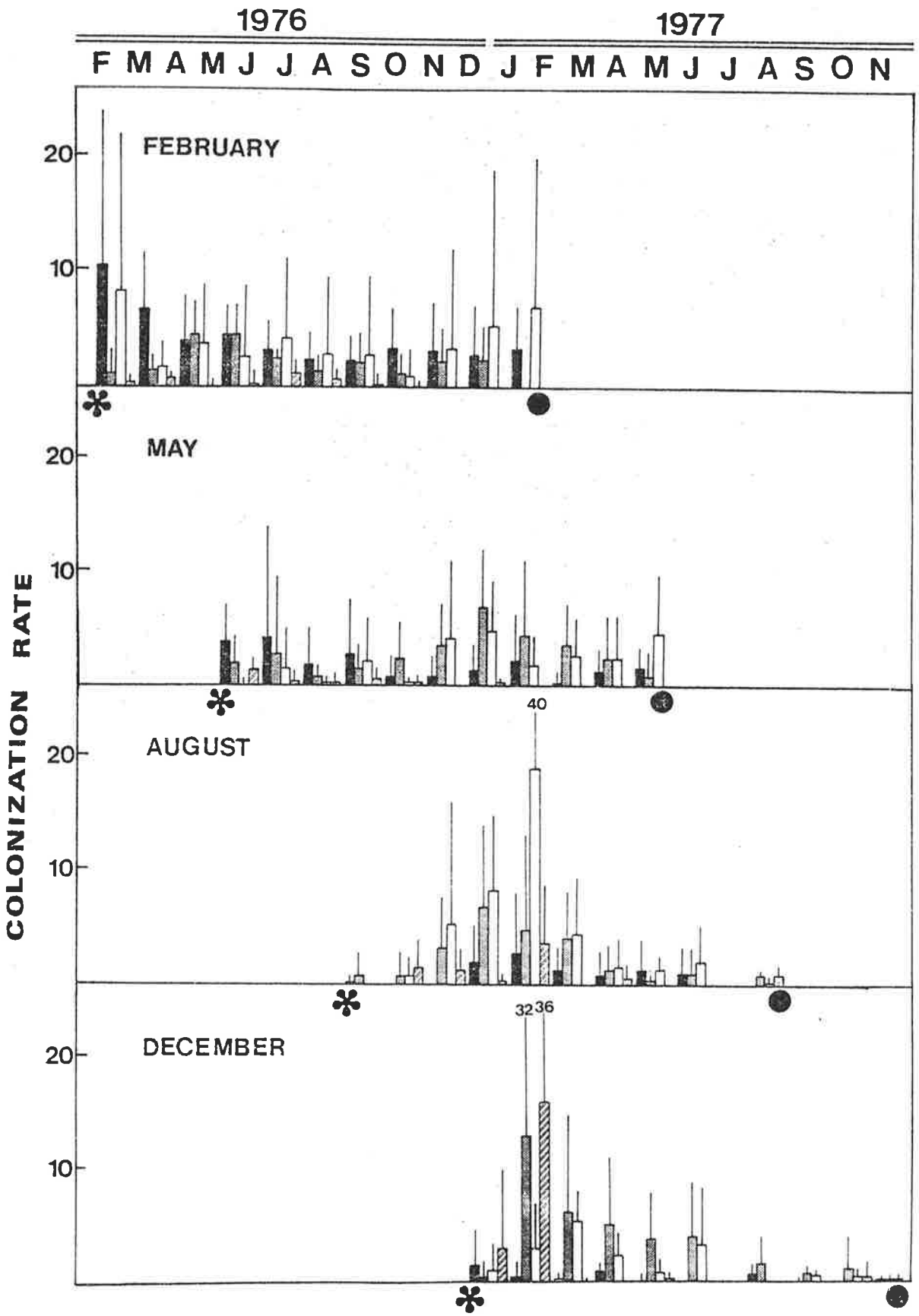

1976
1977
F M A M J J A S O N D J F M A M J J A S O N
FEBRUARY
MAY
AUGUST
DECEMBER
20
10
40
32 36
COLONIZATION RATE

FIGURE 4.6 Bar diagrams showing the mean (bar) and standard deviation (line) of overgrowth (percentage cover of live tissue overgrown/90 days) in all four groups in Experiment I on all sample intervals

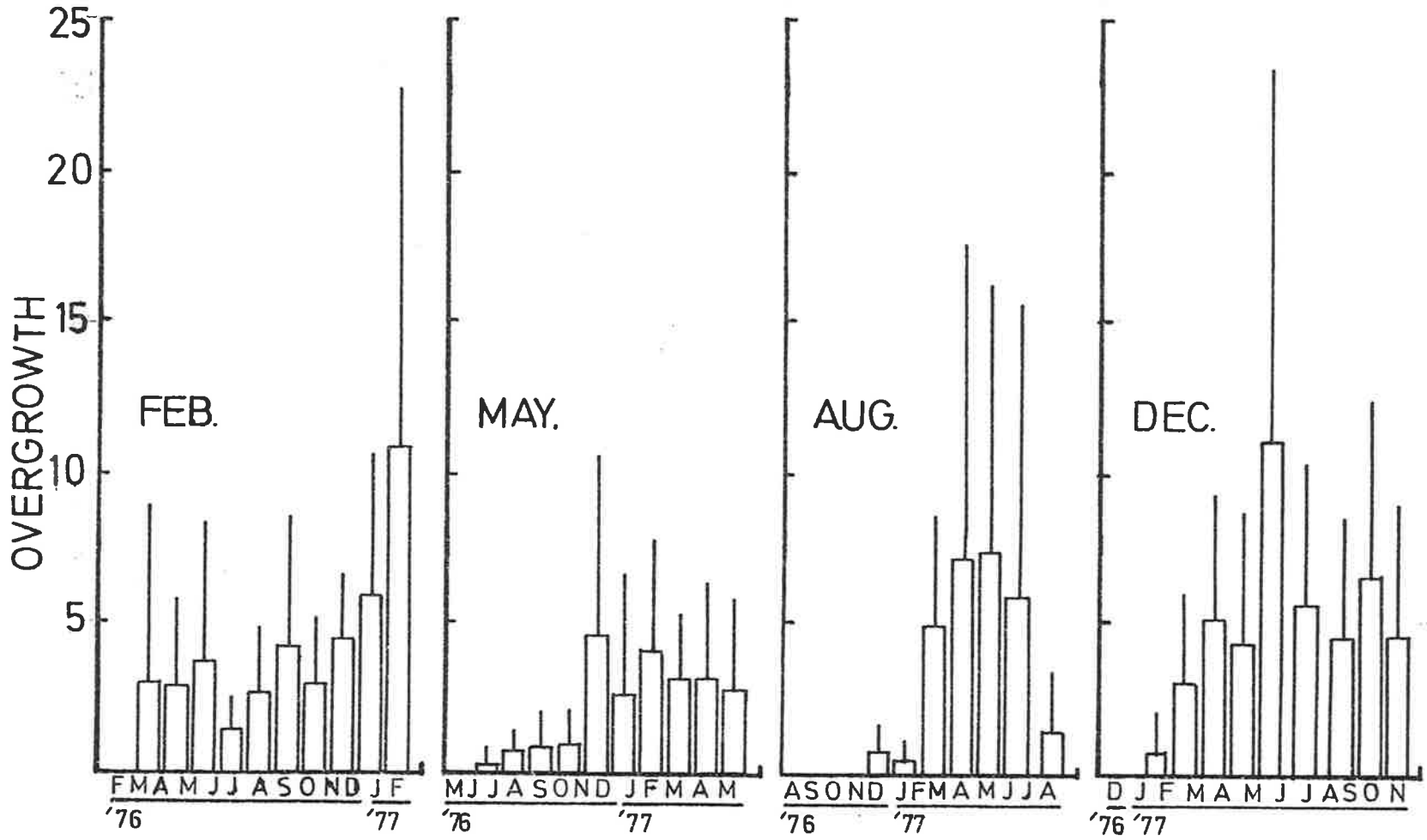

OVERGROWTH
25
20
15
10
5
FEB.
MAY.
AUG.
DEC.
F M A M J J A S O N D J F
'76
'77
M J J A S O N D J F M A M
'76
'77
A S O N D J F M A M J J A
'76
'77
D J F M A M J J A S O N
'76
'77

FIGURE 4.7 Contact matrix of competitive interactions for species pairs where the number of observations were greater than five. Arrows point in the direction of the dominant of each two species pair. An asterisk indicates competitive equivalence. Species code numbers are listed in Table 2.1. For further explanation see text of Section 3.2.1.2.

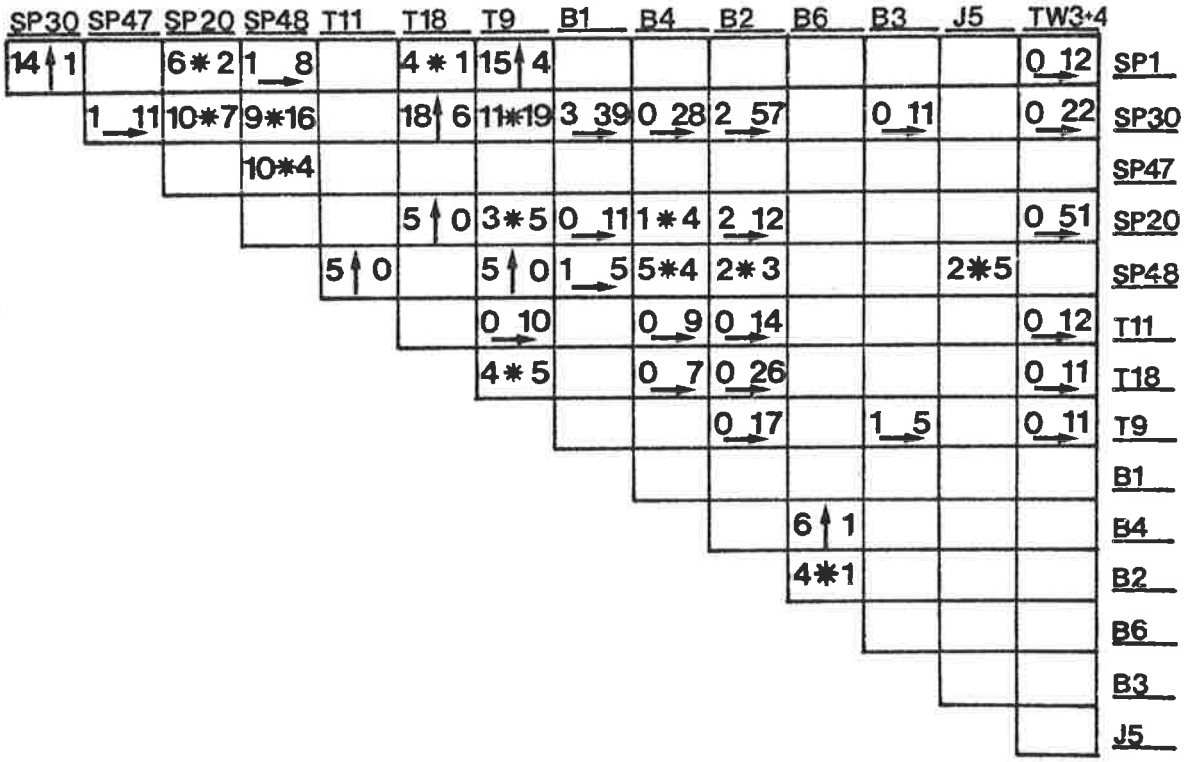
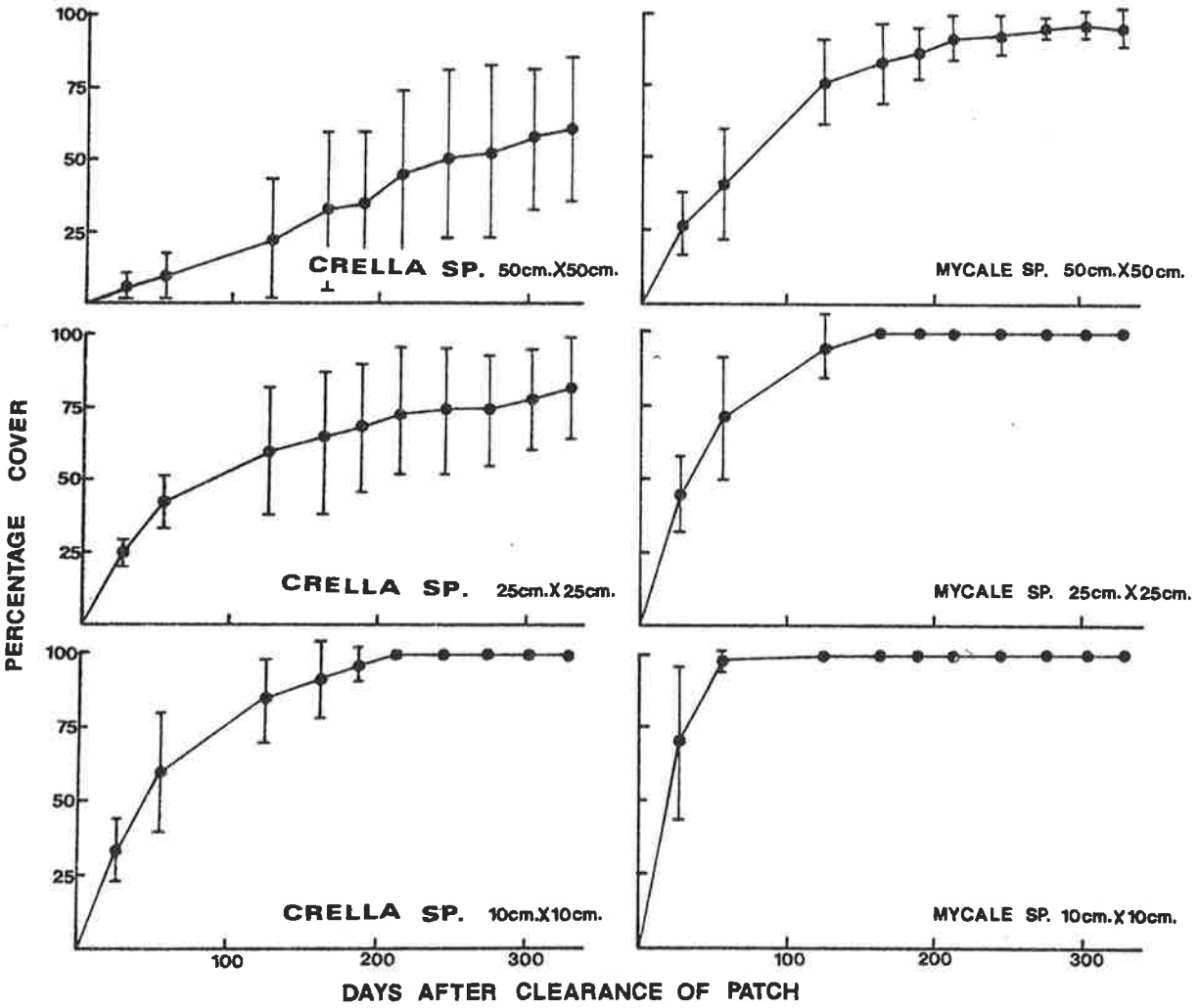

SP30 SP47 SP20 SP48 T11 T18 T9 B1 B4 B2 B6 B3 J5 TW3+4
14 1 6*2 1 8 4*1 15 4 0 12 SP1
1 11 10*7 9*16 18 6 11*19 3 39 0 28 2 57 0 11 0 22 SP30
10*4 SP47
5 0 3*5 0 11 1*4 2 12 0 51 SP20
5 0 5 0 1 5 5*4 2*3 2*5 SP48
0 10 0 9 0 14 0 12 T11
4*5 0 7 0 26 0 11 T18
0 17 1 5 0 11 T9
B1
6 1 B4
4*1 B2
B6
B3
J5

FIGURE 4.8 Mean and standard deviation (line) of percentage cover for the vegetative growth of surrounding sponge tissue after initial patch clearance in all six groups in Experiment II on all sample dates


PERCENTAGE COVER
100
75
50
25
CRELLA SP. 50cm.X50cm.
MYCALE SP. 50cm.X50cm.
CRELLA SP. 25cm.X25cm.
MYCALE SP. 25cm.X25cm.
CRELLA SP. 10cm.X10cm.
MYCALE SP. 10cm.X10cm.
100
200
300
DAYS AFTER CLEARANCE OF PATCH

5.0 DEVELOPMENT OF THE SESSILE GUILD AT RAPID BAY

5.1 Introduction

The word development is commonly used to describe the growth to maturity of an individual organism. Theories of community organization where an analogy is made between the community and an individual organism (e. g. Clements 1916, 1936, Tansley 1935, Margalef 1963, 1969, Odum 1969) have been discredited by a number of authors (e.g. Colinvaux 1972, Ricklefs 1973, Horn 1974). Nevertheless the term community development is frequently used to refer to the process of colonization and the pattern of changes in species composition and abundance on previously unoccupied artificial and natural substrata in the subtidal region of the marine environment (e.g. Goodbody 1961, Sutherland and Karlson 1973, 1977, Jackson 1977a, Osman 1977, Anger 1978). Succession in its broadest sense (e.g. Connell and Slayter 1977, Noble and Slayter In press) is synonymous with this definition. Accordingly the term community development encompasses the variety of models postulated to explain the mechanisms underlying succession (e. g. Odum 1969, Horn 1974, Connell and Slayter 1977, Noble and Slayter In press) and does not necessarily imply that the community under investigation is some kind of organic entity that has emergent properties greater than the sum of its parts.

Community development on hard substrata is the marine environment is acknowledged to be a result of a highly complex combination of biological and physical factors. These are habitat

selection by vagile larvae (Meadows and Campbell 1972, Crisp 1964, Jackson 1977a), seasonal abundance of colonizers (Sutherland 1974, Osman 1977), competitive interactions between established adults and between adults and colonizing larvae (Goodbody 1961, Sutherland 1974, 1977, Osman 1977, Anger 1978, Russ In press) and disturbance by physical factors and/or predators (Sutherland 1974, Osman 1977, Anger 1978, Karlson 1978, Russ In press). Despite this investigations in different localities have shown that there is often a small number of key factors which determine the patterns of species replacement and the final stable community structure (if this is a reality which can be identified) on an individual piece of substratum.

Grazing fish have been shown to be of critical importance in the development of fouling communities in several localities (e.g. Day 1977, Russ In press) by preventing monopolization of space by a dominant competitor which they selectively remove. In other localities the seasonality of larval abundance has been shown to be a key factor in community development (Sutherland 1974, Osman 1977). As explained in Section 4.1 Sutherland (1974, 1975, 1978) demonstrated that differences in the order of larval recruitment onto artificial plates at Beaufort resulted in communities of different structure on different plates (i.e."multiple stable points").

In Section 3.4 I suggested that *Culicia* sp. maintained high abundance in the sessile guild at Rapid Bay as a result of the combined effect of three characteristics: rapid vegetative

growth, long life span and the inhibition of overgrowth and larval settlement. However I cannot assume that these were the only factors or even the key factors responsible for this species first achieving high abundance in this guild. In particular I must acknowledge the possiblity that rapid vegetative growth was a result rather than a partial cause of extremely high abundance. In Chapter 3 the growth rates of *Culicia* sp. were measured in bare patches surrounded by large expanses of this species. It is highly likely that the number of new polyps that a colony can produce is positively correlated with its size. This proposition is given support by Jackson's (In press) analysis of morphological strategies in colonial sessile animals. Thus a newly settled colony of *Culicia* sp. may expand and fill new space much more slowly than the large established colonies seen on the pilings today (see Photograph 6.1). Additionally the bare patches mainly consisted of the remains of *Culicia* sp. skeleton. It is possible that this facilitated the vegetative growth of *Culicia* sp. across these areas. The colonies of *Culicia* sp. which first settled as the pilings would have had to grow over the original bituminous tar surface.

With this in mind I offer three alternative hypotheses which describe how *Culicia* sp. may have reached such high abundance in the sessile guild at Rapid Bay after the pilings of the pier were driven in October and November 1960.

(1) *Culicia* sp. colonized the new pilings sporadically and in lower numbers than other species but rapidly increased

in abundance due to rapid vegetative growth. It has since maintained high abundance due to the three characteristics listed in Chapter 3.

(2) *Culicia* sp. colonized the new pilings sporadically and in low numbers and only slowly increased its abundance by moderately slow vegetative growth, and continued low levels of colonization. It has eventually achieved high abundance through long life and resistance to overgrowth and larvae invasion. This hypothesis is analogous to Karlsons (1978) explanation for the high abundance of the colonial hydroid *Hydractinia echinata* in the fouling community on pier pilings at Beaufort.

(3) *Culicia* sp. colonized the pilings in high numbers immediately after they were driven due to a seasonal or chance peak in the recruitment of this species during construction of the pier. This gave rise almost immediately to relatively high abundance which was increased due to vegetative growth and maintained due to the three characteristics listed in Chapter 3. In this case the structure of the sessile guild at Rapid Bay could be viewed as one of several "multiple stable points" analogous to those observed by Sutherland (1974) at Beaufort as artificial substrata. This view would be applicable if *Culicia* sp. was unable to invade and establish high abundance on pilings which had not been driven during the peak in its recruitment because they had been heavily colonized by different species.

I acknowledge that there may be further alternatives but I feel these were the most likely three possibilities in view

of my own observations and the observations made in other fouling communities. They are also crude descriptions of the possible developmental pattern and are concerned mainly with the mechanisms by which the most abundant species in the sessile guild at Rapid Bay has acquired so much of the space resource. The role that predation may have played in this process is indicated by the experiments reported in Chapter 6.

To distinguish between these alternatives the development of the sessile guild was investigated using large artificial panels simulating the original piling surface. Two groups of long-term panels were submerged at different times of the year to test the effect of differences in the sequence of larval recruitment. One group was installed at the beginning of the season in which the pier pilings were originally driven, the other six months earlier. A series of short-term panels were also used to record the colonization rates of different species onto the original piling surface at different times of the year.

5.2 Methods

5.2.1 Long-Term Panels

Eight experimental panels were submerged at Rapid Bay on March 28, 1976 (March group) and another eight were submerged six months later on October 2, 1976 (October group). In each group two panels were allotted to each of the four piling faces (see Inset in Fig. 2.3). The panels on faces 1 and 2 were constructed of flat pieces of asbestos cement (5mm thick) 40cm x 60cm in size (Fig. 5.1). Those on faces 3 and 4 were constructed of three separate sections of asbestos 60cm in length and attached

together by rope (Fig. 5.1). The central section of these panels was 18cm wide and the two outside sections were 15cm wide. This design permitted these panels to be fitted snugly into the concave faces of the pilings (Fig. 5.1). All panels were strapped to pilings within the study area using rope and pieces of wire were fixed around the central section of the panels on faces 3 and 4 to prevent the outside sections folding over on top of them (Fig. 5.1). Before immersion each panel was given two liberal coatings of bituminous tar paint to simulate the original piling surface.

This field experiment was restricted to the West arm of the pier to facilitate relocation of panels and minimize the time spent diving. The panels were tied to the pilings in pairs; panels for faces 1 and 2 together and panels for faces 3 and 4 together. Pairs of panels were allocated to pilings at random within the study area using the method described in Section 2.4.2.1.

Each panel was photgraphed at approximately three monthly intervals (see Table 5.1 for exact sampling schedule) at a distance of 0.8 metres with an aperture of f8. Photographic sampling was stopped after April 13, 1978 but the panels have been left in place and casual observations have been made on them since. Unfortunately after the first 12 months of immersion some of the panels in the March group fell off the pilings during the Winter of 1977 (see Table 5.1). By April 13, 1978 only three panels were left in this group; one on each of face 1, face 3 and face 4. An area 30cm x 30cm central to each of the panels as faces 1 and 2

TABLE 5.1 Sampling schedule for long-term panels
S: Date of Submergence

Date	Number of panels photographed March group	October group
28/03/76	S	
09/06/76	8	
05/09/76	8	
02/10/76		S
17/12/76	8	8
29/03/77	8	8
20/06/77	6	8
29/09/77	4	8
20/01/78	3	8
13/04/78	3	8

and an area 30cm x 10cm central to each section of the panels on faces 3 and 4 (Fig. 5.1) was used for recording the development of the sessile guild. The abundances of species within these areas were calculated from the transparencies using the method described in Section 2.4.2.2. They were expressed as a percentage of the 900cm^2 area on each panel.

Not all of the species which colonized these long-term panels and could be seen in the transparencies could be accurately identified. The two problematical groups were the bryozoans and the encrusting coralline red algae.

A total of 35 different species of bryozoans (excluding species B1 to B7) were recorded on the short-term panels. Nineteen of these (all encrusting cheilostomate species from the following seven genera; *Membranipora, Electra, Watersipora, Crepidacantha, Microporella, Schizoporella* and *Mucronella*) were capable of forming colonies large enough to be detected in my transparencies but I could only identify them by examination under a low power dissecting microscope. For this reason any bryozoan colony which

could not be identified as B1, B2, B3, B4, B5, B6 or B7 was recorded under the heading "other bryozoan." This category is likely to include several or all of the 19 bryozoans identified on the short-term panels. Regrettably the individual abundances of these species on the long-term panels could not be determined on any sample date.

Similarly the colonies of coralline red algae could not be identified to the species level in the transparencies. I attempted to collect some of the colonies from the edges of the long-term panels outside of the areas used for recording species abundances but, because they were so brittle, it proved impossible. Since these species were not seen on the short-term panels I can only suggest that they were the same as those species seen on small stones and other pieces of litter beneath the pier and as epizooites and epiphytes within the piling study area. These species still await identification and have been lodged in the Botany Department at the University of Adelaide. Any colony of coralline red algae seen on the long term panels was simply recorded under the heading "coralline red algae."

Because of these identification difficulties I have made no attempt to estimate species number and diversity from the data derived from the transparencies. The mean and standard deviation of percentage cover for each species and the two categories "other bryozoan" and "coralline red algae" were calculated for each series of panels on each sample date (Appendix IVa). The mean and standard deviation of percentage cover were plotted against time for:

(1) species which attained a mean percentage cover of at least 1% on at least one sample date in either series

(2) all species present (total cover)

(3) skeletal remains of bryozoans and *Galeolaria* spp. which had been smothered and killed by overgrowth

(4) each of the following six phyletic groups which were recorded on the long-term panels

(a) serpulids

(b) bryozoans

(c) tunicates

(d) sponges

(e) cnidarians

(f) coralline red algae

A Mann-Whitney U-test was used to compare the abundances of individual species which attained a mean percentage cover of at least 1% on at least one sample date in either group between the two groups of panels 3, 6, 12, 15 and 18 months after submergence. The results of these tests are summarized in Table 5.4.

5.2.2 Short Term Panels

Eight short term panels were submerged for approximately two monthly intervals from March 28, 1976 until October 3, 1978 (see Table 5.2 for exact schedule). Two panels in each two monthly groups were allotted to each of the four piling faces. The design of the panels was exactly the same as that described for the long-term panels. The short-term panels were also restricted to the West arm of the pier and each one was randomly

TABLE 5.2 Sampling schedule for short-term panels

Date submerged	Date collected	Duration of submergence days	Number of panels recovered
28/03/76	03/06/76	67	7
03/06/76	14/08/76	72	4
14/08/76	20/10/76	65	8
20/10/76	28/12/76	69	8
28/12/76	28/02/77	62	8
28/02/77	29/04/77	61	7
29/04/77	20/06/77	52	8
20/06/77	25/08/77	65	8
25/08/77	02/11/77	69	8
02/11/77	03/01/78	69	8
03/01/78	10/03/78	66	8

allotted to a piling within the study area using the method described in Section 2.4.2.1. Panels were tied to the pilings in the manner depicted in Fig. 5.1 and each two monthly group was allotted a new set of randomly chosen pilings.

After collection, panels were placed into large plastic bags, taken back to the laboratory and stored in a refrigerator until examination. After the panels had been examined they were scraped clean with a knife and brush, given a new coat of bituminous tar and resubmerged under the pier approximately two months after collection. I used two groups of eight short-term panels which were submerged on successive sample intervals.

An area 60cm x 30cm in size on the panels from faces 1 and 2 and areas 60cm x 10cm in size on the sections of the panels from faces 3 and 4 were searched for colonists. Only colonists of species or species groups (i.e., other bryozoans and coralline red algae) which were recorded in the transparencies of the long-term panels (Table 5.3 lists species) were counted. I have included some notes in Section 5.3.2 about other colonists observed on these panels.

All species could be identified by eye with the exception of some bryozoans which had to be scraped off the panels and examined under a binocular microscope. Colonies of the colonial tunicate *Didemnum* sp.a first appeared on the panels in the August 14, 1976-October 20, 1976 sample interval but due to their small size they were not identified as such and were not counted for this two monthly period. This omission was corrected in subsequent sample intervals. Only one species, *Pycnoclavella diminuta*, that was recorded on the long-term panels and also on the short-term panels did not recruit as distinct individual colonies. This species forms large colonies made up of thousands of zooids (5cm in length) (see Photograph 3.5 Section 3.2.1.1). The zooids are connected to each other via a complex network of stolons adhering to the substratum. I could not determine if the colonies that were seen on both the long-term and short-term panels were the result of the merger of several colonists or not. Therefore the colonization rate of this species has been recorded as a percentage of the area examined on each panel on which the colonies occurred.

The number of colonists within the 1800cm^2 area on each panel was calculated for a standard interval of 60 days. The mean and standard deviation of the colonization rate (no. colonist/ 1800cm^2/60 days) of each species, the "other bryozoan" category and each phyletic group was calculated for each sample interval and plotted against time.

5.3 Results

5.3.1 Long-Term Panels

In June 1977 the mean of total percentage cover reached maxima of 98% and 92% on the March and October groups of panels respectively (Fig. 5.2). This occured 15 months after submergence for the March group and nine months after submergence for the October group. After this peak the means of total percentage cover declined on both groups of panels (Fig. 5.2). At the same time the mean percentage cover of dead skeletal remains increased on both groups of panels (Fig. 5.2).

Galeolaria spp. were the first species to be detected on the panels in both groups (Fig. 5.3 and Fig. 5.4A) but at three months after submergence they occupied only a small proportion of the space resource in both groups (Fig. 5.4A). In the March group *Galeolaria* spp. reached a maximum mean percentage cover of 21% after nine moths but this decreased to 1.3% after 24 months (Fig. 5.3 and Fig. 5.4A to H). In the October group *Galeolaria* spp. only reached a maximum mean percentage cover of 2.7% after six months. For the remaining 12 months of observations made on this group the mean percentage cover of *Galeolaria* spp. remained below 1% (Fig. 5.3 and Fig. 5.4A to H). *Galeolaria* spp. were significantly more abundant on the panels of the March group than the panels of the October group after nine, 15 and 18 months of submergence respectively (Table 5.4) but were equally abundant on both groups of panels three and 12 months after submergence (Table 5.4). Another species of serpulid, *Filograma implexa*, was observed on the panels of the March group 18 months after

submergence and on the panels of the October group six months after submergence but its mean percentage cover was less than 1% in both cases (Appendix IVa).

Tunicates and bryozoans were recorded in both groups of panels six months after submergence (Fig. 5.3). In both groups the mean percentage cover of tunicates increased rapidly to reach a maximum of more than 60% by June 1977, 15 months after submergence for the March group and nine months after submergence for the October group (Fig. 5.3). After this date the mean percentage cover for tunicates declined in both groups to less than 10% by April 1978 (Fig. 5.3). In both groups of panels the mean percentage cover of bryozoans increased more slowly than that of tunicates but it did not show the same rapid decline after reaching a maximum (Fig. 5.3). In the March group bryozoans reached a maximum mean percentage cover of 36% in January 1978, 21 months after submergence and in the October group they reached a maximum mean percentage cover of 28% in June 1977 nine months after submergence (Fig. 5.3). In April 1978 the mean percentage cover of bryozoans was 34% and 19.6% in the March and October groups respectively.

Sponges were not observed on any of the panels of the March group until April 1978, 24 months after submergence (Fig. 5.3). In contrast sponges were recorded on some of the panels of the October group six months after submergence (Fig. 5.3) but they did not attain a mean percentage cover of greater than 1% until April 1978, 18 months after submergence (Fig. 5.3).

"Coralline red algae" was recorded in both groups of panels

in January and April 1978, 21 and 24 months after submergence for the March group and 15 and 18 months after submergence for the October group (Fig. 5.3). This category did not attain a mean percentage cover of greater than 16% on either sample date in either group of panels.

The stony coral *Culicia* sp. was recorded on some of the panels in each group only on the last sample date, April 1978 (Fig. 5.3). On this date the mean percentage cover for *Culicia* sp. was 1.62% in the March group and 0.28% in the October group.

A total of 14 tunicate species were recorded on the long-term panels (Table 5.3). However only four of these, *Atapazoa fantasiana*, *Didemnum* sp.a, *Botrylloides* sp. and *Pycnoclavella diminuta* attained a mean percentage cover of greater than 1% on at least one sample date in each group (Appendix IVa). From nine to 18 months after submergence in the March group and from six to 15 months after submergence in the October group, *Pycnoclavella diminuta* was the most abundant species (Fig. 5.4B, C, D, E, F). It achieved a maximum mean percentage cover of 60% in the March group in June 1977, 15 months after submergence and a maximum mean percentage cover of 54% in the October goup in September 1977, 12 months after submergence. Although this species never completely monopolized all the space on every panel it invaded all panels in both groups and achieved a maximum percentage cover of more than 50% on seven of the eight panels in the March group and five of the eight panels

in the October group. It occupied space on the panels of both groups for approximately one year (Fig. 5.4B, C, D, E, F) during which I observed it growing over many of the bryozoan colonies and *Galeolaria* spp. individuals which had previously settled on the panels. At the end of the one year period the colonies of this species began to slough-off revealing previously covered bryozoans and *Galeolaria* spp. which appeared to be dead when examined in the field. This explains the correlation between the decline in total percentage cover and the increase in the dead skeletal remains in both groups of panels (Fig. 5.2). *Pycnoclavella diminuta* was significantly more abundant in the October group than the March group six months after submergence but nine, 12, 15 and 18 months after submergence it was equally abundant in both groups (Table 5.4).

Atapazoa fantasiana and *Botrylloides* sp. did not attain a mean percentage cover of greater than 5% on any sample date in either group of panels also they were equally abundant in both groups of panels for all sample dates during the first 18 months of submergence (Table 5.4). *Didemnum* sp.a achieved a mean percentage cover greater than 5% on two occasions in the October group, nine and 18 months after submergence (Fig. 5.4B, F). It was more abundant in the October group than the March group six, nine and 18 months after submergence and equally abundant in both groups 12 and 15 months after submergence (Table 5.4).

All the bryozoan species from B1 to B7 and the "other bryozoans" category were recorded on the panels of both groups and attained a mean percentage cover of at least 1% on at least one sample date

in both groups. With the exception of the other bryozoan category *Smittina raigii* and *Biflustra perfragillis* were the only two bryozoan species to attain a mean percentage cover of greater than 5% in either group of panels. (Fig. 5.4B, C, D, E, F, G, H) Considering only the period of submergence common to both groups (i.e. the first 18 months) *Smittina raigii* attained a maximum mean percentage cover of 6.33% in the March group 12 months after submergence and one of 13.09% in the October group nine months after submergence. *Biflustra perfragillis* attained a maximum mean percentage cover of 2.3% and 9.96% in the March group and October group respectively 18 months after submergence. This species increased its abundance in the following three months in the March group to achieve a maximum mean percentage cover of 33.26%. Neither of these two bryozoan species attained a percentage cover of greater than 50% on any long term panel at any time and in most cases it was considerably less. The "other bryozoans" category attained a mean percentage cover of greater than 5% only on two occasions. In the October group its mean percentage cover was 5.64% and 5.51% after nine months and 12 months of submergence respectively. Finally there was no consistently significant difference between the abundances of any bryozoan species on the two groups of panels (Table 5.4 and also see Fig. 5.4B, C, D, E, F) during the first 18 months of submergence.

The preceding evidence indicates that no one species consistently monopolized or was consistently more abundant on the panels of one group and not the other. Furthermore the development of

the sessile guild on the panels of both groups followed the same general pattern. *Galeolaria* spp. were the first species to utilize the space provided by the panels in both groups followed by encrusting bryozoan and tunicates which rapidly became more abundant. In both groups the same species of tunicate was the most abundant species for approximately one year during the first 18 months of submergence. When it sloughed off during the summer months of late 1977 and early 1978 "coralline red algae" and *Culicia* sp. colonized panels in both groups. It is worth noting that the invasion of coralline red algae and *Culicia* sp. occured after a longer period of submergence in the March group than the October group. Although the same general pattern of sessile guild development occured on both groups of panels it occured in a shorter time period in the October group (Fig. 5.2 and Fig. 5.3).

5.3.2 Short Term Panels

Serpulids, bryozoans and tunicates showed a seasonal trend in larval availability with peaks occurring in the warm months of the year from September to April (Fig. 5.5A). Serpulids colonized the short term panels most heavily during these months with mean colonization rates often well over 400 colonists/ 1800cm^2 /60 days (Fig. 5.5A). Tunicates achieved maximum mean colonization rates of between 100 and 250 colonists/1800cm^2/ 60 days during these months (Fig. 5.5A). Bryozoans did not achieve mean colonization rates of greater than 80 colonists/ 1800cm^2/60 days during these months. The mean colonization rates of all three phyletic groups dropped to below 30 colonists

/1800cm^2/60days at least once during the winter months of 1976 and 1977.

Graphs for the colonization rates of the three individual serpulid species *Galeolaria hystrix*, *Galeolaria caespitosa* and *Filograma implexa* indicate that each species had peaks of larval availability during the warmer months of the year but not necessarily of the same magnitude and in exactly the same two months each year (Fig. 5.6A). *Galeolaria hystrix* attained maximum mean colonization rates of 269.6 and 490 colonists/1800cm^2/60 days during November 1976 and December 1977 respectively. *Galeolaria caespitosa* attained maximum mean colonization rates of 149 and 145 colonists/1800cm^2/60 days November 1976 and December 1977 respectively. *Filograma implexa* attained maximum mean colonization rates of 538 and 172 during April 1977 and December 1977 respectively. The mean colonization rates of all three species dropped to less than 2 colonists/1800cm^2/60 days between peaks (Fig. 5.6A).

Only four of the colonial tunicates which were recorded on the longterm panels colonized the short term panels. These were *Botrylloides leachii*, *Botrylloides* sp., *Didemnum* sp.a and *Pycnoclavella diminuta*. *Botrylloides leachii* and *Botrylloides* sp. colonized the short term panels extermely rarely (Fig. 5.5B) with mean colonization rates always less than 2 colonists/1800cm^2/60 days. *Pycnoclavella diminuta* colonized a short term panel once only. One patch of this species covering 5.78% of a panel from face 4 was recorded in the December 1977-February 1977 time interval. In contrast *Didemnum* sp.a colonized short

term panels very heavily and showed increases in larval abundance during the warmer months of the year (Fig. 5.5C). It attained a maximum mean colonization rate of 240 colonists/ 1800cm^2/60 days during January 1977 and a minimum of 0 colonists/ 1800cm^2/60 days during April-May-June of 1976 and May-June-July of 1977 (Fig. 5.5C).

With the exception of *Celleporaria pigmentaria* and the Mustard encrusting bryozoan (B7) all bryozoan species recorded on the long term panels colonized short term panels. *Smittina raigii* and *Biflustra perfragillis* had peaks of larval availability in the warmer months of the year (Fig. 5.6B, C). *Smittina raigii* had maximum mean colonization rates of 52 and 22 colonists/1800cm^2/ 60 days during March 1977 and December 1977 and *Biflustra perfragillis* had maximum mean colonization rates of 11 and 14 colonists/1800cm /60 days during December 1976 and September 1977. Both species had low mean colonization rates of 2.5 colonists/ 1800cm^2/60 days during the winter months of 1976 and 1977 (Fig. 5.6C). *Celleporaria fusca* and *Celleporaria valligera* were recorded on short term panels in late 1977 and early 1978 only. (Fig. 5.6C, D) and their mean colonization rate during this period was extremely low; less than one colonist/1800cm^2/60 days. *Cryptosula pallasiana* colonized short term panels on most sample intervals but the mean colonization rate of this species was always less than 1.3 colonists/1800cm^2/60 days. There was no good evidence of a seasonal trend. The "other bryozoans" colonized panels on all sample intervals with the mean coloniza-

nization rate ranging between 30 and nine colonists/1800cm^2/ 60 days (Fig. 5.6D). There was no obvious seasonal trend in the colonization rate of this group, probably as a result of grouping together a large number of species which had different seasonal trends in larval abundance.

The standard deviations of the colonization rates of all the species discussed were usually quite large (greater than 50% of the mean value) indicating that there was considerable variability in the number of colonizers between panels.

Culicia sp. and the "coralline red algae" did not colonize any of the short term panels.

A number of other organisms were seen on these panels. These included seven species of cyclostomate bryozoans, nine species of cheilostomate bryozoans, small and delicate creeping hydroids, tiny spirorbids, an occasional small bivalve or barnacle and small tufts of algae. Anyone or all of these species may have colonized the long-term panels but I never detected their presence in the transparencies. This indicates that they occupied only a very small fraction of the space resource on these panels if any at all and their omission in this analysis of sessile guild development was considered unimportant.

5.4 Discussion

The high abundance of *Pycnoclavella diminuta* in both groups of long term panels was remarkable in view of the fact that it colonized only one short term panel on one occasion. This indicates that the larvae of this species recruited on to the long term panels in preference to the short term panels. The mech-

anisms underlying this selection cannot be determined from the observations I have made but the period of substrate submersion appears to be a critical factor. If this were not so then this species would have recruited onto the long term panels of both groups at approximately the same date. Instead *Pycnoclavella diminuta* was first recorded in the March group three months before it was recorded in the October group (six and nine months after submergence respectively). One possible explanation is that some compound in the bituminous tar paint inhibited settlement of this species and it leached out of the panels after approximately six months. Another is that the presence of serpulids and/or bryozoans on the long term panels facilitated the recruitment of this species. The larvae of *Pycnoclavella diminuta* may not be able to recruit successfully onto a smooth surface such as that offered by a newly submerged panel. The rough surface of the calcareous tubes produced by adult *Galeolaria* spp. may have provided a more suitable substratum.

The results also indicate that the period of substrate immersion was a critical factor in the recruitment of *Culicia* sp. and the "coralline red algae." Neither was recorded on any short term panels and both colonized the long term panels in the March and October groups after the senescence of *Pycnoclavella diminuta*. Again the mechanisms responsible for this cannot be determined from the observations I have made. Additionally it is possible that the appearance of the stony coral *Culicia* sp. was causally connected with the appearance of the "coralline red algae." Coral-

line red algae can provide suitable substrata for colonization by corals (Birkeland 1977).

Further experimental investigations are needed to determine whether the invasion of *Pycnoclavella diminuta*, *Culicia* sp., and the "coralline red algae" onto bituminous tar covered surfaces at Rapid Bay is facilitated by previous occupants or not. Despite this the development of the sessile guild on the long term panels was clearly directional in both groups (Fig. 5.3). Up until the time when *Pycnoclavella diminuta* sloughed off it resembled those patterns of development in the fouling communities studied by Anger (1978) and Osman (1977). In both these investigations solitary species which initially colonized the substratum in high numbers were later overgrown and surpassed in abundance by colonial species. At Rapid Bay *Galeolaria* spp. which were the first species recorded on the long term panels (Fig. 5.4A) were surpassed in abundance by both bryozoan and tunicate species during the course of the development of the sessile guild in both groups of these panels (Fig. 5.4B, C, D, E, F, G, H). Additionally I observed a large number of *Galeolaria* spp. being overgrown by the vegetative extension of both tunicate and bryozoan colonies but never the reverse during the course of the experiment.

All the species which were recorded on the long term panels had peaks of larval abundance in the summer months or showed no particular seasonal trend (Fig. 5.5A, B, C; Fig. 5.6A, B, C, D). This suggests that the time of initial substrate availability would not be a key factor in the pattern of development of the sessile guild at Rapid Bay. The similarity of the development of the

sessile guild on both groups of long term panels supports this proposition. Furthermore comparison of the identity of recruits between short term and long term panels suggests that *Culicia* sp. did not become the dominant species in the sessile guild at Rapid Bay as a result of a heavy period of recruitment after the pilings were first driven. As was argued earlier in this discussion the length of substrate immersion appears to be a critical factor in the recruitment of *Culicia* sp.

Additionally casual observations suggest that *Culicia* sp. typically has very low levels of recruitment. During the four years that I have been diving at Rapid Bay I have never seen any evidence of a heavy spatfall of *Culicia* sp. onto any piece of substratum under or near the pier despite the high abundance of this species in the sessile guild. Further observations are required to rule out the possibility that *Culicia* sp. has occassional periods of heavy recruitment that are often spaced more than four years apart.

I have made casual observations of the long term panels in both groups since April 1978 and *Culicia* sp. has only slowly increased its abundance. On the last visit in August 1979 *Culicia* sp. did not occupy more than 40% of the space on any panel. Obviously the newly settled colonies of *Culicia* sp. were unable to extend rapidly over the long term panels.

In summary, the evidence presented in this chapter and in Chapter 3 suggests that *Culicia* sp. has attained high abundance in the sessile guild at Rapid Bay by a process of slow accumulation permitted by long life, resistance to overgrowth and resis-

tance to larval invasion. This is similar to the conclusions arrived at by Karlson (1978) to explain the high abundance of the colonial hydroid *Hydractinia echinata* on pier pilings at Beaufort, North Carolina.

The results presented in this Chapter also demonstrate that larval recruitment plays an important role in the competitive repertoire of *Galeolaria* spp. and bryozoans at Rapid Bay. Despite their extremely low abundance in the sessile guild on the pilings (Appendix Ib and Fig. 2.8 Section 2.4.3.3) inspection of the transparencies of the long term panels indicated that over a hundred larvae from both groups had recruited onto each of the long term panels during the first three months of submergence. Additionally *Galeolaria* spp. and bryozoans attained high colonization rates on the short term panels (Figs. 5.5A, 5.6A). These observations, the results of the experiments reported in Chapter 4 and the assessment of competitive ability reported in Chapter 3 suggest that these groups have an "opportunistic" competitive strategy. Opportunistic species have "high dispersibility, reduced long term competitive ability and a propensity to occupy ephemeral or highly disturbed habitats" (Vermeij 1979). Both bryozoans and *Galeolaria* spp. were poor interference competitors and were unable to exploit free space by vegetative growth as well as most other species in both sessile guilds (Chapter 3). However the vagile larvae of both groups rapidly invaded unoccupied substratum in both sessile guilds. Moreover *Galeolaria* spp. and bryozoans were more abundant on substrata that had been recently cleared (i.e. a newly

formed patch as in Chapter 4 or a newly submerged panel as in this Chapter) than on substrata which had not been cleared for many years (e.g. the pilings of Edithburgh and Rapid Bay piers see Chapter 2).

TABLE 5.3 Species recorded on the long term panels

Sponges
SP1 *Aplysilla rosea* Schulze
SP2 *Aplysilla sulphurea* Schulze
SP20 *Mycale* sp.
SP13 *Callyspongia* sp.
SP33 *Sycon* sp.
SP7 Large orange sponge
SP5 Red encrusting sponge
SP4 Green encrusting sponge
SP54 Mauve spiky sponge
SP57 Cream lumpy sponge

Colonial Tunicates
T13 *Botryllus schlosseri* (Pallas)
T11 *Botrylloides leachii* (Savigny)
T20 *Botrylloides* sp.
T12 *Didemnum patulum* (Herdman)
T9 *Didemnum* sp.a
T18 *Didemnum* sp.b
T5 *Podoclavella cylindrica* (Quoy & Gaimard)
T19 *Pycnoclavella diminuta* (Kott)
T25 *Atapazoa fantasiana* (Kott)
T37 *Polysyncraton orbiculum* Kott
T23 Chestnut encrusting tunicate
T39 Opaque orange encrusting tunicate

Solitary Tunicates
T7 *Phallusia depressiuscula* (Heller)
T28 *Cnemidocarpa etheridgii* (Herdman)

Bryozoans
B1 *Celleporaria fusca* (Busk)
B2 *Celleporaria valligera* Harmer
B3 *Celleporaria pigmentaria* (Waters)
B4 *Smittina raigii* (Audouin)
B5 *Cryptosula pallasiana* (Moll)
B6 *Biflustra perfragillis* McGillivray
B7 Mustard encrusting bryozoan
BO "Other bryozoans"

Cnidarians
J5 *Culicia* sp.

Serpulids
TW3/4 *Galeolaria* spp.
TW2 *Filograma implexa* Berkley

Algae
A14 *Zonaria augustata* Paperfuzz
A17 *Rodymenia australis* Harvey
CR "Coralline red algae"

TABLE 5.4 Summary of results of Mann-Whitney U-tests comparing species abundances between the two groups of long term panels. The value of the statistic "U" for each comparison is listed in the table in parenthesis. The sample sizes for all comparisons a a given sample date are given at the top of the table.

NS: no significant difference

O: abundance in October group significantly greater than abundance in March group

M: abundance in March group significantly greater than abundance in October group

A significance level of .05 and a one tailed test was used.

	Months after immersion of panels:	3	6	9	12	15	18
Species	Sample Sizes:	8,8	8,8	8,8	8,8	6,8	4,8
TW3/4	*Galeolaria* spp.	NS(29)	NS(27.0)	M(0)	NS(16.5)	M(0)	M(1.0)
T25	*Atapazoa fantasiana*		NS(28.0)	NS(28.0)	NS(25.5)	NS(21.0)	NS(15.0)
T9	*Didemnum* sp.a		O(12.0)	O(4.0)	NS(25.0)	NS(18.0)	O(3.5)
T20	*Botrylloides* sp.			NS(31.5)			
T19	*Pycnoclavella diminuta*		O(4.0)	NS(24.0)	NS(31.0)	NS(17.0)	NS(9.0)
B1	*Celleporaria fusca*		NS(22.5)	NS(29.0)	NS(28.0)	NS(22.0)	NS(12.5)
B2	*Celleporaria valligera*		O(12.0)	NS(28.0)	NS(28.0)	NS(12.0)	O(2.5)
B3	*Celleporaria pigmentaria*		NS(28.0)	NS(24.0)	NS(24.0)	NS(20.0)	NS(12.0)
B4	*Smittina raigii*		O(11.0)	NS(29.0)	NS(30.0)	NS(22.5)	NS(11.0)
B5	*Cryptosula pallasiana*		NS(31.5)	NS(20.0)	NS(27.0)	NS(12.0)	NS(14.5)
B6	*Biflustra perfragillis*		O(8.0)	NS(26.0)	M(7.0)	M(6.0)	NS(7.0)
B7	Mustard encrusting bryozoan		NS(32.0)	NS(28.0)	NS(20.0)	NS(11.5)	O(0)
BO	"other bryozoan"		NS(24.0)	NS(26.0)	NS(20.0)	NS(21.0)	NS(8.0)
J5	*Culicia* sp.						NS(12.0)
CR	Coralline red algae					NS(14.0)	O(2.5)

FIGURE 5.1 The design and dimensions of the panels in the long term groups and short term series

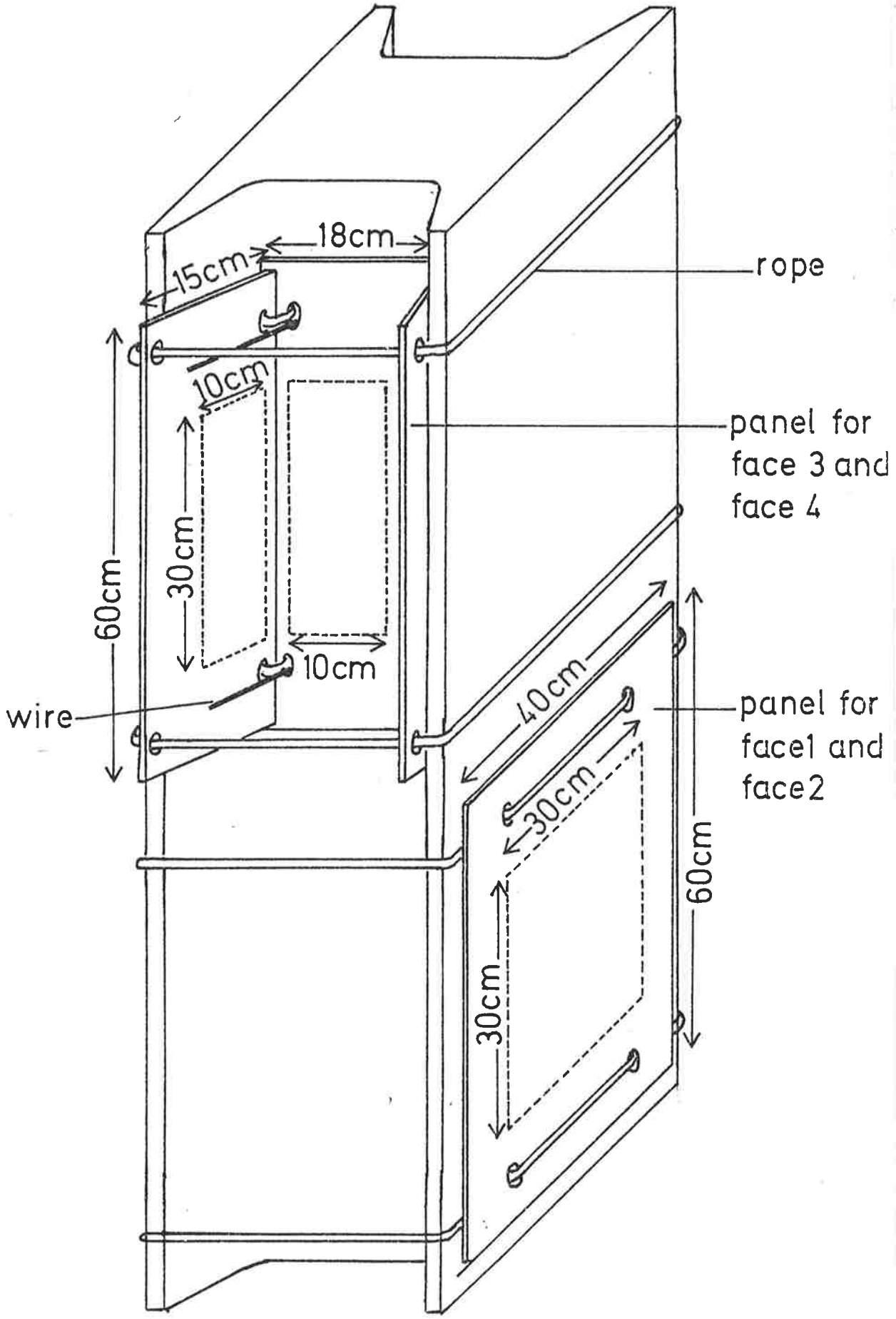

18cm
15cm
rope
10cm
panel for
face 3 and
face 4
60cm
30cm
10cm
wire
40cm
panel for
face1 and
face2
30cm
60cm
30cm

FIGURE 5.2 Change in percentage cover after the two groups of long term panels were submerged. Graphs show mean (spot) and standard deviation (line) of total live cover (O) and total dead cover (●) at three monthly intervals.

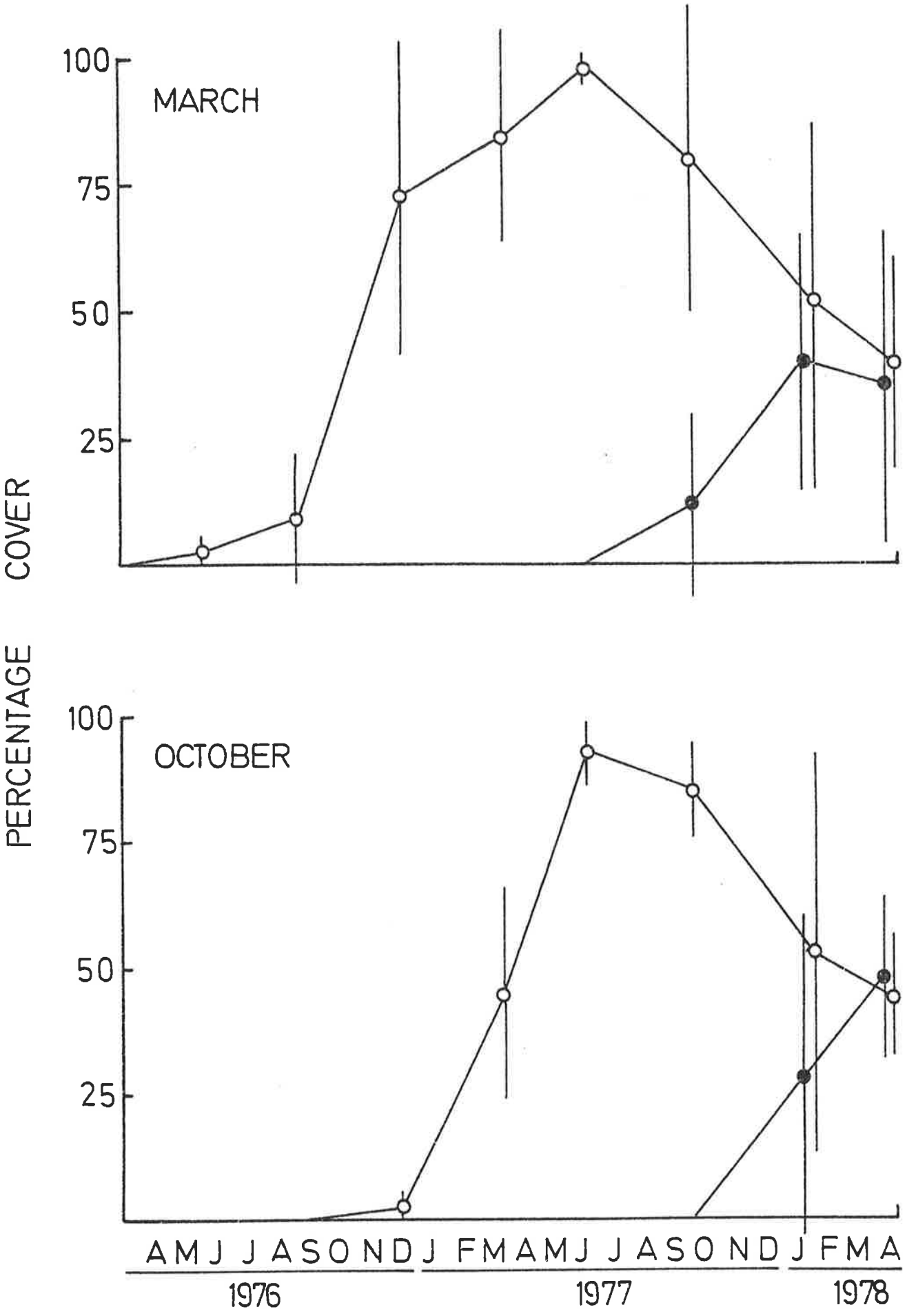

PERCENTAGE COVER
100
75
50
25
MARCH
100
75
50
25
OCTOBER
A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 5.3 Bar diagrams showing the mean (bar) and standard deviation (line) of percentage cover for the following six phyletic groups on both groups of long term panels at three monthly intervals after submergence.

serpulids: horizontal stripes
bryozoans: spots
tunicates: open bars
sponges: solid bars
cnidarians: diagonal stripes
coralline red algae: vertical waves

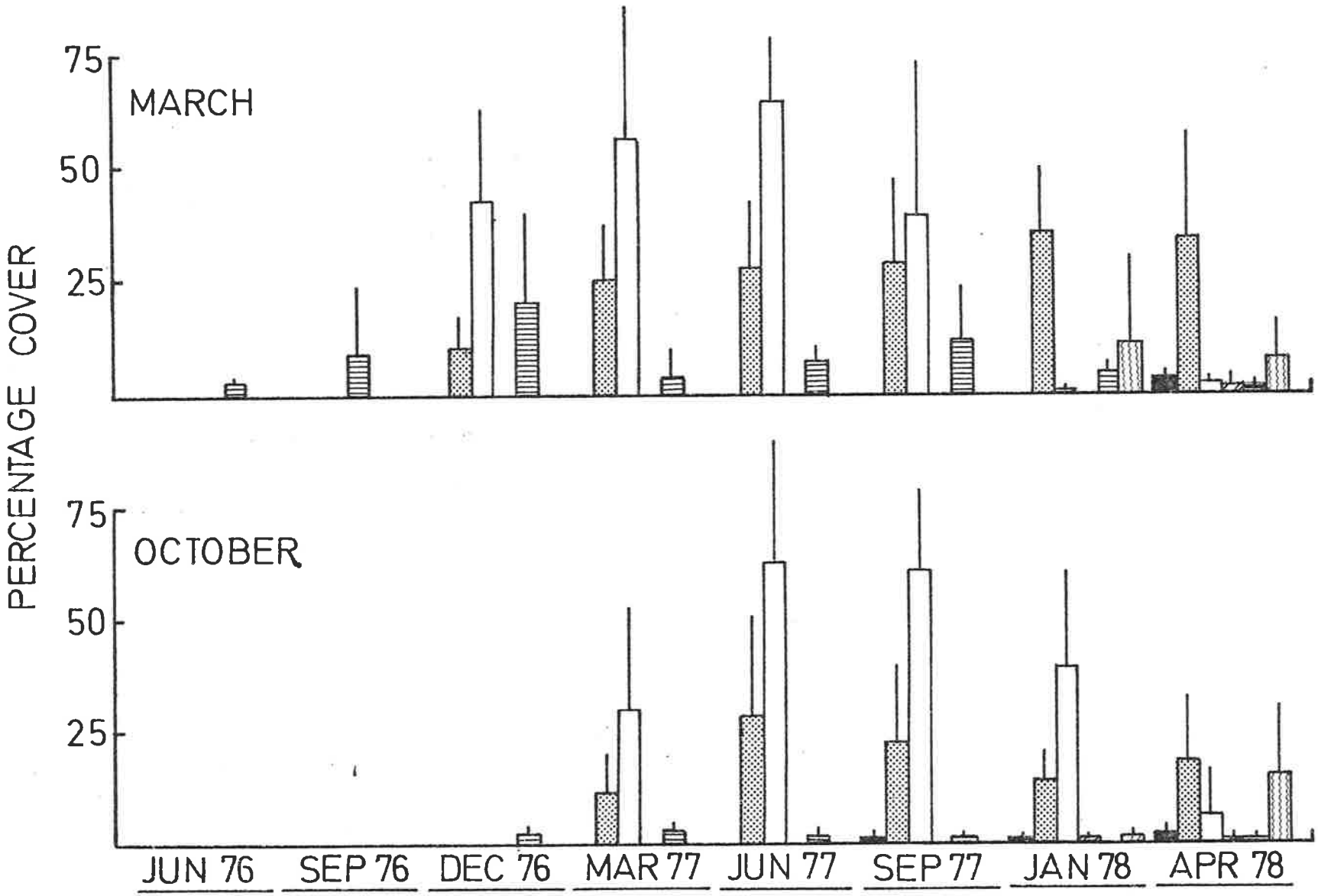
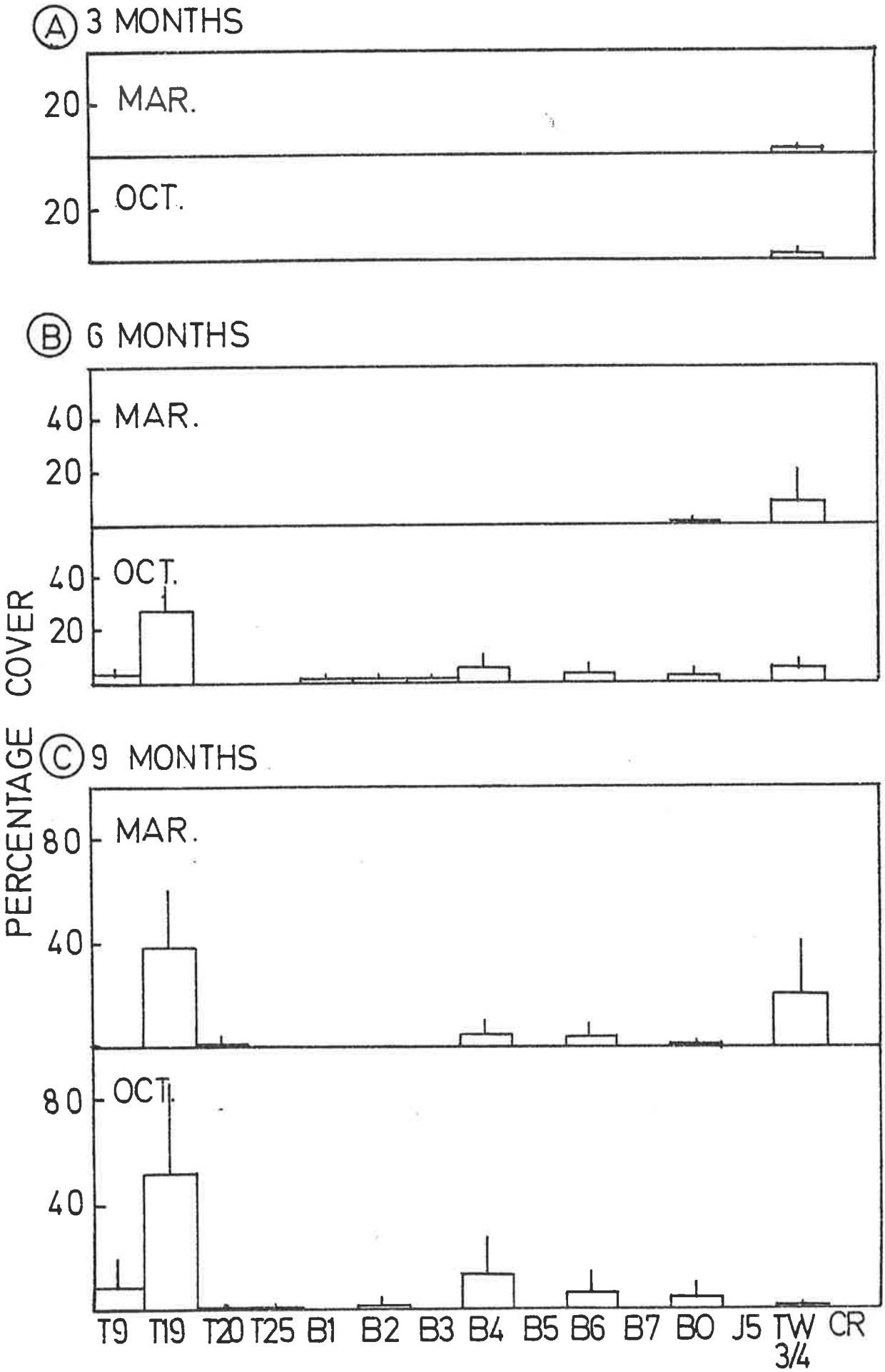
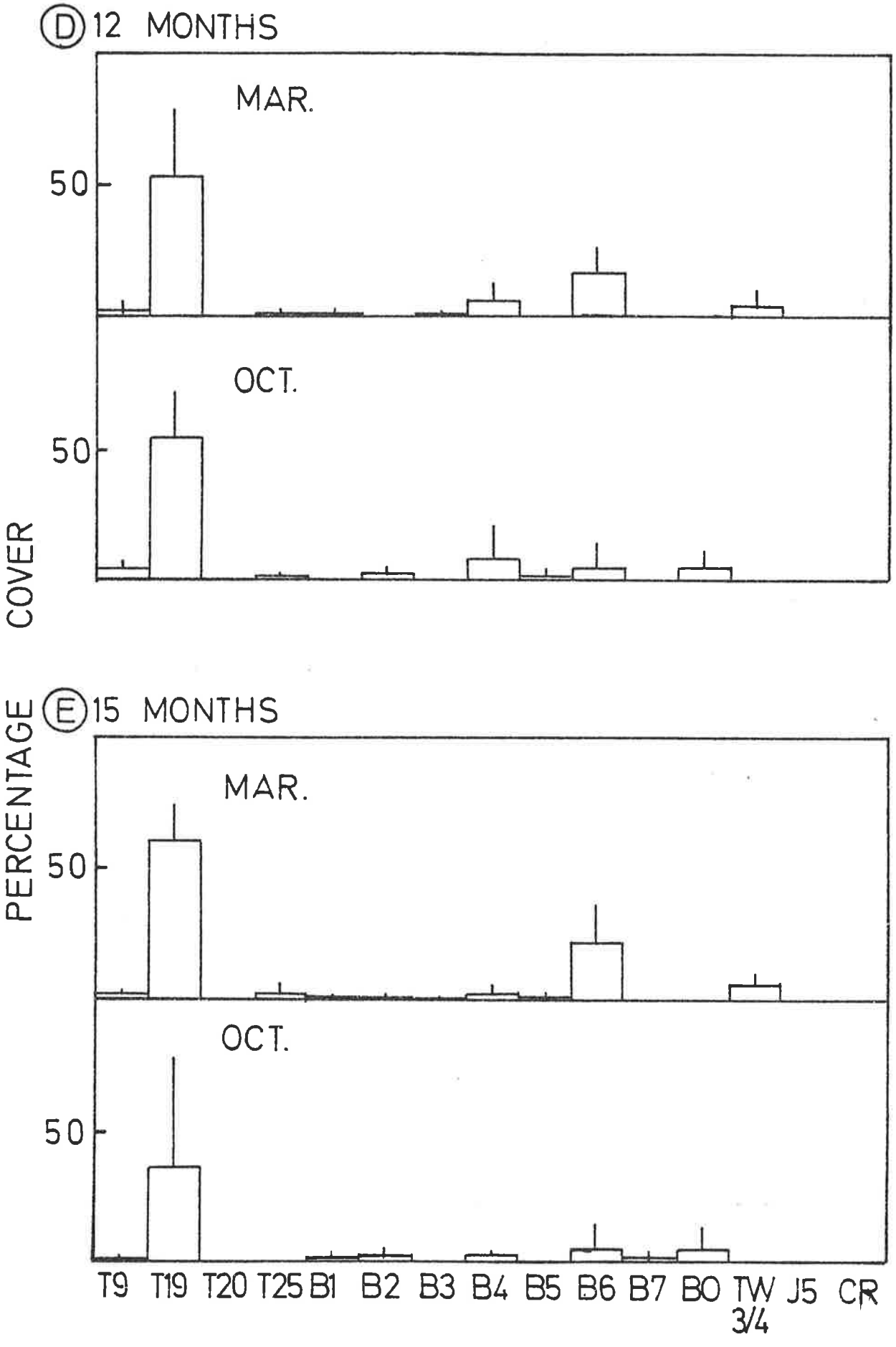

PERCENTAGE COVER
75
50
25
MARCH
75
50
25
OCTOBER
JUN 76
SEP 76
DEC 76
MAR 77
JUN 77
SEP 77
JAN 78
APR 78

FIGURE 5.4 Bar diagrams showing the mean (bar) and standard deviation (line) of percentage cover for individual species on both groups of long term panels at three monthly intervals after submergence. The species corresponding to the code numbers on the X axis are listed in Table 5.3

A 3 months
B 6 months
C 9 months
D 12 months
E 15 months
F 18 months
G 21 months
H 24 months


A 3 MONTHS
20
MAR.
20
OCT.
B 6 MONTHS
40
MAR.
20
40
OCT.
20
PERCENTAGE COVER
C 9 MONTHS
80
MAR.
40
80
OCT.
40
T9 T19 T20 T25 B1 B2 B3 B4 B5 B6 B7 BO J5 TW 3/4 CR


Ⓓ 12 MONTHS
MAR.
50
OCT.
50
COVER
Ⓔ 15 MONTHS
PERCENTAGE
MAR.
50
OCT.
50
T9 T19 T20 T25 B1 B2 B3 B4 B5 B6 B7 BO TW 3/4 J5 CR

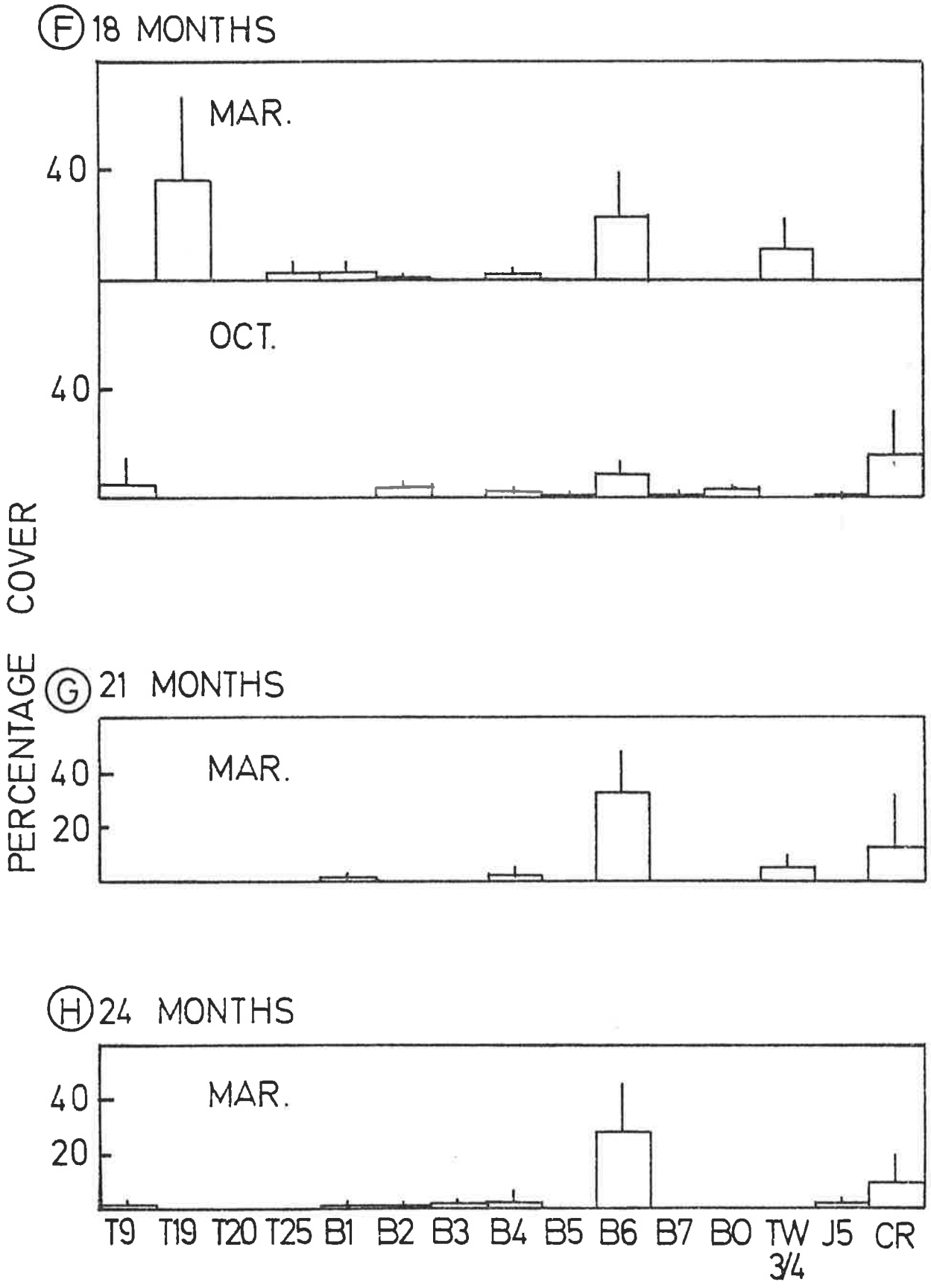

Ⓕ 18 MONTHS
MAR.
40
OCT.
40
PERCENTAGE COVER
Ⓖ 21 MONTHS
MAR.
40
20
Ⓗ 24 MONTHS
MAR.
40
20
T9 T19 T20 T25 B1 B2 B3 B4 B5 B6 B7 B0 TW 3/4 J5 CR

FIGURE 5.5 A Bar diagram showing the mean (bar) and standard deviation (line) of the colonization rates (no. colonists/1800cm^2/60 days) of

serpulids: horizontal stripes

tunicates: open bar

bryozoans: spots

on the short term panels for each two monthly period of submergence

FIGURE 5.5 B Graph showing the mean (spot) and standard deviation (line) of the colonization rate (no. colonists/1800 cm^2/60 days) of *Botrylloides leachii* (●) and *Botrylloides* sp. (O) on the short term panels for each two monthly period of submergence

FIGURE 5.5 C Graph showing the mean (spot) and standard deviation (line) of the colonization rate (no. colonists/1800cm^2/60 days) of *Didemnum* sp.a on the short term panels for each two monthly period of submergence.

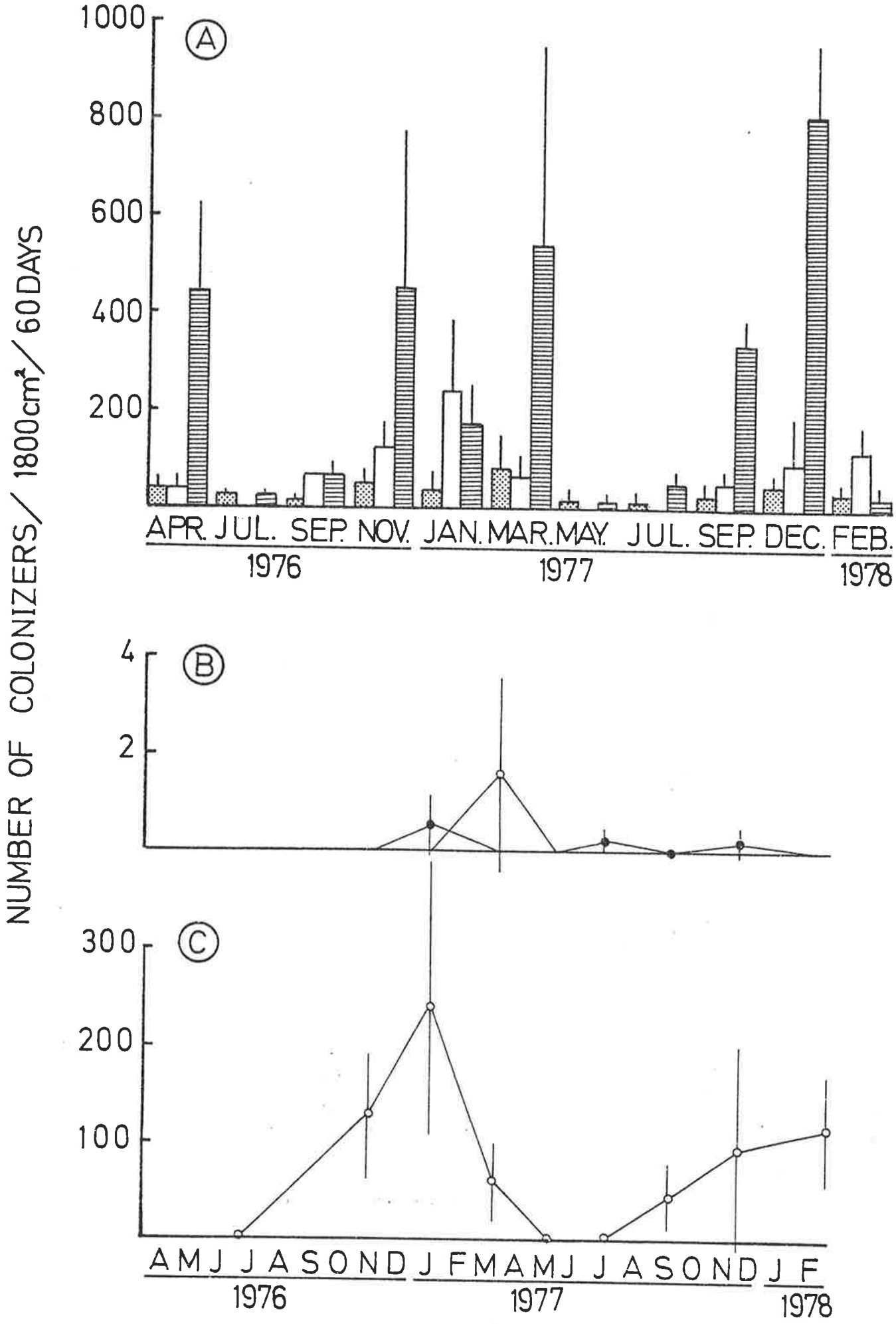
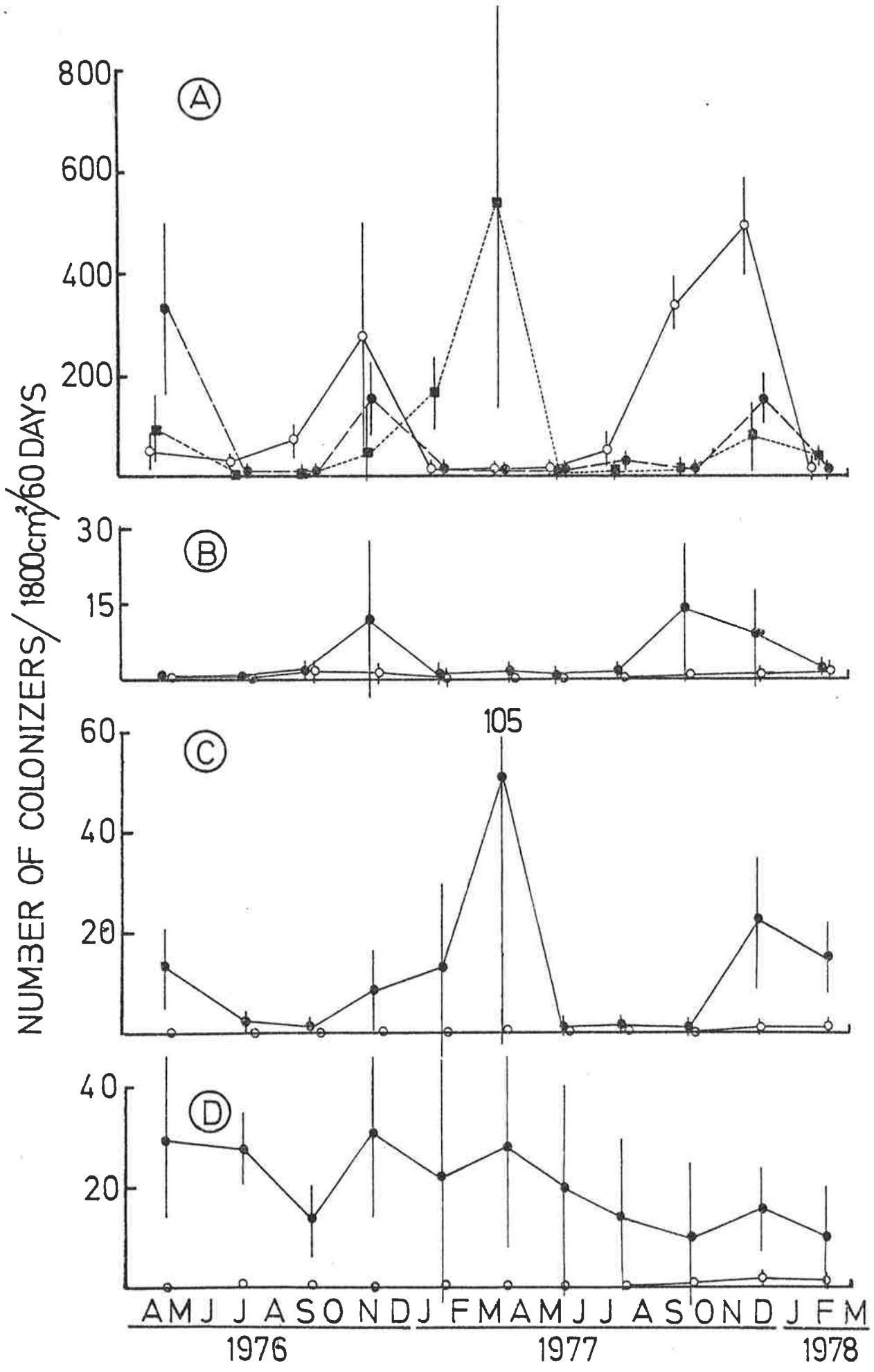

NUMBER OF COLONIZERS/ 1800cm²/ 60 DAYS
A
1000
800
600
400
200
APR. JUL. SEP. NOV. JAN. MAR. MAY. JUL. SEP. DEC. FEB.
1976
1977
1978
B
4
2
C
300
200
100
A M J J A S O N D J F M A M J J A S O N D J F
1976
1977
1978

FIGURE 5.6 Graphs show the mean and standard deviation of the colonization rate (no. colonists/1800 cm^2/ 60 days) of the following individual species on the short term panels for each two monthly period of submergence

A. *Filograma implexa* (■)
Galeolaria caespitosa (●)
Galeolaria histrix (0)
B. *Smittina raigii* (●)
Cryptosula pallasiana (0)
C. *Biflustra perfragillis* (●)
Celleporaria fusca (0)
D. "Other Bryozoans" (●)
Celleporaria valligera (0)


NUMBER OF COLONIZERS/1800cm²/60 DAYS
800
600
400
200
A
30
15
B
105
60
40
20
C
40
20
D
A M J J A S O N D J F M A M J J A S O N D J F M
1976
1977
1978

6.0 FUNCTIONAL ROLES OF PREDATION AND *CULICIA* SP. IN THE SESSILE GUILD AT RAPID BAY AND OF PREDATION IN THE SESSILE GUILD AT EDITHBURGH

6.1 Introduction

As was pointed out in Section 1.1 of the introductory chapter predation may have a considerable effect on community structure but this effect will vary in degree and nature in different situations. Numerous experimental investigations have demonstrated that predation increases diversity in communities where a dominant competitor is preyed upon in preference to other species sharing a limited resource (see Section 1.1). Examples of generalized non-selective predation increasing community diversith (e.g. Dayton and Hessler 1972) are rare. However it is commonly recognized that non-selective predation can stabilize competition between two species if the inferior competitor has a higher reproductive rate (Addicott 1974). Non-selective predation has also been shown to reduce community diversity (Day 1977). Additionally in situations where predation is selective but not on the dominant competition it has been shown to decrease diversity (Glynn 1976, Lubchenco 1978).

When I first commenced my investigation of the sessile guilds at Rapid Bay and Edithburgh in late 1975 one of my primary concerns was to identify from amongst a very large number of possibilities those factors and processes which played a significant role in the structure of these guilds. Since predation had been shown to be an important structuring agent in a variety of sessile communities in the marine environment at that time (Paine 1966, 1969, 1971, 1974 Dayton 1971, 1975 in the intertidal;

Sutherland 1974, Porter 1972, 1974 and Dayton et al. 1979 in the subtidal) it seemed probable that predation would also play a role in these two guilds.

I had also been impressed during the first months of diving at Rapid Bay by the high abundance of the stony coral *Culicia* sp. on the pilings (see Photographs 6.1 and 6.2). Subjective impressions then suggested that this species resisted larval invasion and overgrowth by potential competitors keeping their abundance extremely low.

This chapter reports on two field experiments. The experiment at Rapid Bay was designed to evaluate the functional roles of predators and an extremely abundant sessile organism in sessile guild structure. The experiment at Edithburgh was designed to evaluate the functional role of predators in sessile guild structure.

6.2 Methods

6.2.1 Predator Exclusion and *Culicia* sp. Removal Experiment at Rapid Bay

6.2.1.1 Experimental Design and Field Methods

Forty-eight rectangular quadrats, 20cm x 30cm, were randomly allocated to pilings within the study area on the East arm of the tee-head in the manner described in Section 2.4.2.1. They were divided into two groups of 24 quadrats each. All colonies of *Culicia* sp. were cleared from the quadrats of one group at the beginning of the experiment using a hammer and chisel. It was extremely difficult to remove completely all of the skeletal portions of these colonies from the original piling surface.

However in all cases all the live portions of the colonies and at least .5cm of the underlaying skeletal structure were removed. Any regrowth of *Culicia* sp. back into these quadrats was removed after the quadrats had been photographed on subsequent sampling dates. Each of these two groups were divided into three groups of eight quadrats each representing the following three treatments.

1) exclusion quadrats; predators were excluded from the quadrat by enclosing it in a plastic mesh cage.

2) control quadrats; quadrats were partially enclosed in plastic mesh but predators still had access to the quadrat

3) uncaged quadrats; no further manipulation of the quadrat.

If it can be assumed that the experimental side effects due to the presence of the plastic mesh were the same for the exclusion and control quadrats then differences in the composition of the quadrats between these three treatments arising during the course of the experiment could be attributed either to the absence of predation (comparison of exclusion and control quadrats) or the presence of the mesh (comparison of control quadrats and uncaged quadrats). This assumption is partially tested by the water flow experiment detailed in Section 6.2.1.3 and is considered further in the discussion, Section 6.4.

In each group of eight, two quadrats were allocated to face 1, face 2, face 3 and face 4 of the pilings respectively. The design of this experiment is summarized in Table 6.1. There is a total of six separate treatments with eight replicates for each treatment.

TABLE 6.1 Design and sampling schedule of the predator exclusion and *Culicia* sp. removal experiment at Rapid Bay

	Uncaged quadrats	Control quadrats	Exclusion quadrats
Culicia sp. removed	8 replicates	8 replicates	8 replicates
Culicia sp. not removed	8 replicates	8 replicates	8 replicates

Sample dates: 29/03/76, 28/07/76, 13/11/76, 10/03/77, 29/09/77, 13/04/78

The exclusion and control cages were constructed of ¼ x ¼ inch black plastic mesh (plastic diameter = 1/16 inch.) This material did not corrode and was therefore more suitable for a long term field experiment in the marine environment than galvanized wire which corroded after about 10-12 months. It was also relatively inexpensive and did not tear easily. The mesh size was sufficient to exclude all potential predators including the smaller species of nudibranchs which could penetrate the next larger sized mesh (½ x ½ inch).

The design of the cages is illustrated in Figure 6.1. The top and bottom ends of the control cages were left open to allow crawling and swimming predators free access to the quadrat. Casual observations during dives suggested that the fish, crabs, molluscs and echinoderms seen on and around the pilings were

were able to move in and out of these control cages without any trouble. Each cage had a rectangular metal frame which was hinged to metal straps that were bolted around the pilings (Fig. 6.1). A latch at the top of each cage connecting the metal frame with the upper metal strap held the cage closed over the quadrat (Fig. 6.1). A quadrat could be exposed for photographs by undoing the latch and swinging the cage back on its hinges like a door. The bottom side of each cage was approximately one metre above the ocean floor.

The cages were considerably larger than the actual quadrats and enclosed rectangular sections of piling approximately 40cm x 60cm in dimension on all faces (Fig. 6.1). Each quadrat was centrally located in this area and thus its centre was positioned approximately 1.3 metres above the ocean floor. Uncaged quadrats were positioned at the same height.

The experiment was begun in March 1976 and lasted for two years until April 1978. Quadrats were photographed (for details of method see Section 2. 2.) and cleared of *Culicia* sp. at approximately four monthly intervals for the first year and at approximately six monthly intervals for the second year. The exact sampling schedule may be found in Table 6.1.

On each sampling visit the mesh of the cages was cleaned inside and out with a knife and a stiff brush to prevent a build up of fouling organisms. Records were kept of predators which managed to find their way onto exclusion quadrats and any significant effects they were thought to have caused were noted. Casual observations were made on predator-prey interactions in the

undisturbed sessile guild and are reported in Section 6.3.2.5 of the results.

6.2.1.2 Calculations and Analysis

The mean and standard deviation of species number and of percentage cover for each species was calculated on each sample date for all six experimental treatments. The percentage cover data for the last two sample dates common to all six experimental treatments is listed in Appendix Va.

The mean and standard deviation of percentage cover was plotted against time for

1) Species whose abundance differed significantly between experimental treatments
2) All solitary tunicate species
3) *Culicia* sp.
4) Unoccupied substratum
5) All species together excluding *Culicia* sp. (Total cover minus *Culicia* sp.)
6) Each of the following phyletic groups.
   a) sponges
   b) bryozoans
   c) colonial tunicates
   d) solitary tunicates

The mean and standard deviation of species number was also plotted against time.

Since this experiment had a 2x3 factorial design (Cochran and Cox 1957) it was particularly desirable that the data be

analysed using a two-way ANOV so that interaction between the two fixed factors (*Culicia* sp. removal and caging) could be identified. As a result of the extreme patchiness in the distribution of species in relation to quadrat size the percentage cover data displayed a most unusual distribution (note large standard deviations in Appendix Va). Attempts to normalize it using, for example, the arcsine transformation (see Zar 1974 pp 185-186) were not successful. Additionally the variances of these data were heteroscedastic more often than not, a situation which was not markedly improved in the trial transformations. Since two basic requirements of parametric ANOV, that is homoscedastricity and normality, were not met I had to resort to nonparametric methods.

A Kruskal-Wallis one-way ANOV (Siegel 1956) was used to test whether the percentage cover of a given species or species group was homogenous between caging treatments within either the *Culicia* sp. removed or *Culicia* sp. not removed groups. If that test showed heterogeneity a nonparametric multiple comparisons test (Zar 1974 pp. 156-157) was used to identify significant differences between pairs of the three caging treatments. Mann-Whitney U-tests were used to identify significant differences in the percentage cover between the *Culicia* sp. removed and *Culicia* sp. not removed treatments within each of the three caging treatments. This series of comparisons permitted identification of interactions between the two treatment factors, caging and *Culicia* sp. removal, as well as individual factor effects.

All preceding statistical analyses were carried out on the

last two sample dates only. The September 1977 sample date, 18 months after the commencement of the experiment, represented the case where the annual tunicates were likely to be in greatest abundance just before their summer senescence. On the next sample date, April 1978, the newly settled colonies of these tunicates would have had only a short time to grow and therefore would be in relatively low abundance at this time. Therefore any seasonal interaction with either treatment could be identified by this choice of sample dates.

Unlike the percentage cover data the species number data approached normality and variances did not deviate significantly from homoscedasticity. Parametric two-way ANOV (Zar 1974) was used to test for treatment interactions and effects on the last three sample dates.

6.2.1.3 Water Flow Measurements

Since the diameter of the plastic of the plastic mesh was a quarter the length of the open squares of the mesh it was highly likely that water flow would be decreased on caged quadrats compared to uncaged quadrats. Providing the control cages restricted water flow as much as the exclusion cages changes in species abundances due to this factor would be the same in both types of cages. To test this assumption and also to establish whether the plastic mesh in both fouled and unfouled conditions significantly restricted the flow of water over the quadrats the following experiment was set up.

A modified version of the plaster of Paris clod method (Muus

1967, Doty 1971) was used to measure water flow over a quadrat. Plaster of Paris blocks were made in plastic ice cube trays using 1,000g of plaster per litre of water. These blocks were allowed to dry in air for one month. They were individually weighed and then arranged end to end into rectangular "bags" constructed of ½ x ½ inch plastic mesh as illustrated in Figure 6.2. There were 24 bags containing five blocks each. The bags were divided into four groups of four bags and one group of eight bags. Each group of four bags was then allocated to one of the following four treatments

1) quadrats in fouled exclusion cages.
2) quadrats in unfouled exclusion cages.
3) quadrats in fouled control cages.
4) quadrats in unfouled control cages. Cages were designated as fouled if at least 25% of the mesh surface was covered by sessile organisms. Unfouled cages were completely free of sessile organisms. One bag in each group was allocated to face 1, face 2, face 3 and face 4 of the pilings respectively. The bags in the group of eight were allocated to uncaged quadrats. Two bags were allocated to each of face 1, face 2, face 3 and face 4 respectively.

The quadrats for this experiment were randomly chosen from those used in the predator exclusion and *Culicia* sp. removal experiment. Each bag was attached to the uppermost metal strap above the appropriate quadrat with a piece of wire (Fig. 6.1) so that it hung parallel to and just above the piling surface across the centre of the quadrat.

Each bag was submerged for a period of 24 hours from approximately midday on 3/1/79 to midday 4/1/79. After the bags were collected they were rinsed in fresh water and allowed to air dry for one month. The blocks were then removed and reweighed.

For plaster blocks of the same weight and size which have been submerged in water of the same temperature for the same length of time weight loss is directly proportional to overall water movement (Muus 1967, Doty 1971). There was some variability in the initial weight of the 24 groups of five blocks (mean = 94.57g, S.D. = 2.62g). In order to minimize bias in weight loss associated with differences in initial weight of a group I expressed weight loss as a percentage of initial weight.

The data from the four groups of four bags were analysed in terms of two fixed factors (cage design, fouling) using a parametric two-way ANOV. Student's t-test (Zar 1974) was used to compare percentage weight loss between quadrats in fouled cages and uncaged quadrats and between quadrats in unfouled cages and uncaged quadrats.

6.2.2 Predator Exclusion Experiment at Edithburgh

6.2.2.1 Experimental Design and Field Methods

Ten, 20cm x 30cm quadrats were randomly allocated to pilings within the study area using the method described in Section 2.4.2.1. They were divided into two groups of five quadrats each representing the following two treatments which were described in Section 6.2.1.1

1) exclusion quadrats
2) control quadrats.

Additionally five quadrats were randomly selected from the 16 permanent quadrats to represent the third treatment: uncaged quadrats.

The design of this experiment is summarized in Table 6.2. There is a total of three separate treatments and five replicates in each treatment.

TABLE 6.2 Design and sampling schedule of the predator exclusion experiment at Edithburgh

	Uncaged quadrats	Control quadrats	Exclusion quadrats
	5 replicates	5 replicates	5 replicates
Sample Dates:	14/03/76, 20/06/76, 26/09/76, 08/12/76, 18/03/77, 11/06/77, 24/09/77, 28/12/77, 14/03/78		

The experiment began in March 1976 and all quadrats were photographed (for details of method see Section 2. 2.) at approximately three monthly intervals until December 1977. The exclusion and control quadrats were photographed again after this in March 1978. The exact sampling schedule may be found in Table 6.2.

The exclusion and control cages were constructed of the same plastic mesh and were of the same basic design as those cages used in the Rapid Bay experiment (see Fig. 6.3). However they were smaller in size and enclosed rectangular areas of approximately 40cm x 30cm on the pilings. Quadrats were centrally located in this area. The vertical height of the centre of each

ranged between one and two metres and corresponded to the height of the diver on arrival at the piling when the cages were first installed. Cages were attached to the pilings using nails and were removed and reattached each time a photograph was taken.

On each visit cages were cleaned and casual observations were made on predators in precisely the same way as at Rapid Bay (see Section 6.2.1.1). Casual observations on predator prey interactions are reported in Section 6.3.3.2 of the results.

6.2.2.2 Calculations and Analysis

The mean and standard deviation of species number and of percentage cover for each species was calculated on each sample date for all three experimental treatments. The percentage cover data for the last two sample dates common to all three experimental treatments is listed in Appendix Vb.

The mean and standard deviation of percentage cover was plotted against time for

1) Species whose abundance differed significantly between experimental treatments
2) All solitary tunicate species
3) All species together (Total cover)
4) Each of the following phyletic groups
   a) sponges
   b) colonial tunicates
   c) solitary tunicates
   d) bryozoans.

The mean and standard deviation of species number was also plotted against time.

The percentage cover data could not be analysed using parametric ANOV for the reasons outlined in Section 6.2.1.2 and the non-parametic methods used to analyze the Rapid Bay data were employed here. These tests were carried out for the September 1977 and December 1977 sample dates. As was explained in Section 6.2.1.2 this choice of sample dates would allow identification of a possible treatment x season interaction associated with the seasonal fluctuations in abundance of the annual tunicates.

The data of species number were analysed using parametric one-way ANOV (Zar 1974) on the last four sample dates common to all treatments.

6.3 Results

6.3.1 Note on Interpretation of Results

Before evaluating the results of these experiments I would like to point out that the initial composition of the quadrats (number of species, abundances of species and identity of species) was extremely variable within and between experimental treatments (see Appendices Va, b and Figs. 6.4, 6.5, 6.6 and 6.7). This was due mainly to the small quadrat size in relation to the uneven distribution of species on the pilings in both sessile guilds. The small number of quadrats used in each treatment contributed to the variability between treatments. This fact severely hampered the identification of experimental effects and side effects and only the most obvious trends could be evaluated unambiguously.

In addition to this I had to perform a very large number of individual statistical tests (see Appendix Vc) which meant that there was a high probability of obtaining a significant result in the absence of a real experimental effect. In order to establish whether an experimental effect had caused the abundance of a species or the number of species to differ significantly between experimental treatments I have reviewed the effects of the treatments suggested by the results of the statistical tests in respect to the changes in the species abundance or in the number of species over time in the different experimental groups. This has been done by visual appraisal of graphs. Any other incidental observations which I felt had some bearing on the results are also included.

6.3.2 Predator Exclusion and *Culicia* sp. Removal Experiment at Rapid Bay

6.3.2.1 Replicate Reduction

During the two year period of this experiment a number of exclusion and control cages were lost due to the combined effects of rough weather and snagging by fishing lines. The sequence of cage loss is summarized in Table 6.3. Because of this and also to facilitate statistical analysis I have reduced the replicate number in each treatment to four. One quadrat in each treatment came from one of each of the four piling faces. These quadrats were chosen at random from those remaining in the experiment on the last sample date. All means and standard deviations presented in this section are thus based on a sample size of four.

TABLE 6.3 Cage Loss at Rapid Bay

	Number of cages remaining intact			
	Culicia sp. not removed		*Culicia* sp. removed	
Date	Exclusion	Control	Exclusion	Control
29/03/76	8	8	8	8
28/07/76	8	8	8	8
13/11/76	7	8	8	8
10/03/77	6	7	6	6
29/09/77	6	4	6	6
13/04/78	6	4	6	5

6.3.2.2 Species Number

On the March 1977 sample date approximately one year after the experiment began there was no significant difference in species numbers between treatments (Table 6.4). Six months later on the September 1977 sample date species number was significantly higher on quadrats cleared of *Culicia* sp. than on those that were not (Table 6.4 and Fig. 6.4 A). There was no evidence of a caging X *Culicia* sp. removal interaction (Table 6.4). On the last sample date, April 1978, there was significant heterogeneity in species number between caging treatments. Since there was no longer a significant difference between *Culicia* sp. removal treatments and there was no evidence of a caging X removal interaction (Table 6.4) pairwise comparisons were performed between caging treatments on data pooled from the two removal treatments (Table 6.5). Species number was significantly greater on exclusion quadrats than on control and uncaged quadrats (Table 6.5 and Fig. 6.4A). There was no significant differ-

ence in species number between control quadrats and uncaged quadrats which suggests that an absence of predators has resulted in increased species number.

Figure 6.4A indicates that there was not a clearly defined trend towards increasing species numbers on quadrats cleared of *Culicia* sp. Therefore despite the significant result on September 1977 I conclude that removal of *Culicia* sp. in this experiment did not increase species number. Additionally there was not a consistent increase in the mean of species number in the exclusion treatment (Fig. 6.4A) although in the last year of the experiment the difference in the mean species number between exclusion and control treatments and exclusion and uncaged treatments clearly increased giving rise to a significant difference. These data suggest but do not clearly demonstrate that an absence of predators increased the number of species.

6.3.2.3 Species Abundances

Visual appraisal of Figures 6.4C, D, E, F suggests that the mean abundance of only one phyletic group, the bryozoans, was increased by the removal of *Culicia* sp. During the experiment the mean abundance of bryozoans increased in all three caging treatments in which *Culicia* sp. was removed compared to a barely perceptible change in the mean abundance in the treatments where *Culicia* sp. was not removed (Fig. 6.4F). However only one of the pairwise comparisons between removal treatments for each caging treatment in September 1977 and April 1978 was significant (Table 6.6). Bryozoans were more abundant in the exclu-

sion/*Culicia* sp. removed treatment than in the exclusion/*Culicia* sp. not removed treatment in April 1978 (Table 6.6 Fig. 6.4F). Observations made on individual quadrats from which *Culicia* sp. had been removed indicated that bryozoans settled on the remains of the *Culicia* sp. skeleton and often formed encrusting colonies up to 25cm^2 in area. This rarely occurred on quadrats where *Culicia* sp. was not removed. Although the data presented are inconclusive they suggest that *Culicia* sp. decreases the abundance of bryozoans in this sessile guild. None of the comparisons between removal treatments were significant for individual bryozoan species (Appendix Vc).

Colonial tunicates were significantly more abundant on quadrats from which *Culicia* sp. had been removed than on quadrats on which *Culicia* sp. had been left in the uncaged treatments on April 1978 sample date (Table 6.5 Fig. 6.4D). However Figure 6.4D shows that the mean abundance of colonial tunicates in the uncaged/*Culicia* sp. removed treatment was at least twice that in the uncaged/*Culicia* sp. not removed treatment on every sample date during the experiment. Furthermore the value of the difference between those means decreased rather than the opposite in the last six months of the experiments. This provides no support at all for the proposition that the abundance of colonial tunicates increased in the absence of *Culicia* sp. on uncaged quadrats. The mean abundances of this group in exclusion and control treatments did not show any consistent changes over time that suggested a removal treatment effect of any sort (Fig. 6.4D). Since there was no significant difference in the abundance of colonial

tunicates between removal treatments in either exclusion or control treatments on the last two sample dates (Table 6.6) I conclude that *Culicia* sp. removal had no discernible effect on the abundance of this phyletic group.

There was no significant difference in the abundance of the other two phyletic groups sponges and solitary tunicates, and the total cover minus *Culicia* sp. group between removal treatments in any cage treatment on the last two sample dates (Appendix Vc). Additionally inspection of Figures 6.4B, 6.4C and 6.4E indicate that there was no trend of increasing or decreasing mean abundances associated with removal treatments for any of these three groups during the two year period of the experiment.

With the exception of *Culicia* sp. and *Galeolaria* spp. the abundance of all individual species did not differ significantly between removal treatments on the last two sample dates (Appendix Vc).

In the exclusion treatment in September 1977 *Galeolaria* spp. were significantly more abundant on quadrats from which *Culicia* sp. had been removed than on quadrats on which *Culicia* sp. had been left (Table 6.6, Fig. 6.5J). Inspection of Figure 6.5J suggests that *Galeolaria* spp. increased in abundance in all caging treatments from which *Culicia* sp. had been removed in the first year of the experiment and maintained higher abundances in these treatments than in the caging treatments where *Culicia* sp. had not been removed for the following year. With the exception of the first sample date the mean abundance of *Galeolaria* spp. in the *Culicia* sp. removed treatment was at least twice that of

Galeolaria spp. in the *Culicia* sp. not removed treatment for all caging treatments (Fig. 6.5J). In most cases it was considerably more. This suggests, despite the lack of significant statistics, that *Culicia* sp. decreases the abundance of *Galeolaria* spp. in this sessile guild.

Without further qualification these results suggest that *Culicia* sp. had little effect on the number of species and the abundances of most species in the sessile guild at Rapid Bay. However for the following reasons I think this conclusion is unjustified.

Culicia sp. grew back into the quadrats from which it was periodically removed remarkably rapidly so that on each visit a substantial area of the quadrats had to be recleared (see Fig. 6.4G). This reduced the effectiveness of the *Culicia* sp. removed treatment since few quadrats remained free of this species between sample dates. Statistical comparison of the abundance of *Culicia* sp. between removal treatments indicated that *Culicia* sp. was not necessarily significantly more abundant in the *Culicia* sp. not removed treatment in every caging treatment on the last two sample dates (Table 6.6).

Additionally it is possible that the artificially sheared *Culicia* sp. skeleton was an unsuitable substratum for invasion by the colonists of many species in the sessile guild due to the release of some inhibitory substance during the clearing process. Also colonies of other species beside *Culicia* sp. were occasionally damaged or dislodged from a quadrat while *Culicia* sp. was being removed. It is noteworthy that the total cover minus *Culicia* sp. group did not increase in abundance during the experimental period

in the *Culicia* sp. removed treatment (Fig. 6.4B, Appendix Vc) although on the majority of sample dates during the experiment over 10% of the substratum was unoccupied in all caging treatments in this removal treatment (Fig. 6.4H).

Accordingly I conclude that I have not adequately tested the functional role of *Culicia* sp. by this experiment.

Only one phyletic group, the solitary tunicates, showed an obvious change in abundance associated with caging treatments (Fig. 6.4E). During the experiments the mean abundance of solitary tunicates increased from .8% and 4.20% to 15.29% and 18.59% in the exclusion/*Culicia* sp. not removed and exclusion/*Culicia* sp. removed treatments respectively (Fig. 6.4E). The mean abundance of this group was less than 2.6% on all sample dates in the remaining four treatments and there was no trend of increasing abundance during the experimental period (Fig. 6.4E). Solitary tunicates were significantly more abundant on exclusion quadrats than on control or uncaged quadrats in the *Culicia* sp. not removed treatments in September 1977 and in both removal treatments in April 1978 (Tables 6.7 and 6.8). There was no significant difference in the abundance of solitary tunicates between control and uncaged quadrats in either removal treatments on both sample dates (Table 6.8). These results indicate that the abundance of this group of species is kept low in the sessile guild at Rapid Bay by predation.

Five species of solitary tunicates were recorded in the exclusion quadrats of this experiment. Three of these, (T10) *Polycarpa pedunculata* Heller, (T2) *Ascidia gemmata* Sluiter and (T7) *Phallusia*

depressiuscula (Heller) were not included as members of this sessile guild in Section 2.3. The two other species (T40) *Ascidia thompsoni* and (T28) *Cnemidocarpa etheridgii* were included as members of the sessile guild in Section 2.3. Figures 6.5E, F, G, H, I show the changes in mean abundances of each of these species for all six treatments during the experiment. Considered individually the trend of increasing abundance in the exclusion quadrats is not as convincing as it was for the group as a whole. (compare Fig. 6.4E with Figs. 6.5E, F, G, H, I). Nevertheless the mean abundances of all these species increased to a maximum on the last sample date in exclusion quadrats in at least one removal treatment whereas mean abundances in control and encaged quadrats did not show similar increases. There was one exception to this (Fig. 6.5I). The mean abundance of *Cnemidocarpa etheridgii* steadily increased in the control/*Culicia* sp. not removed treatment. However inspection of the transparencies revealed that this was due to the growth of one individual present in one of the quadrats at the beginning of the experiment. In the exclusion treatments the increase was due to an increase in the number of surviving recruits.

With the exception of *Ascidia gemmata* and *Phallusia depressiuscula* there was no significant heterogeneity between caging treatments on the last two sample dates in the abundance of individual species of solitary tunicates (Table 6.7, Appendix Vc). Additionally the multiple comparisons test indicated that there was no significant difference in the abundances of either *Ascidia gemmata* and *Phallusia depressiuscula* between caging treatments on the occasions where the Kruskal-Wallis ANOV had indicated

that there was significant heterogeneity between caging treatments (Table 6.8). Thus there is only weak evidence, provided by inspection of graphs, that the abundance of each individual solitary tunicate is kept low in the sessile guild at Rapid Bay by predation.

There was no significant heterogeneity in the abundances of the three other phyletic groups, sponges, colonial tunicates and bryozoans, between caging treatments in either removal treatment on the last two sample dates (Appendix Vc). This indicates as does visual appraisal of Figures 6.4C, 6.4D and 6.4F that the abundances of these groups were not affected by any of the caging treatments. However the abundances of two sponge species, two colonial tunicate species, *Culicia* sp. and *Galeolaria* spp. were significantly heterogenous between caging treatments on at least one of the last two sample dates in one or the other of the two removal treatments (Table 6.7).

Aplysilla rosea was significantly more abundant on uncaged quadrats than exclusion quadrats in September 1977 in the *Culicia* sp. not removed treatment (Table 6.8 Fig. 6.5A). There was no significant difference between exclusion and control quadrats and between control and uncaged quadrats. This result suggests that a combination of the experimental side effects of enclosing a quadrat with mesh and the absence of predators reduced the abundance of this species on exclusion quadrats. However Figure 6.5A gives no support for such an interpretation of the results of the statistical tests. Clearly the difference in mean abundance of *Aplysilla rosea* between the uncaged/*Culicia* sp. not removed

treatment and the exclusion/*Culicia* sp. not removed treatment was less in the second year of the experiment than in the first (Fig. 6.5A). This suggests that the significant difference between uncaged and exclusion quadrats was due to initial sampling bias. Additionally the multiple comparisons test indicated that there was no significant difference in the abundance of *Aplysilla rosea* in April 1978 between caging treatments in the *Culicia* sp. not removed treatment (Table 6.8) although the Kruskal-Wallis ANOV had indicated that there was significant heterogeneity between caging treatments on that occasion (Table 6.7). Thus I conclude that the caging treatments had no real effect on the abundance of this species and the significance of the statistical tests is not indicative of an experimental effect.

Aplysilla sulphurea was significantly more abundant in the exclusion/*Culicia* sp. not removed treatment compared to the control/*Culicia* sp. not removed and uncaged/*Culicia* sp. not removed treatments in September 1977 (Table 6.7, 6.8). There was no significant difference between the control and uncaged treatments suggesting that an absence of predators had increased the abundance of this species. However the mean abundance of *Aplysilla sulphurea* did not show a steady increase in the exclusion/*Culicia* sp. not removed treatment during the experiment and it was actually a little lower on the last sample date compared to the first (Fig. 6.5B). This indicates, that *Aplysilla sulphurea* did not increase its abundance in the absence of predators. Since the mean abundance of this species showed barely perceptible fluctuations over time in the uncaged/*Culicia* sp. not removed

treatment (Fig. 6.5B) it is unlikely that an absence of predators prevented a decrease in species abundance. These observations and the fact that the abundance of *Aplysilla sulphurea* was not heterogenous between caging treatments in April 1978 in both *Culicia* sp. removal treatments (Table 6.7) strongly suggests that predators do not reduce the abundance of *Aplysilla sulphurea*.

The abundances of both *Botryllus schlosseri* and *Atapazoa fantasiana* were significantly heterogenous between caging treatments in September 1977 in the *Culicia* sp. removed treatment (Table 6.7). However the multiple comparisons test indicated that there were no significant differences in the abundances of either species between caging treatments on these occasions (Table 6.8).

Figures 6.5C and 6.5D show that the mean abundances of both these species are at least twice as great on the last two sample dates as on the preceding four sample dates in the uncaged/*Culicia* sp. removed treatment. No such increase in mean abundances occurs in the exclusion/*Culicia* sp. removed and control/*Culicia* sp. removed treatments for either species although for the first year of the experiment the mean abundances of each of these species are similar in all three caging treatments in the *Culicia* sp. removed treatment (Fig. 6.5C, D). These observations suggest that the presence of mesh around a quadrat decreased the abundance of these two species in the *Culicia* sp. removed treatment. It is worth noting that the mean abundances of both species remain uniformly low in all caging treatments in the *Culicia* sp. not removed treatment during the last year of the experiment (Fig. 6.5C, D).

This suggests that there are interactions between caging and removal treatments. One interpretation is that both the presence of *Culicia* sp. and the presence of mesh inhibits the abundance of these two species. However no definitive conclusions can be made because there are no significant statistics supporting the preceding proposals.

The abundance of *Galeolaria* spp. was heterogenous among caging treatments in the *Culicia* sp. removed treatment in September 1977 (Table 6.7). Although there was no significant difference in the abundance of this species group between exclusion and control treatments and between control and uncaged treatments its abundance in the exclusion treatment was significantly greater than in the uncaged treatment (Table 6.8). Figure 6.5J shows that the mean abundance of *Galeolaria* spp. was greater in the exclusion/*Culicia* sp. removed treatment than the control/*Culicia* sp. removed and uncaged/*Culicia* sp. removed treatments during the last year of the experiment. Similarly the mean abundance of this group in the control/*Culicia* sp. removed treatment was greater than that in the uncaged/*Culicia* sp. removed treatment during the last year of the experiment (Fig. 6.5J). It is possible that both the absence of predators and the presence of mesh around a quadrat increased the abundance of *Galeolaria* spp. on quadrats from which *Culicia* sp. was removed but only when these two factors are in combination is the effect great enough for a significant difference to be detected. However there is little evidence for this hypothesis in the absence of more convincing data and statistical tests.

The abundance of *Galeolaria* spp. was not significantly heterogenous between caging treatments in the *Culicia* sp. not removed treatment on the last two sample dates (Table 6.7). Also the mean abundance of *Galeolaria* spp. was always less than .15% in all caging treatments in the *Culicia* sp. not removed treatment on all sample dates (Fig. 6.5J). It appears, therefore, that the abundance of *Galeolaria* spp. may only be responsive to caging treatments in the absence of *Culicia* sp.

The abundance of *Culicia* sp. was heterogenous among caging treatments on the April 1978 sample date in the *Culicia* sp. removed treatment (Table 6.7). However the multiple comparisons test indicated that there was no significant difference in the abundance of this species between caging treatments on this occasion (Table 6.8). Inspection of Figure 6.4G suggests that the mean abundance of *Culicia* sp. decreased more in the exclusion/*Culicia* sp. removed treatment than in the control/*Culicia* sp. removed treatment or the uncaged/*Culicia* sp. removed treatment during the experiment. Additionally the mean abundance of *Culicia* sp. decreased in the exclusion/*Culicia* sp. not removed treatment but it did not decrease in the control/*Culicia* sp. not removed or the uncaged/*Culicia* sp. not removed treatments (Fig. 6.4G). These observations suggest that the abundance of *Culicia* sp. decreased in the absence of predators but the results of the statistical tests (Tables 6.7 and 6.8) give very little support to this hypothesis.

6.3.2.4 Water Flow Measurements

Water flow did not differ significantly between exclusion

quadrats and control quadrats (Table 6.9) but fouled mesh restricted water flow to a greater extent than unfouled mesh (Table 6.9 and 6.10). There was no evidence of an interaction between fouling and caging (Table 6.9) indicating that fouling restricts water movement over exclusion quadrats and control quadrats equally.

Data from exclusion quadrats and control quadrats were pooled to give one group of weight loss data for quadrats enclosed by unfouled mesh and one for quadrats enclosed by fouled mesh. Each of these groups was then statistically compared to the weight loss data from uncaged quadrats. There was no significant difference in water movement across uncaged quadrats compared to quadrats enclosed in unfouled mesh ($t = 0.7477$ $df = 14$ $P > .05$). However water movement was significantly less across quadrats enclosed in fouled mesh than across uncaged quadrats ($t = 3.8483$ $df = 14$ $P < .001$ Table 6.10). These results indicate that unfouled exclusion and control cages do not significantly restrict water flow but that fouled exclusion and control cages do significantly restrict water flow.

However, inspection of Table 6.10 shows that there are noticeable trends in the weight loss data suggesting that exclusion cages restricted water flow a little more than control cages and that water flow across quadrats is restricted to a small extent by unfouled cages. Nevertheless the effect of fouling is clearly far greater than the effect (non-significant) of clean mesh (Table 6.10).

The results indicate that differences in the abundance of a

species between exclusion quadrats and control quadrats are unlikely to be due to differences in water flow. Additionally they indicate that differences in species abundances between quadrats enclosed by mesh and uncaged quadrats using the cage design and material as was used at Rapid Bay and Edithburgh are unlikely to be due to differences in water flow, provided the cage surfaces are kept clean.

6.3.2.5 Predator-Prey Observations

The sessile guild at Rapid Bay is part of a trophically complex community which inhabits the general pier environment (Keough and Butler 1979). A very large number of mobile animals belonging to various phyla (Chordata, Mollusca, Echinodermata, Arthropoda, Platyhelminthes) have been recorded in the area. However in this section I shall consider only those species which I have observed eating members of the sessile guild or whose predatory habits have been studied by others.

Keough and Butler (1979) have demonstrated that the four common asteroids at Rapid Bay, *Coscinasterias calamaria* (Gray), *Patiriella brevispina* H.L. Clark, *Tosia australis* Gray and *Petricia vernicina* (Lamarck) are unimportant in influencing the the utilization of space by sessile fauna although the last three species were reported to feed on common species in the sessile guild. The largest and most common of these asteroids, *Coscinasterias calamaria* which feeds mainly on molluscs and moribund items (Keough and Butler 1979), was often found inside cages which had been damaged and torn open by fishing hooks or particularly bad weather. Bivalve molluscs, mainly *Chlamys asperrimus*

and *Electroma* spp., frequently colonized the inside of the mesh of exclusion cages. Any invading *Coscinasterias calamaria* rapidly consumed these as indicated by individuals feeding in the cages and by the numerous empty valves still stuck to the remains of the mesh. For example I deliberately introduced one individual of *Coscinasterias calamaria* into a test exclusion cage originally installed in late 1975 as a trial run for the predator exclusion experiment at Rapid Bay. A large number of *Chlamys asperrimus* and *Electroma* spp. had settled both on the inside of the mesh and amongst the sessile fauna on the piling inside this cage. Within three weeks this one individual asteroid consumed 51 individuals of *Chlamys asperrimus* and 26 individuals of *Electroma* spp. and as far as I could ascertain left the other species in the cage untouched.

I have observed only three species of fish frequently feeding on sessile organisms on the pier. The magpie perch *Goniistius vizonarius* (Saville-Kent) was often observed biting off small pieces of sponge and colonial tunicate colonies as well as picking off small newly settled colonial tunicates. I have also seen the mosaic leather jacket, *Eubalichthys mosaicus* (Ramsay and Ogilby) picking off small tunicate colonies. Other casual observations suggest that the coral fish *Chelmonops truncatus* (Kner) forages in the sessile guild for crevice fauna such as small crustaceans and polycheates.

Of the mobile molluscs in the community the nudibranch *Ceratosoma brevicaudatum* Abraham was often observed eating sponges and algae and the whelk *Thais orbita* Gmelin was occasionally ob-

erved drilling bivalve molluscs such as *Malleus meridianus* Cotton and *Chlamys asperrimus*.

Despite the large number of crabs in the area I have never seen them feeding on anything except moribund items. However the sponge crab, *Cryptodromia octodentata* (Haswell) carries pieces of sponge or tunicate colonies on its back as camouflage. Presumably it obtains these pieces from colonies on the pilings as well as from other pieces of hard substrata in the area.

Finally I have never seen any species clearing areas of substrate larger than 16cm^2 in the sessile guild at Rapid Bay.

6.3.3 Predator Exclusion Experiment at Edithburgh

6.3.3.1 Species Number

In March 1977 and December 1977 species number was heterogenous between caging treatments but it was not heterogenous on the intervening two sample dates (Table 6.11). Pairwise comparisons between caging treatments on the former two sample dates indicated that the number of species was not significantly different between exclusion and control treatments but both these treatments had significantly higher species number than the uncaged treatment (Table 6.12 Fig. 6.6A). This suggests that enclosing a quadrat with mesh rather than predator exclusion resulted in an increase in species number. However by inspecting Figure 6.6A it can be seen that only the mean of species number in the exclusion treatment shows a convincing increase during the experimental period. No such upward trend is shown for the mean of species number in the control and the uncaged treatments.

This suggests that predator exclusion did increase species number but without more convincing statistical tests the results must remain inconclusive.

6.3.3.2 Species Abundances

As was the case at Rapid Bay only one phyletic group, the solitary tunicates, showed an obvious change in abundance associated with caging treatments (Fig. 6.6B, C, D, E F). The mean abundance of this group was zero in both the uncaged and control treatments for the duration of the experiment (Fig. 6.6E). In contrast the mean abundance of solitary tunicates steadily increased in the exclusion treatment from 0% to over 20% on the last sample date (Fig. 6.6E). As expected there was significant heterogeneity in the abundance of solitary tunicates between caging treatments in September 1977 and December 1977 (Table 6.13). Solitary tunicates were significantly more abundant in the exclusion treatment than either the control or uncaged treatment on both the September 1977 and December 1977 sample dates (Table 6.13). There was no significant difference in abundance between uncaged and control treatments (Table 6.13). This evidence indicates that the abundance of solitary tunicates increased due to the absence of predators.

Five species of solitary tunicate were recorded in the exclusion treatment and none had previously been included as members of this sessile guild (Table 2.1 Section 2.3). They were T4 *Halocynthia hispida* (Herdman), T2 *Ascidia gemmata,* T40 *Ascidia thompsoni,* T6 *Ciona intestinalis* Linnaeus and T7 *Phallusia depressiuscula.*

Photograph 6.3 shows an exclusion quadrat at Edithburgh on which two of these species, *Ciona intestinalis* and *Phallusia depressiuscula*, are growing. Considered individually the abundance of only one of the five tunicate species, *Halocynthia hispida*, was significantly heterogenous between caging treatments (Appendix Vd, Table 6.13). However the multiple comparisons test indicated that the abundance of this species did not differ significantly between caging treatments on the last two sample dates where the Kruskal-Wallis ANOV had indicated that there was significant heterogeneity (Table 6.13).

The mean abundance of three of the tunicate species, *Halocynthia hispida*, *Ascidia thompsoni* and *Phallusia depressiuscula* increased in the exclusion treatment during the experiment to a maximum on the last sample date (Fig. 6.7B). The mean abundances of the two other species, *Ascidia gemmata* and *Ciona intestinalis* initially increased in the exclusion treatment and then decreased again near the end of the experiment (Fig. 6.7B). Thus, as was the case at Rapid Bay, there is only weak evidence, provided by inspection of graphs, that the abundance of each individual solitary tunicate is kept low in the sessile guild at Edithburgh by predation.

There was no significant heterogeneity in the abundance of any of the other phyletic groups between caging treatments (Appendix Vd). Additionally there was no obvious or consistent change in the mean abundances of these groups in any treatment during the experiment with one possible exception (Figs. 6.6B, C, D, F). The mean abundance of bryozoans decreased from 32%

to 4% during the last 18 months of the experiment in the exclusion treatment (Fig. 6.6F). The death of an extremely large colony of *Biflustra perfragillis* which occupied a large proportion of one of the exclusion quadrats was responsible for this decrease. Although the reason for the death of this colony cannot be determined conclusively it is likely that it was already dying before the experiment commenced. Approximately 20% of the zooid cases of this colony were empty when the exclusion cage was first installed.

The abundance of total cover was significantly heterogenous between caging treatments in September 1977 but not in December 1977 (Appendix Vd, Table 6.13). In September the abundance of total cover was significantly greater in the uncaged treatment compared to the control and exclusion treatments (Table 6.13). There was no significant difference between exclusion and control treatments. This suggests that total cover was reduced in September due to an experimental side effect of enclosing a quadrat with mesh. However there was no great or consistent change in the mean abundance of total cover in any treatment during the experimental period and it was initially more than 10% higher in the uncaged treatment than in the exclusion or control treatment (Fig. 6.6B). Additionally the mean abundance of total cover was not heterogenous between caging treatments on the December 1977 sample date (Appendix Vd). This evidence suggests that the abundance of total cover was not significantly reduced by enclosing a quadrat with mesh. The significant result on the September sample date is most likely to have been rela-

ted to initial sampling bias.

The abundance of only one further individual species, *Didemnum* sp.a was significantly heterogenous between caging treatments (Appendix Vd, Table 6.13). In September 1977 the abundance of this species was significantly greater in the exclusion treatment than the control and uncaged treatments (Table 6.13). There was no significant difference between control and uncaged treatments (Table 6.13). This suggests that the abundance of this species increased in the absence of predators. However in December 1977 the multiple comparisons test indicated that there were no longer any significant differences in the abundance of this species between caging treatments although the Kruskal-Wallis ANOV had indicated that there was significant heterogeneity between caging treatments (Table 6.13).

This species is an annual and colonizes pilings most heavily during January, February and March each year. It usually sloughs off the pilings during October and November as indicated by the drop in mean abundances during these months in all caging treatments (Fig. 6.7A). The lack of significant differences between caging treatments in December 1977 could be interpreted to mean that predators do not reduce the abundance of this species during its seasonal low. However inspection of Figure 6.7A shows that the mean abundances of *Didemnum* sp.a increases in the exclusion treatment during the course of the experiment (Fig. 6.7A). No such increase occurs in the uncaged and control treatments (Fig. 6.7A). Thus it is more likely that the abundances of *Didemnum* sp. did not differ significantly between caging treat-

ments on December 1977 because it decreased slightly in the exclusion treatment due to the senescence of old colonies (Fig. 6.7A).

In summary I think the evidence is sufficient to conclude that predators decrease the abundance of *Didemnum* sp. a in the sessile guild at Edithburgh at all times of the year.

6.3.3.3 Predator-Prey Observations

The sessile guild at Edithburgh, like that at Rapid Bay, is part of a trophically complex community containing a large number of mobile animals.

Five asteroids were common at Edithburgh (Keough In press). These were the four common asteroids at Rapid Bay and also *Uniophora granifera* (Lamarck). Casual observations suggest that the latter species frequently feeds on bivalve molluscs and that the former four species have diets similar to those outlined for Rapid Bay.

The magpie perch, *Goniistius vizonarius*, and the mosaic leather jacket, *Eubalichthys mosaicus*, were the only two fish which I frequently observed feeding on sessile organisms on the pilings. I have seen both species biting off small pieces of large sponge and tunicate colonies. Additionally on a number of occasions I have seen *Gonniistius vizonarius* pick off newly settled colonies of *Didemnum* sp. a in bare patches on the pilings.

Incidental observations on the feeding activity of *Ceratozoma brevicaudatum* and *Thais orbita* suggested that their general food preferences were the same as those observed at Rapid Bay. Additionally the sponge crab *Cryptodromia octodentata* was relatively

common on the pilings of this pier.

The large patches of bare substratum at Edithburgh (see Section 4.1) were not caused by predator activity. I have never seen any predatory species clearing areas of substratum larger than 16cm at this pier.

6.4 Discussion

6.4.1 The Role of *Culicia* sp. at Rapid Bay

Although experimental quadrats at Rapid Bay could not be kept completely free of *Culicia* sp. the data suggested that the presence of this species decreased the abundance of two other species groups, bryozoans and *Galeolaria* spp. It was surprising that both sponges and colonial tunicates, which are able to exploit unoccupied substratum by vegetative extension of established colonies (see Section 3.3.2.1) did not show significant increases in abundance in the *Culicia* sp. removed treatment. Since the amount of substratum occupied by the vegetative extension of a colony in a given time will be a function of colony size as well as growth rate, this result is likely to be partly due to the low abundance and small colony size of sponges and colonial tunicates in comparison to *Culicia* sp.

Both bryozoans and *Galeolaria* spp. had extremely low growth rates compared to sponges and tunicates (Section 3.3.2.1). However inspection of transparencies of experimental quadrats indicated that they increased their abundance in the *Culicia* sp removed treatment by larval recruitment on the sheared *Culicia* sp. skeleton. Sponges and tunicates colonized the sheared *Culicia* sp.

skeleton very rarely, possibly because it was an unsuitable substratum for their larvae as was suggested in Section 6.2.2.3. Another alternative is that these phyletic groups have naturally very low colonization rates. The results reported in Section 5.3.2 give some support to this hypothesis. The colonization rates of most sponge and tunicate species onto bituminous tar surfaces were extremely low. However the hypothesis of low colonization rates is certainly incorrect for the colonial tunicate *Didemnum* sp. a which colonized bituminous tar surfaces in high numbers (Section 5.3.2).

Although the functional role of *Culicia* sp. was not adequately tested the evidence suggests that it was resistant to larval recruitment by bryozoans and *Galeolaria* spp., keeping their abundance in the sessile guild low. Sutherland (1975, 1978) argues that both *Schizoporella unicornis* (an encrusting bryozoan) and *Styela plicata* (a solitary tunicate) stabilize the fouling community at Beaufort by resisting larval invasion by other species. Larval invasion is an event capable of altering community structure (Sutherland 1975, 1978). Since the results of the experiment reported here are not conclusive I can only suggest that *Culicia* sp. may play a similar role in the sessile guild at Rapid Bay by resisting larval invasion by bryozoans and *Galeolaria* spp.

In view of the remarkable regenerative powers of large established colonies of *Culicia* sp. any further experiments to test its role would be best performed using artificial panels. These could be isolated from large *Culicia* colonies capable of invasion by vegetative growth. Any colonies of *Culicia* sp. recruiting on-

to such panels could be removed easily and the panels could probably be kept absolutely free of *Culicia* sp. during community development. The role of *Culicia* sp. could be evaluated by comparison of community development on such panels with that on panels where *Culicia* sp. is not removed.

6.4.2 The Role of Predation at Rapid Bay and Edithburgh

In hard substrate marine communities where a dominant competitor is prevented from monopolizing the space resource by a predator, species number decreases in the absence of that predator (Paine 1966, 1971, 1976, Dayton 1971, Porter 1972, 1974, Day 1977, Lubchenco and Menge 1978, Russ, In Press). In the sessile guilds at Rapid Bay and Edithburgh the data suggested that species number was rising rather than falling in the absence of predation. However the experimental results did not indicate whether this elevation in species number was temporary or permanent. It may be argued, as follows, that it was a temporary rise which was part of a process analogous to that described by the above authors.

In both sessile guilds, species of solitary tunicate that eigher were very rare or had not previously been recorded in the guilds colonized exclusion quadrats. Inspection of the successive transparencies of individual quadrats indicated that an increase in the number of species on an exclusion quadrat was often a direct result of the recruitment of one or more of these species. This suggests that an increase in the abundance of the solitary tunicates due to the absence of predation was responsible for the

trend of rising species numbers in exclusion treatments.

During the course of the experiments at both Rapid Bay and Edithburgh the mean percentage cover of the solitary tunicates displayed a more or less steady increase up until the last sample date (Figs. 6.4E, 6.6E). Whether this increase would have continued had the experiments been conducted for a longer period of time can not be determined conclusively, but the following circumstantial evidence suggests that it may have done so.

Inspection of sequential transparencies of individual exclusion quadrats indicated that the exhalent and inhalent siphons of each individual solitary tunicate were never overgrown. Additionally, in the last year of the experiments a number of the larger individuals appeared to be crowding and crushing other sessile organisms adjacent to them. Furthermore, most individuals which colonized exclusion quadrats in the first year of the experiment survived until the end of the experiment and casual observations in the unmanipulated guilds suggested that all the solitary tunicate species had life-spans of at least three years. Therefore it seems likely that this group of species would continue to increase in abundance on the exclusion quadrats, possibly resulting in the competitive exclusion of other species and a simultaneous drop in species number. The downward trend in the abundance of *Culicia* sp. in the exclusion treatment in the Rapid Bay experiment may have been caused by the recruitment and growth of these solitary tunicates.

Inspection of successive transparencies on individual exclusion quadrats indicated that the increased percentage cover of

solitary tunicates was due to recruitment of larvae and their subsequent growth after metamorphosis rather than the growth of established individuals. After both experiments were terminated several cages were removed from a few of the exclusion quadrats at both study sites. Casual observations made on subsequent field trips indicated that the solitary tunicates on these quadrats survived for at least nine months and continued to grow in size although no further recruits were seen on the quadrats. This suggests that the low abundance of solitary tunicates in these sessile guilds may be accounted for by predation on newly settled individuals.

Numerous sessile invertebrates in various marine habitats have been reported to have a size refuge from predation (see Connell 1975 for review). It is possible that the thickening tests of the growing juvenile tunicates eventually serve as a mechanical barrier to predation. Alternatively it is possible that some or all of the solitary tunicate species reported here may produce substances toxic or distasteful to predators as adults but not as newly settled juveniles. Many solitary tunicates are known to be toxic to potential predators (Burkholder 1973, Russell 1966).

At Edithburgh it is noteworthy that most solitary tunicates grow out of the shells of dead *Pinna bicolor* or out of the crevices among the wood and rock debris underneath the pier. This could be explained by one or more of at least three mechanisms. Firstly there may be habitat selection by vagile larvae so that the small and vulnerable juvenile tunicates are protected from

predation; secondly predators may remove new recruits from more exposed sites; thirdly the cryptic sites may have provided better conditions for adhesion by larvae and later by adults than the exposed sites. Although further experimental work is required to provide clear disproof of any one of these alternatives the results of the predator exclusion experiment at Edithburgh are consistent with the second explanation.

Although water flow as measured by the plaster of Paris blocks did not differ significantly between exclusion and control quadrats it could be argued that other experimental side-effects of enclosing a quadrat with mesh, namely reduced light intensity and increased sedimentation, were not equivalent between these two caging treatments. These side effects may have enhanced the abundance of solitary tunicates on exclusion quadrats. However, since solitary tunicates were never seen on either control or uncaged quadrats at Edithburgh and as a group did not increase in abundance on these quadrats at Rapid Bay, one would have to postulate that the other experimental side-effects of exclusion cages were completely absent from control cages before concluding that predation had no effect on the abundance of solitary tunicates. Some sedimentation was observed on both control and exclusion quadrats and no difference in light intensity could be detected between control quadrats and exclusion quadrats using a hand held photographic light-meter (all f2 at 1/30 sec. at ASA 125). Sedimentation was never observed on uncaged quadrats and light meter readings were often but not in every case one "f stop" higher on uncaged quadrats than on con-

trol and exclusion quadrats. Thus, even though these two experimental side-effects may have enhanced the recruitment of solitary tunicates, they are likely to have occured on both control and exclusion quadrats. It is also worth reporting that I never observed predatory organisms congregating in unusually high numbers in control cages. Therefore it is unlikely that the presence of a control cage produced artificially elevated levels of predation on a control quadrat. Accordingly the two types of cages appear to provide a valid test for the effects of predators and the results indicate that predators reduce the abundance of solitary tunicates in these two sessile guilds.

Sutherland (1974) has demonstrated that predation by fish is an important source of mortality to young individuals of the solitary tunicate *Styela plicata* at Beaufort and can therefore play an important role in community development in this locality. Additionally both Day (1977) and Russ (In Press) have shown that predation by fish prevents monopolization of space by a competitively dominant colonial tunicate in a tropical and temperate fouling community respectively. Since I have never witnessed a juvenile solitary tunicate being preyed upon in the sessile guilds at Edithburgh and Rapid Bay I am unable to determine which predator/s are responsible for their low abundance. However the results suggest that the magpie perch *Goniistius vizonarius* may be largely responsible for the low abundance of the colonial tunicate *Didemnum* sp. a at Edithburgh. *Goniistius vizonarius* often feeds on newly settled colonies of *Didemnum* sp. a at Edithburgh and the latter species increased in abundance in exclusion cages.

Goniistius vizonarius is an obvious candidate as an important predator on juvenile solitary tunicates.

As pointed out in Chapter 3 the colonial tunicates at Edithburgh are good overgrowers and are able to exploit newly available free space rapidly due to fast growth rate. In spite of this *Didemnum* sp.a could only monopolize space in this guild temporarily due to its annual life-span. Nevertheless relaxation of predation certainly elevated its abundance during the winter months (Fig. 6.7A) and it is possible that if predators were absent for a longer period its winter peak in abundance would become increasingly elevated in successive years. Whether this species would eventually be out competed and excluded by solitary tunicates under conditions of prolonged predator removal is difficult to determine. Since it often occurs as an epizooite on the tests of the larger solitary tunicates it is unlikely to be completely excluded from the study site although it may eventually lose access to the primary substratum.

Whether the solitary tunicates at Rapid Bay and Edithburgh can be viewed as competitive dominants needs further experimental confirmation. However, it can be concluded that predation does play a role in the structure of these two sessile guilds. This conclusion contradicts that made by Keough and Butler (1979) for the sessile guild at Rapid Bay but it should be pointed out that their predator exclusion experiments lasted only six months. As can be seen in Fig. 6.4E solitary tunicates showed a detectable rise in mean percentage cover only after approximately nine months. Furthermore, their experiment was conducted during the

winter months of the year and casual observations suggested that solitary tunicates recruited onto exclusion quadrats most frequently in the summer months.

Finally it is significant that in three other predator exclusion studies done with subtidal sessile communities (Day 1977, Russ In Press, Sutherland 1974) predation has suppressed the abundance of tunicates. Whether this is mere coincidence or is associated with a common feature in the biology of different tunicate species setting them apart from other phyletic groups requires further investigation.

TABLE 6.4 Summary of two-way ANOV of species number in the Rapid Bay experiment.

ns: not significant at the .05 significance level

*: .05>P>.01

Source of Variation	F_s 10/03/77	29/09/77	13/04/78	d.f.
Removal treatment	3.6 ns	5.56 *	2.17 ns	1,18
Caging treatment	1.71 ns	1.87 ns	8.51 *	2,18
Interaction (Removal x caging)	0.24 ns	0.08 ns	0.27 ns	2,18

$F_{.05(1,18)} = 4.41$ $F_{.01(1,18)} = 8.28$ $F_{.05(2,18)} = 8.28$

TABLE 6.5 Summary of Newman-Keuls multiple range test (Zar 1974, pp. 151-155) for pairwise comparisons of species number betwen caging treatments on 13/04/78 in the Rapid Bay experiment

ns: not significant at the .05 significance level

*: .05>P>.01 Sample size = 8 for all groups

**: .01>P>.001

Comparison	Differences in means	S.E.	q	P
Exclusion vs. Control	4.75	.9732	4.88**	2
Control vs. Uncaged	0.375	.9732	0.385ns	2
Exclusion vs. Uncaged	5.125	.9732	5.266**	3

$q_{.05,21,2} = 2.95$ $q_{.05,21,3} = 3.57$

$q_{.01,21,2} = 4.024$ $q_{.01,21,3} = 4.639$

TABLE 6.6 Summary of Mann-whitney U-tests comparing the abundances of species between *Culicia* sp. removal treatments for each caging treatment in the Rapid Bay experiment. Only those species or groups for which there was a significant difference in at least one comparison on either of the last two sample dates are included. The test was one-tailed and a .05 significance level was used. Sample size = 4 for all groups.

NR: Abundance in *Culicia* sp. not removed group significantly greater

R: Abundance in *Culicia* sp. removed group significantly greater

U values are listed for each comparison

Date	Caging treatment	Colonial tunicates	Bryozoans	*Culicia* sp.	*Galeolaria* spp.
29/09/77	Exclusion	2.0 ns	3.0 ns	1.0 NR	1.0 R
	Control	7.0 ns	2.5 ns	3.0 ns	2.0 ns
	Uncaged	3.0 ns	7.5 ns	0.0 NR	4.0 ns
13/04/78	Exclusion	5.0 ns	0.0 R	2.0 ns	3.0 ns
	Control	6.0 ns	5.0 ns	4.0 ns	2.0 ns
	Uncaged	0.0 R	2.0 ns	0.0 NR	6.0 ns

TABLE 6.7 Summary of Kruskal-Wallis ANOV comparing the abundances of species between caging treatments for each *Culicia* sp. removal treatment in the Rapid Bay experiment on the last two sample dates. Only those species or species groups for which there was significant heterogeneity between caging treatments in at least one comparison on either of the last two sample dates are included. Sample size = 4 for all groups

ns: not significant at the .05 significance level

NR: *Culicia* sp. not removed group

R: *Culicia* sp. removed

	Culicia sp. Treatment	Kruskal-Wallis ANOV 29/09/77 H	P	13/04/78 H	P
Solitary tunicates	NR	8.3	<.008	8.3	<.008
	R	5.2	ns	10.4	<.008
Culicia sp.	NR	2.4	ns	2.6	ns
	R	0.9	ns	5.7	<.05
Aplysilla rosea	NR	6.3	<.05	10.4	<.008
	R	2.8	ns	4.8	ns
Aplysilla sulphurea	NR	8.0	<.008	5.7	ns
	R	1.0	ns	0.6	ns
Botryllus schlosseri	NR	2.0	ns	1.9	ns
	R	7.2	<.01	1.1	ns
Atapazoa fantasiana	NR	1.9	ns	0.0	ns
	R	7.2	<.01	1.9	ns
Ascidia gemmata	NR	1.9	ns	4.3	ns
	R	2.8	ns	7.2	<.01
Phallusia depressiuscula	NR	4.3	ns	7.2	<.01
	R	2.4	ns	1.9	ns
Galeolaria spp.	NR	1.6	ns	2.7	ns
	R	5.6	<.05	0.2	ns

TABLE 6.8 Summary of nonparametric multiple comparisons tests comparing the abundances of species or groups between caging treatments in the Rapid Bay experiment on those occasions when the Kruskal-Wallis ANOV had indicated that there was significant heterogeneity between caging treatments.

Sample size = 4 for all groups

ns: not significant at the .05 signficance level

U: Abundance in the uncaged treatment significantly greater

E: Abundance in the exclusion treatment significantly greater

DIR: Difference between rank sums

NR: *Culicia* sp. not removed

R: *Culicia* sp. removed

S.E = 4.9 when p = 2; S.E. = 7.21 when p = 3

	Date	*Culicia* sp. treatment	Non parametric multiple comparisons test, pairwise comparison between caging treatments: Exculsion vs. Control DIR	p	q		Control vs. Uncaged DIR	p	q		Exclusion vs. Uncaged DIR	p	q	
Solitary tunicates	29/09/77	NR	20	2	4.08	E	5	2	1.02	ns	25	3	3.47	E
	13/04/78	NR	20	2	4.08	E	5	2	1.02	ns	25	3	3.47	E
	13/04/78	R	24	3	3.33	E	0	2	0	ns	24	3	3.33	E
Culicia sp.	13/04/78	R	10	2	2.04	ns	7	2	1.43	ns	17	3	2.36	ns
Aplysilla rosea	29/09/77	NR	12	2	2.45	ns	12	2	2.45	ns	24	3	3.33	U
	13/04/78	NR	0	2	0	ns	23	3	3.19	ns	23	3	3.19	ns
Aplysilla sulphurea	29/09/77	NR	25	3	3.47	E	2	2	0.41	ns	23	2	4.69	E
Botryllus schlosseri	29/09/77	R	0	2	0	ns	18	3	2.5	ns	18	3	2.5	ns
Atapazoa fantasiana	29/09/77	R	0	2	0	ns	18	3	2.5	ns	18	3	2.5	ns
Ascidia gemmata	13/04/78	R	18	3	2.5	ns	0	2	0	ns	18	3	2.5	ns
Phallusia depressiuscula	13/04/78	NR	18	3	2.5	ns	0	2	0	ns	18	3	2.5	ns
Galeolaria spp.	29/09/77	R	11	2	2.24	ns	13.5	2	2.76	ns	24.5	3	3.4	E

$q_{.05,\infty,3} = 3.314$ $q_{.05,\infty,2} = 2.772$ $q_{.01,\infty,3} = 2.902$ $q_{.01,\infty,2} = 2.326$

TABLE 6.9 Summary of two-way ANOV of percentage weight loss of plaster of Paris blocks in cages at Rapid Bay

ns: not significant at the .05 significance level

*: .05>P>.01

Source of variation	d.f	SS	MS	Fs.	
Subgroups	3	278.4	92.8		
Exclusion vs. Control	1	5.76	5.76	.1508	ns
Fouled vs.Unfouled	1	272.41	272.41	7.133	*
Interaction	1	.23	.23	.006	ns
Within groups	12	458.22	38.19		
Total	15	736.62			

$F_{.05(1,12)} = 4.75$

TABLE 6.10 Mean and standard deviation of percentage weight loss in the five groups of bags containing the plaster of Paris blocks

	$\bar{X}$ (S.D.)	Sample size
Fouled Exclusion	24.08 (3.59)	4
Fouled Control	25.52 (5.93)	4
Unfouled Exclusion	32.57 (7.49)	4
Unfouled Control	33.53 (6.97)	4
Uncaged quadrat	35.49 (6.37)	8

TABLE 6.11 Summary of one-way ANOV of species number in the Edithburgh experiment
Sample size = 5 for all groups
ns: not significant the .05 significance level
**: .01>P>.001

Source of Variation	Fs. 18/03/77	11/06/77	24/09/77	28/12/77
Caging Treatments	8.52**	2.76 ns	3.71 ns	8.02**

$F_{.05(2,12)} = 3.89$ $F_{.01(2,12)} = 6.93$

TABLE 6.12 Summary of Newman-Keuls multiple range test (Zar 1974, pp. 151-155) for pairwise comparisons of species number between caging treatments on March 18, 1977 and December 28, 1977 in the Edithburgh experiment
Sample size = 5 for all treatments
ns: not significant at the .05 significance level
*: .05>P>.01
**: .01>P>.001

Date	Comparison	Difference in Means	S.E.	q	P
18/03/77	Exclusion vs. Control	0.8	.9198	0.869 ns	2
18/03/77	Control vs. Uncaged	4.2	.9198	4.57 **	2
18/03/77	Exclusion vs. Uncaged	5.0	.9198	5.43 **	3
28/12/77	Exclusion vs Control	0.8	.7874	1.016 ns	2
28/12/77	Control vs. Uncaged	3.4	.7874	4.32 *	2
28/12/77	Exclusion vs. Uncaged	4.2	.7874	5.33 **	3

$q_{.05(12,2)} = 3.082$ $q_{.05(12,3)} = 3.773$
$q_{.01(12,2)} = 4.32$ $q_{.01(12,3)} = 5.046$

TABLE 6.13 Summary of Kruskal-Wallis one-way ANOV and of the nonparametric multiple comparisons test comparing the abundances of species or groups between caging treatments in the Edithburgh experiment. Only those species or groups where the Kruskal-Wallis ANOV had indicated that there was significant heterogeneity between caging treatments are included.

E: Abundances in exclusion treatment significantly greater

U: Abundance in uncaged treatment significantly greater

ns: not significant at the .05 signficance level

DIR: Difference between rank sums

For the multiple comparisons test S.E=10.0 when p=3 and S.E.=6.77 when p=2

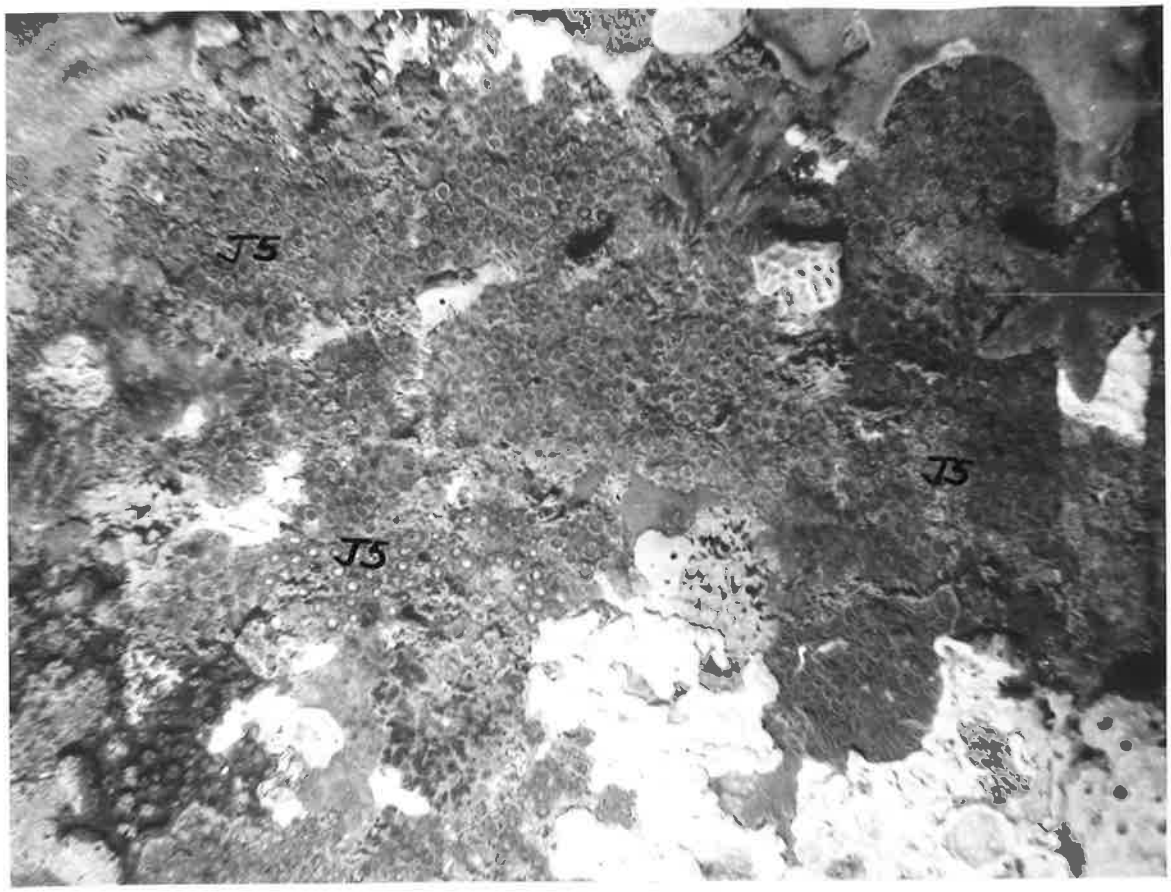
Sample size = 5 for all groups

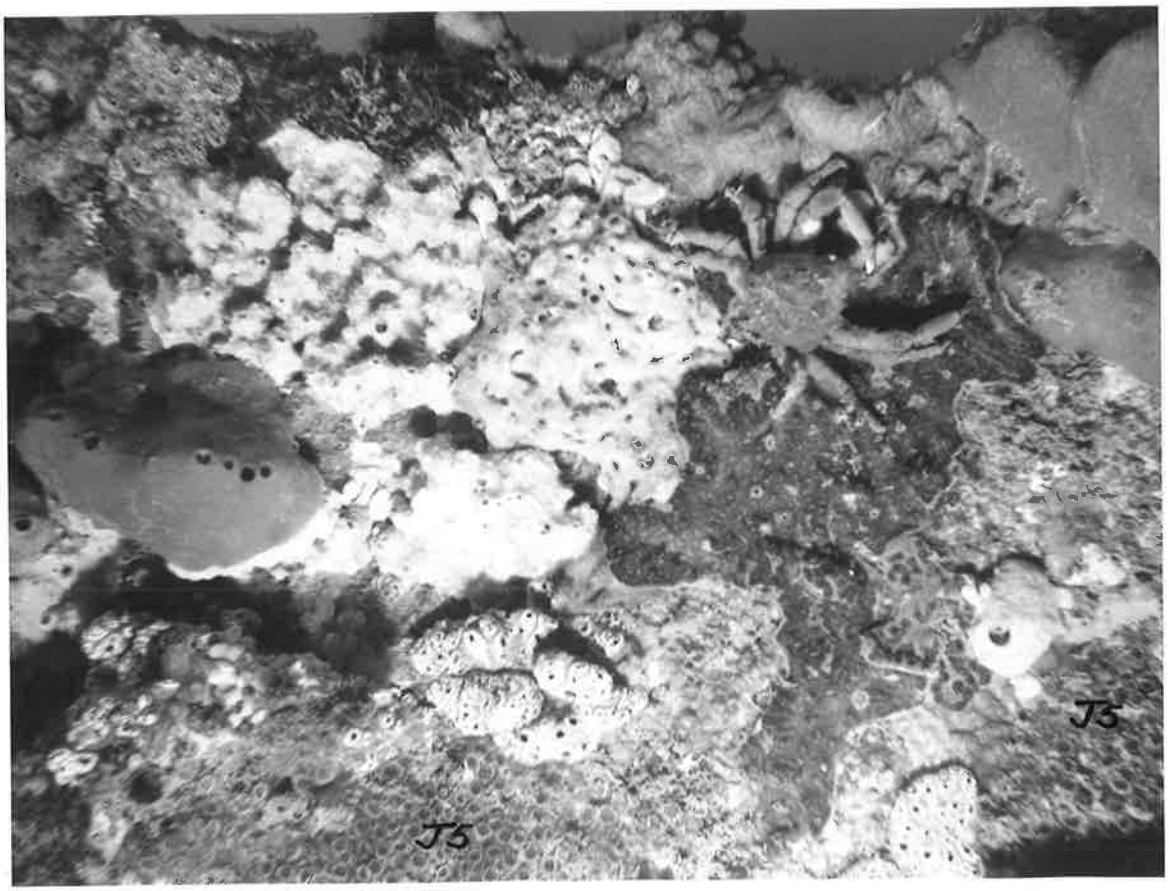
Species or Group	Date	Kruskal-Wallis ANOV H	P	Non parametric multiple comparisons test, pairwise comparison between caging treatments: Exculsion vs. Control DIR	p	q		Control vs. Uncaged DIR	p	q		Exclusion vs. Uncaged DIR	p	q	
Total cover	24/09/77	6.32	<.05	8.0	2	1.18	ns	34.0	3	3.4	U	26.0	2	3.84	U
Solitary tunicates	24/09/77	13.29	<.009	37.5	3	3.75	E	0.0	2	0.0	ns	37.5	3	3.75	E
	28/12/77	13.29	<.009	37.5	3	3.75	E	0.0	2	0.0	ns	37.5	3	3.75	E
Didemnum sp.a	24/09/77	9.54	<.009	26.5	2	3.91	E	13.0	2	1.92	ns	39.5	3	3.95	E
	28/12/77	6.03	<.05	20.5	2	3.03	ns	8.5	2	1.26	ns	29.0	3	2.9	ns
Halocynthia hispida	24/09/77	9.88	<.009	30.0	3	3.0	ns	0.0	2	0.0	ns	30	3	3.0	ns
	28/12/77	6.90	<.05	22.5	3	2.25	ns	0.0	2	0.0	ns	22.5	3	2.25	ns

$q_{.05,\infty,3} = 3.314$ $q_{.05,\infty,2} = 2.772$ $q_{.01,\infty,3} = 2.902$ $q_{.01,\infty,2} = 2.326$

PHOTOGRAPH 6.1 An area of piling at Rapid Bay approximately 40cm x 50cm in size. Most of the area is covered by the stony coral *Culicia* sp. (J5) (tightly packed small white rings on a flattened grey background) which is typical of most of the piling surfaces at Rapid Bay.

PHOTOGRAPH 6.2 The photograph shows an area of piling at Rapid Bay approximately 40cm x 50cm in size which is mainly occupied by species other than *Culicia* sp. (J5). These species are growing on top of the skeletal remains of *Culicia* sp. They form an irregular clump which is more or less surrounded by live *Culicia* sp. colonies parts of which are visible along the bottom edge and the right side of the photograph.


J5
J5
J5


J5
J5

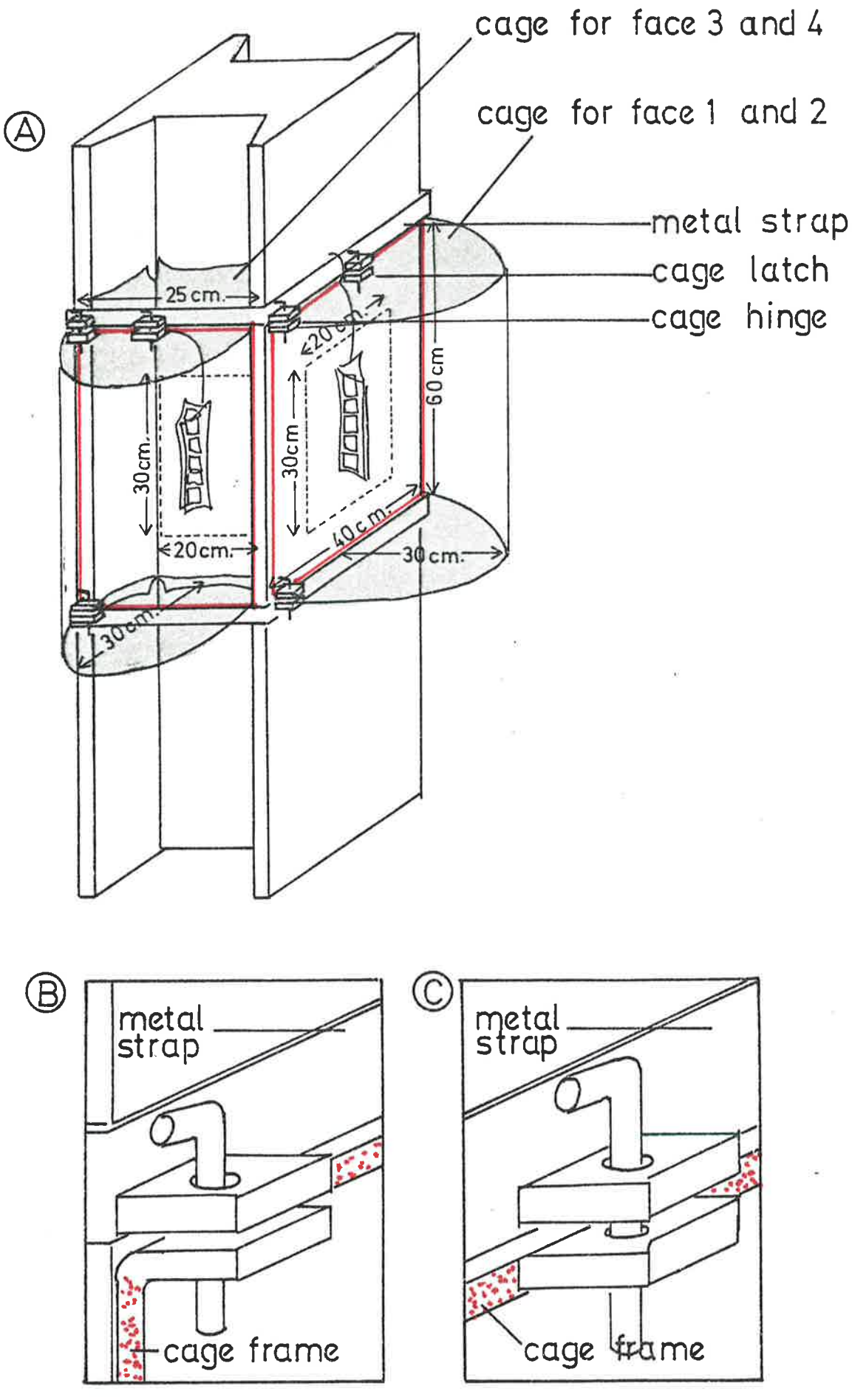
PHOTOGRAPH 6.3 An exclusion quadrat at Edithburgh 18 months after the cage was installed.

Organisms marked with a red X are young individuals of the solitary tunicate *Phallusia depressiuscula*. Organisms marked with a blue X are young individuals of the solitary tunicate *Ciona intestinalis*.

FIGURE 6.1A The cage design used in the predator exclusion and *Culicia* sp. removal experiment at Rapid Bay. The top and bottom ends of the control cages are stippled. The rectangular metal frames of the cages are red. The approximate positions of the quadrats enclosed by the cages are outlined with dashes. The positions of the bags of plaster of Paris blocks above the quadrats are also shown.

B. Detail of cage hinge

C. Detail of cage latch


A
cage for face 3 and 4
cage for face 1 and 2
metal strap
cage latch
cage hinge
25 cm.
20 cm.
60 cm
30cm.
30cm
20cm.
40cm.
30 cm.
30cm.
B
metal strap
cage frame
C
metal strap
cage frame

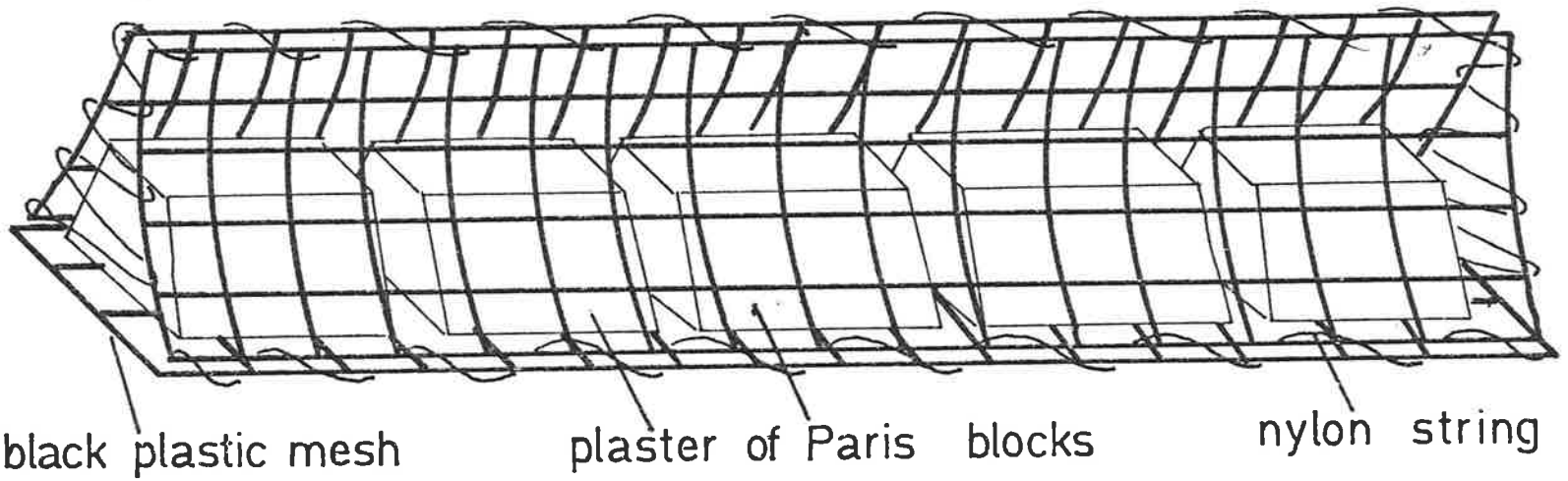

black plastic mesh
plaster of Paris blocks
nylon string

FIGURE 6.2 A plastic mesh bag containing five plaster of Paris blocks.

FIGURE 6.3 The cage design used in the predator exclusion experiment at Edithburgh. The top and bottom ends of the control cages are stippled. The approximate position of the quadrat enclosed by the cage is outlined with dashes.

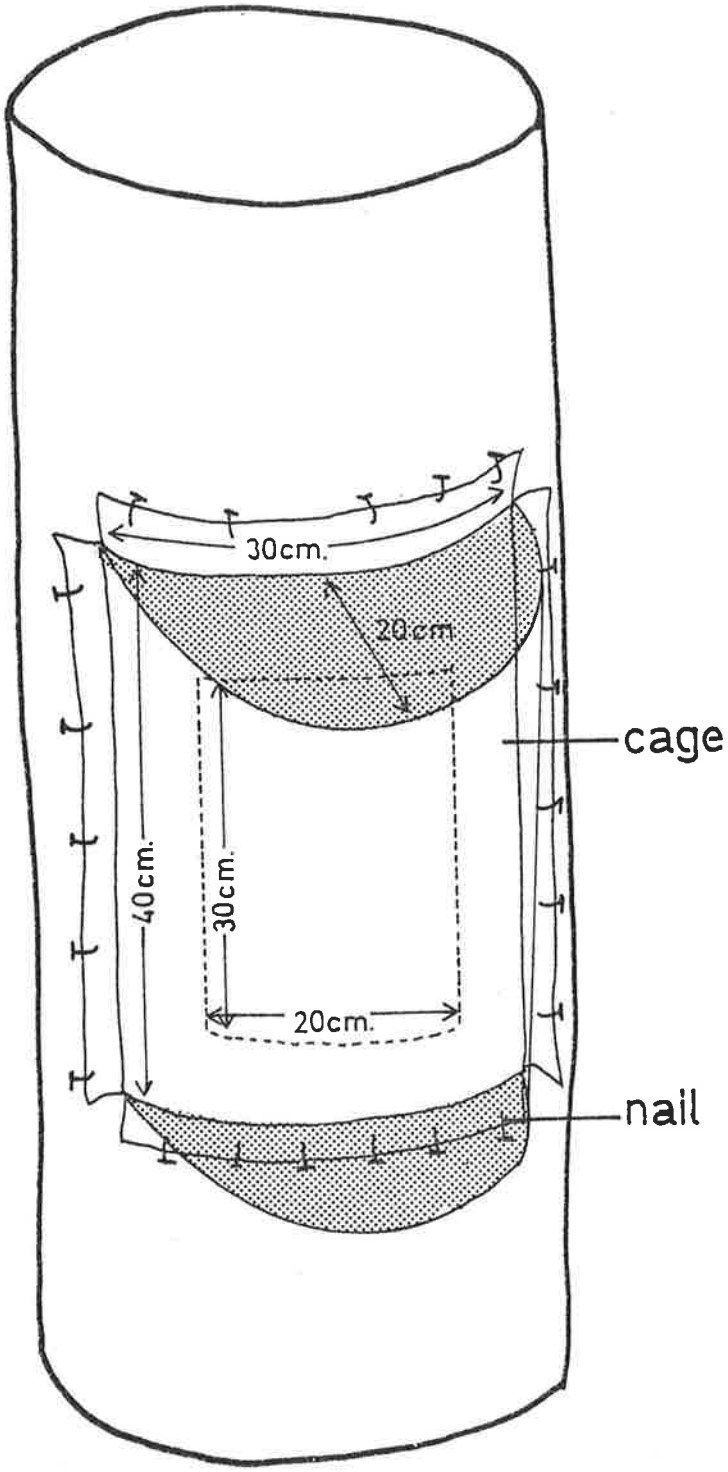

30cm.
20cm.
cage
40cm.
30cm.
20cm.
nail

FIGURE 6.4A The mean and standard deviation (vertical line) of species number in the six experimental treatments at Rapid Bay on every sample date

NR: *Culicia* sp. not removed treatment

R: *Culicia* sp. removed treatment

●: mean in exclusion treatment

O: mean in control treatment

□: mean in uncaged treatment

FIGURE 6.4B The mean and standard deviation (vertical line) of the percentage cover of all species together excluding *Culicia* sp. (Total cover minus *Culicia* sp.) in the six experimental treatments at Rapid Bay on every sample date. See caption Figure 6.4A for further details.

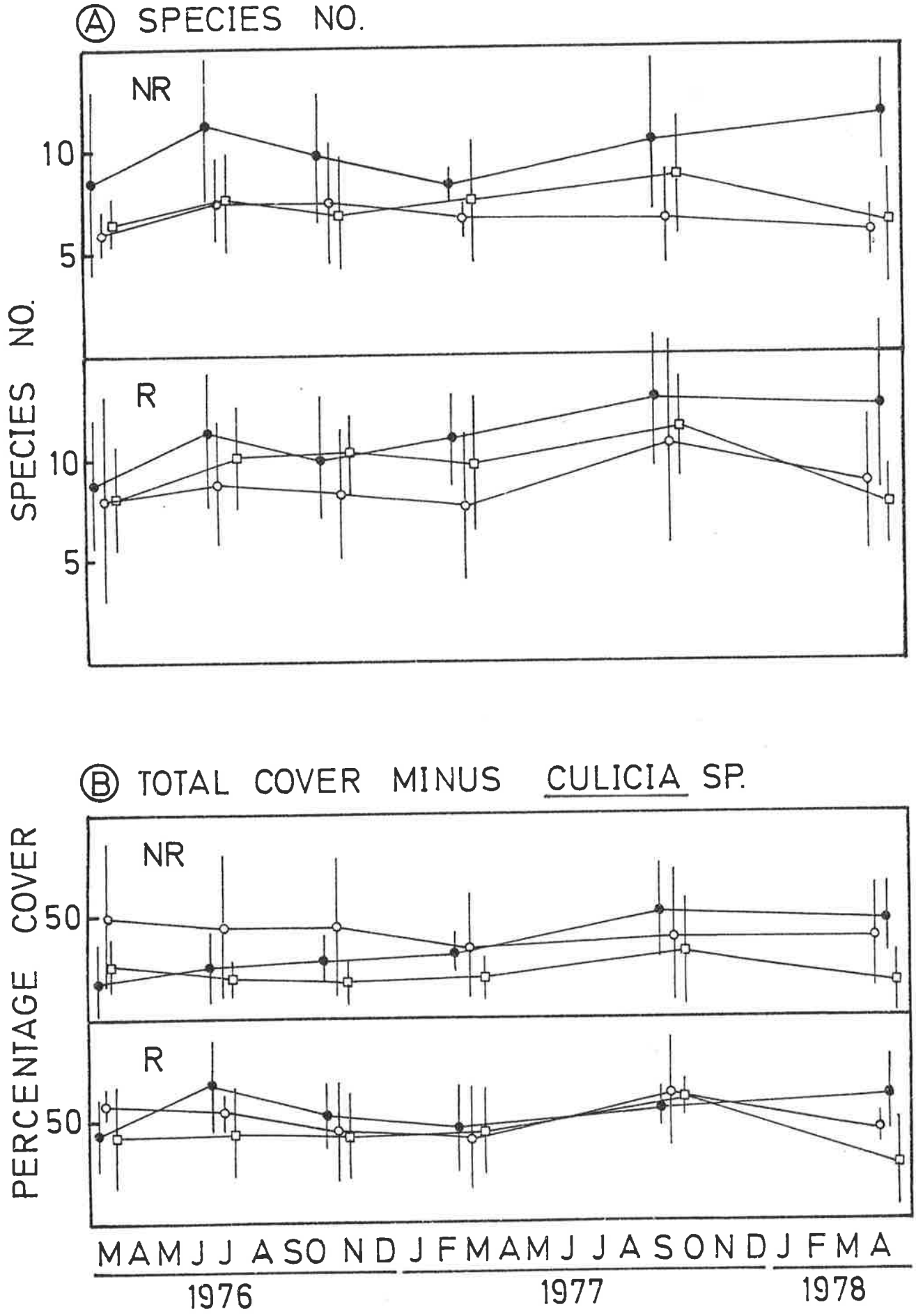

Ⓐ SPECIES NO.
NR
R
10
5
10
5
SPECIES NO.
Ⓑ TOTAL COVER MINUS CULICIA SP.
NR
R
50
50
PERCENTAGE COVER
M A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 6.4C, D, E The mean and standard deviation (vertical line) of the percentage cover of the three following phyletic groups

C. Sponges

D. Colonial tunicates

E. Solitary tunicates

in the six experimental treatments at Rapid Bay on every sample date.
See caption to Figure 6.4A for further details.

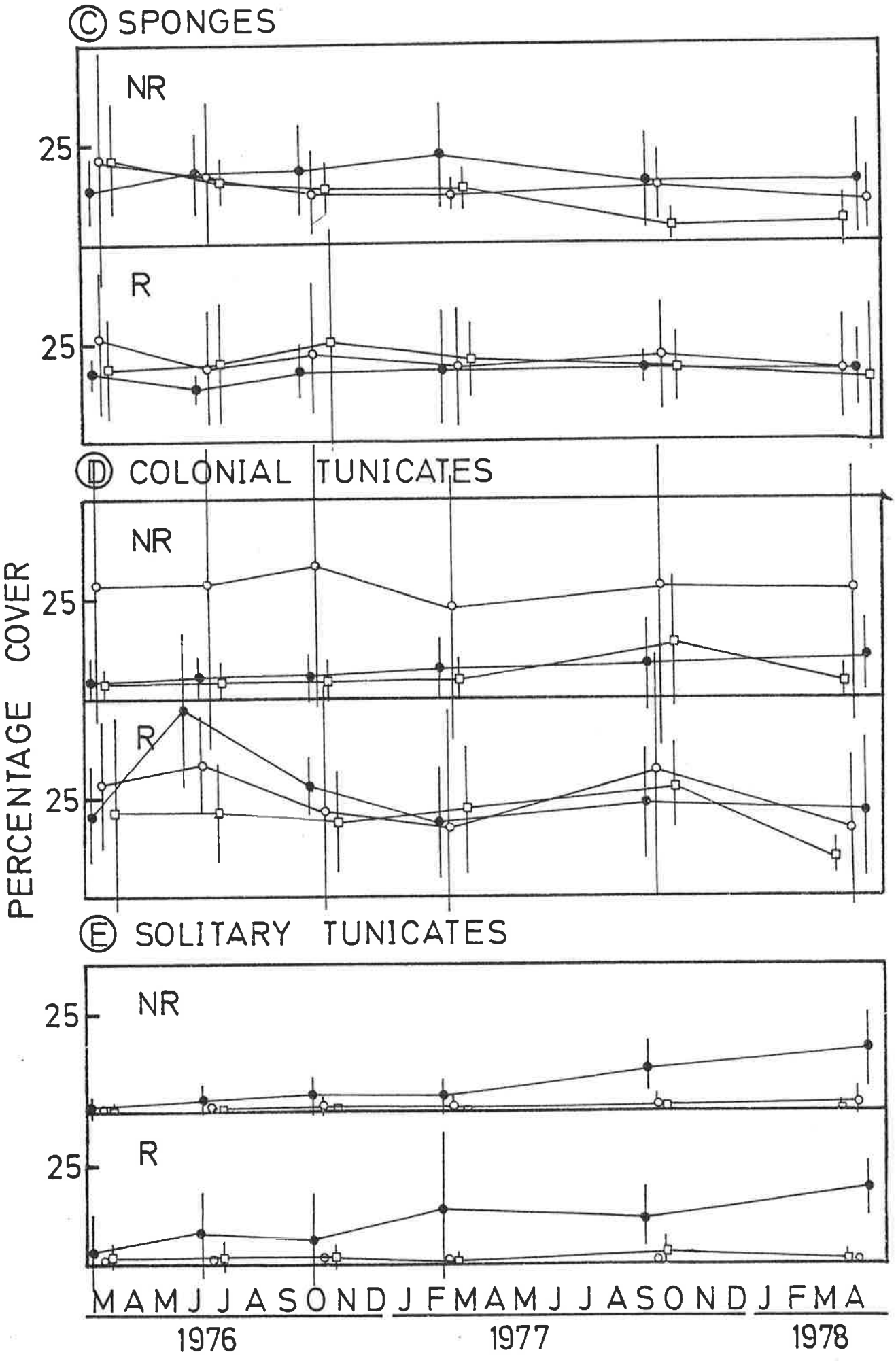

© SPONGES
NR
R
25
25
Ⓓ COLONIAL TUNICATES
NR
R
25
25
PERCENTAGE COVER
Ⓔ SOLITARY TUNICATES
NR
R
25
25
M A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 6.4F, G, H The mean and standard deviation (vertical line) of the percentage cover of

F. Bryozoans

G. *Culicia* sp.

H. Unoccupied substratum

in the six experimental treatments at Rapid Bay on every sample date

See caption to Figure 6.4A for further details.

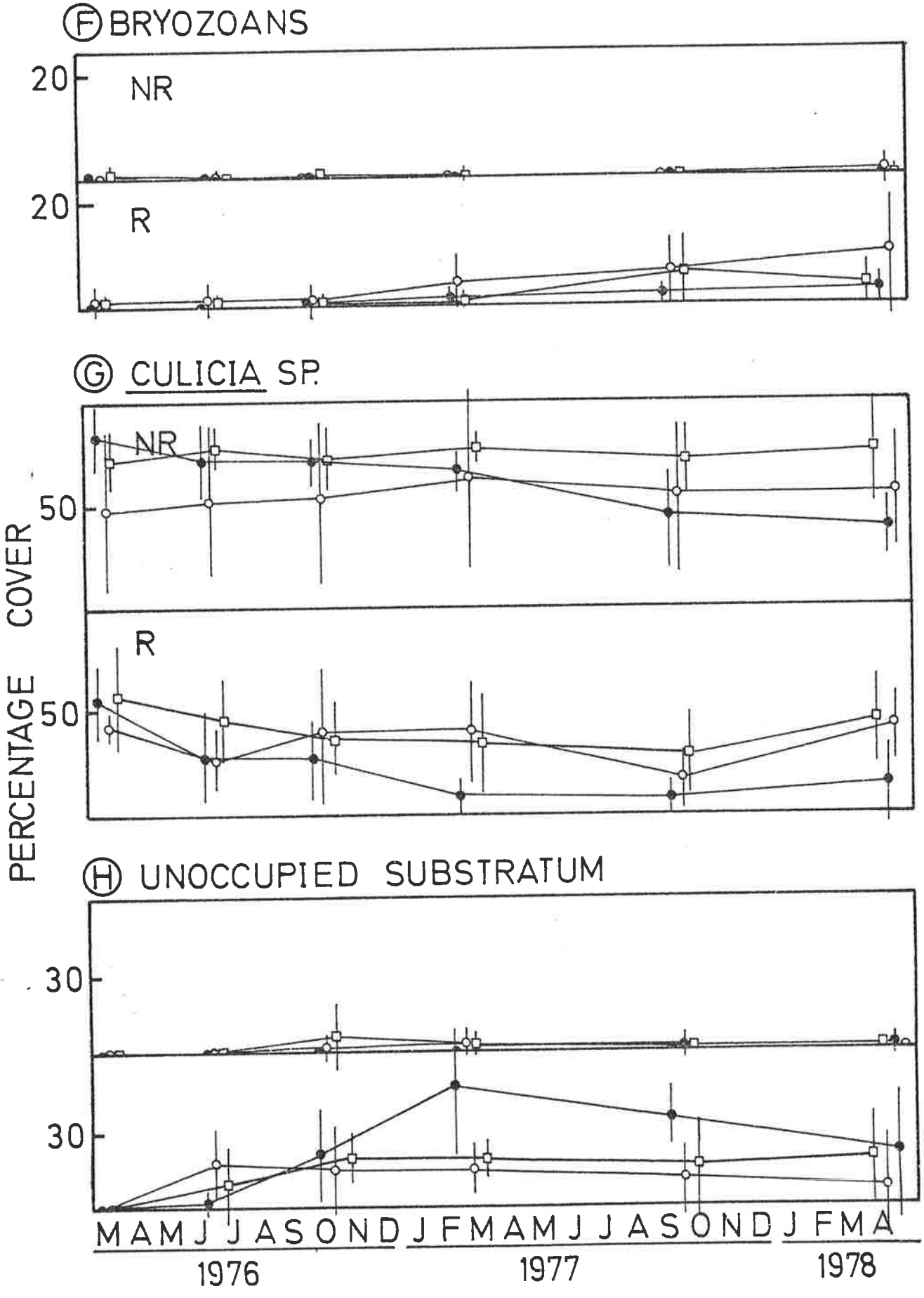

Ⓕ BRYOZOANS
20
NR
20
R
Ⓖ CULICIA SP.
NR
50
R
50
PERCENTAGE COVER
Ⓗ UNOCCUPIED SUBSTRATUM
30
30
M A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 6.5A, B, C, D The mean and standard deviation (vertical line) of the percentage cover of the following species

A. SP1 *Aplysilla rosea*
B. SP2 *Aplysilla sulphurea*
C. T13 *Botryllus schlosseri*
D. T25 *Atapazoa fantasiana*

in the six experimental treatments at Rapid Bay on every sample date See caption to Figure 6.4A for further details.

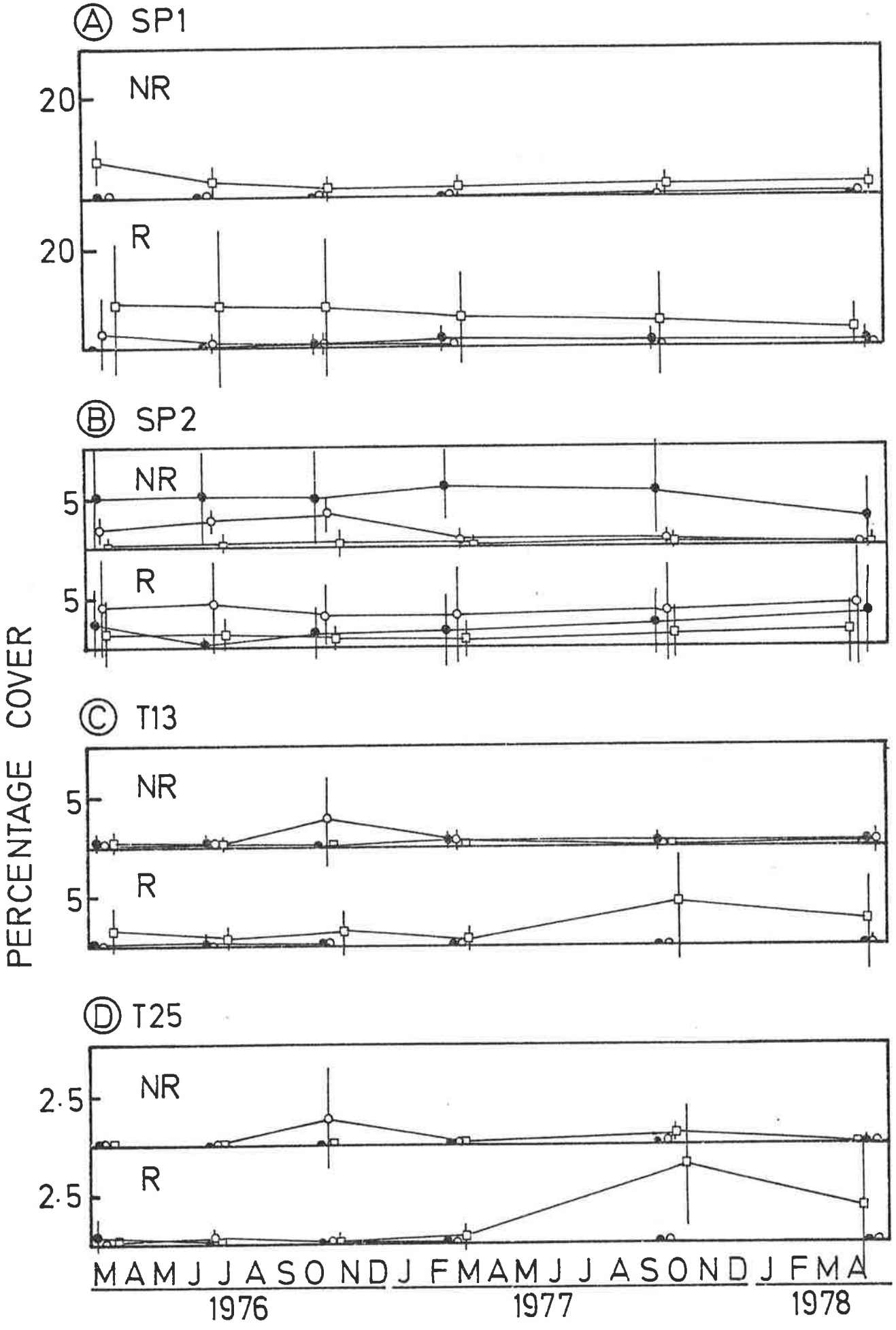

Ⓐ SP1
NR
20
R
20
Ⓑ SP2
NR
5
R
5
Ⓒ T13
NR
5
R
5
Ⓓ T25
NR
2·5
R
2·5
PERCENTAGE COVER
M A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 6.5E, F, G, H

The mean and standard deviation (vertical line) of the percentage cover of the following species

E. T10 *Polycarpa pedunculata*

F. T2 *Ascidia gemmata*

G. T40 *Ascidia thompsoni*

H. T7 *Phallusia depressiuscula*

in six experimental treatments at Rapid Bay on every sample date
See caption to Figure 6.4A for further details.

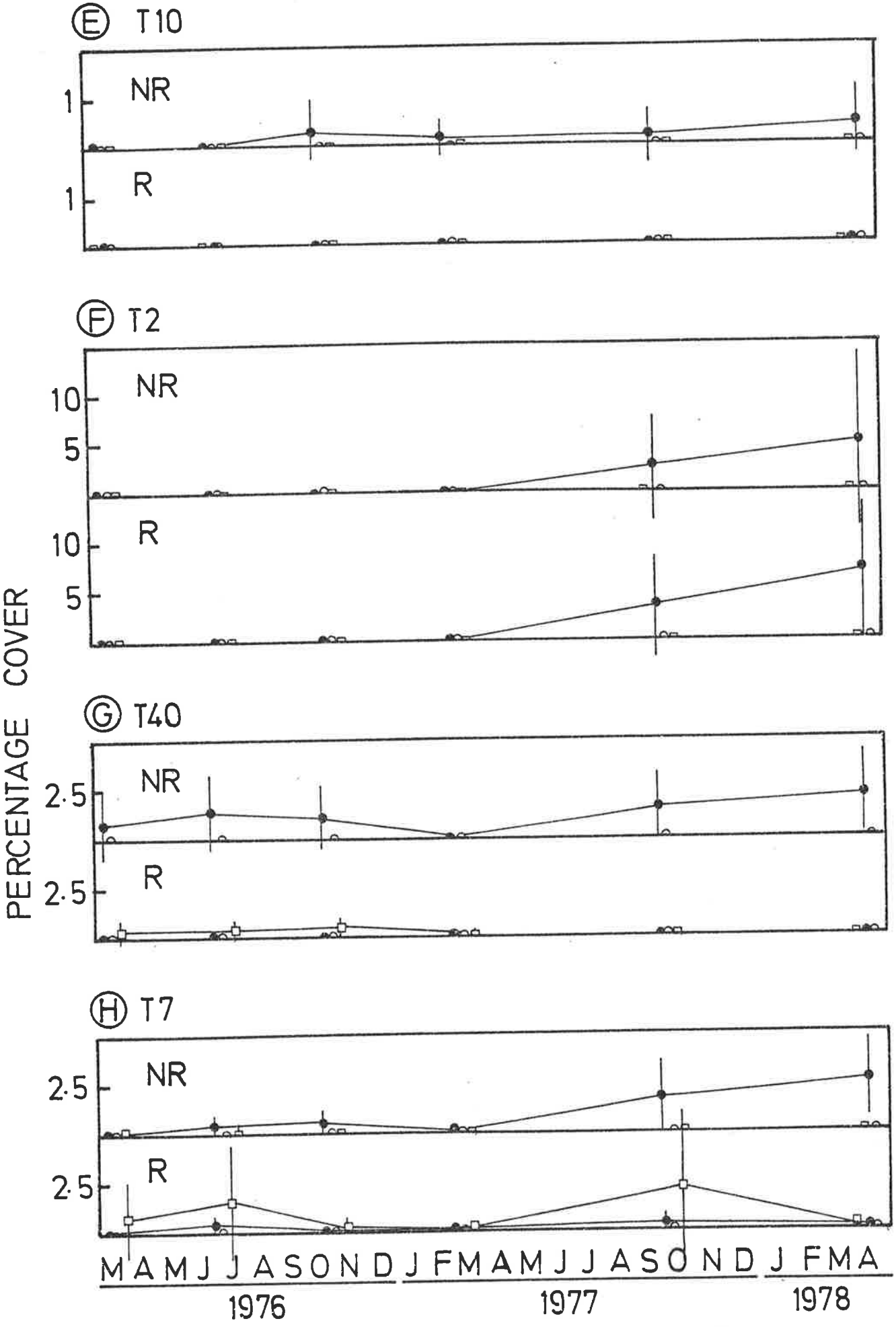

Ⓔ T10
NR
1
R
1
Ⓕ T2
NR
10
5
R
10
5
Ⓖ T40
NR
2·5
R
2·5
Ⓗ T7
NR
2·5
R
2·5
PERCENTAGE COVER
M A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 6.5I, J The mean and standard deviation (vertical line) of the percentage cover of

I. T28 *Cnemidocarpa etheridgii*

J. TW3/4 *Galeolaria* spp.

in six experimental treatments at Rapid Bay on every sample date.

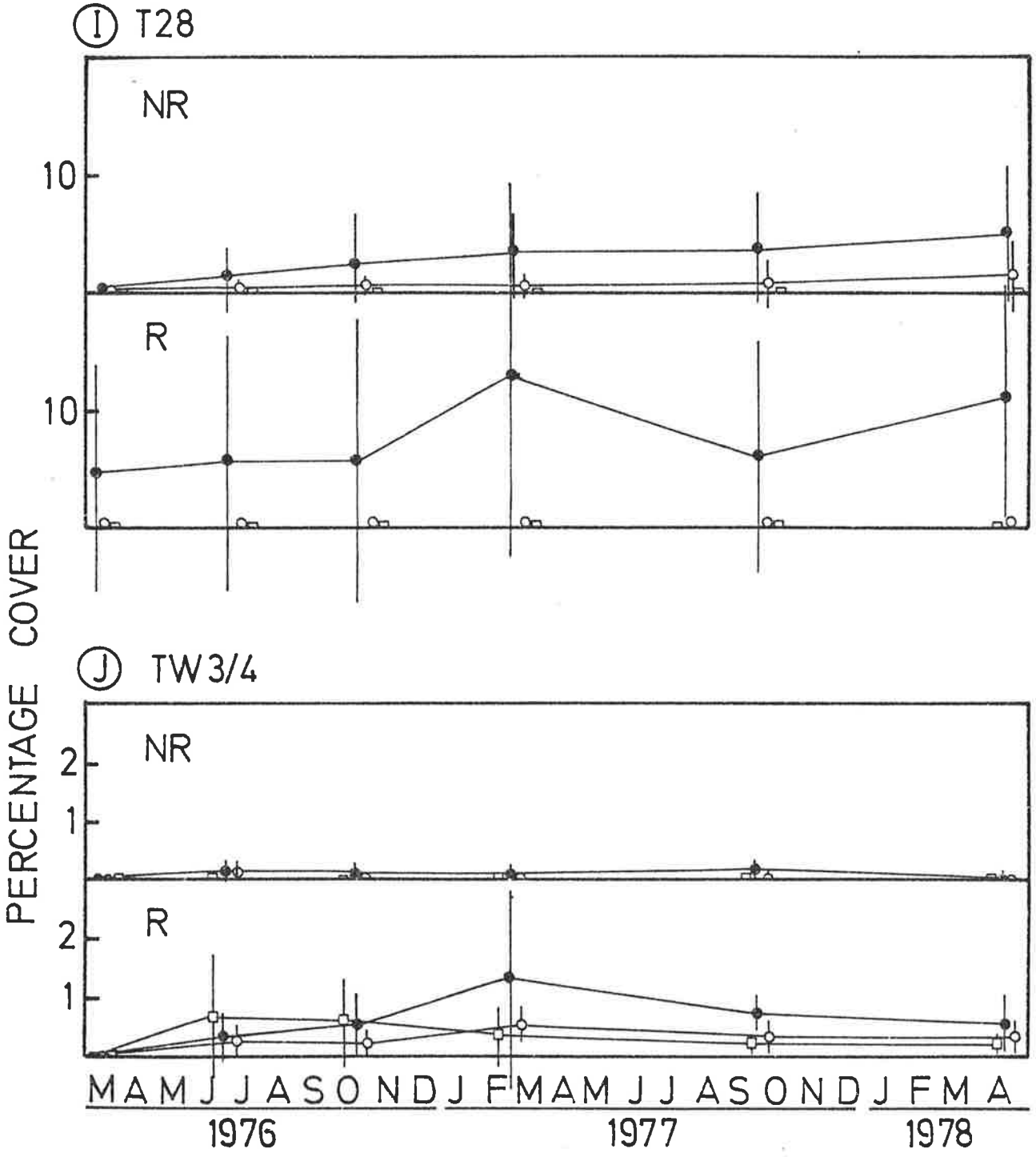

(I) T28
NR
R
10
10
(J) TW3/4
NR
R
2
1
2
1
PERCENTAGE COVER
M A M J J A S O N D J F M A M J J A S O N D J F M A
1976
1977
1978

FIGURE 6.6A The mean and standard deviation (vertical line) of species number in the three experimental treatments at Edithburgh on every sample date.

● mean in exclusion treatments

O mean in control treatment

□ mean in uncaged treatment

FIGURE 6.6B, C, D, E, F

The mean and standard deviation (vertical line) of the percentage cover of

B. Total cover

C. Sponges

D. Colonial tunicates

E. Solitary tunicates

F. Bryozoans

in the three experimental treatments at Edithburgh See caption to Figure 6.6A for further details.

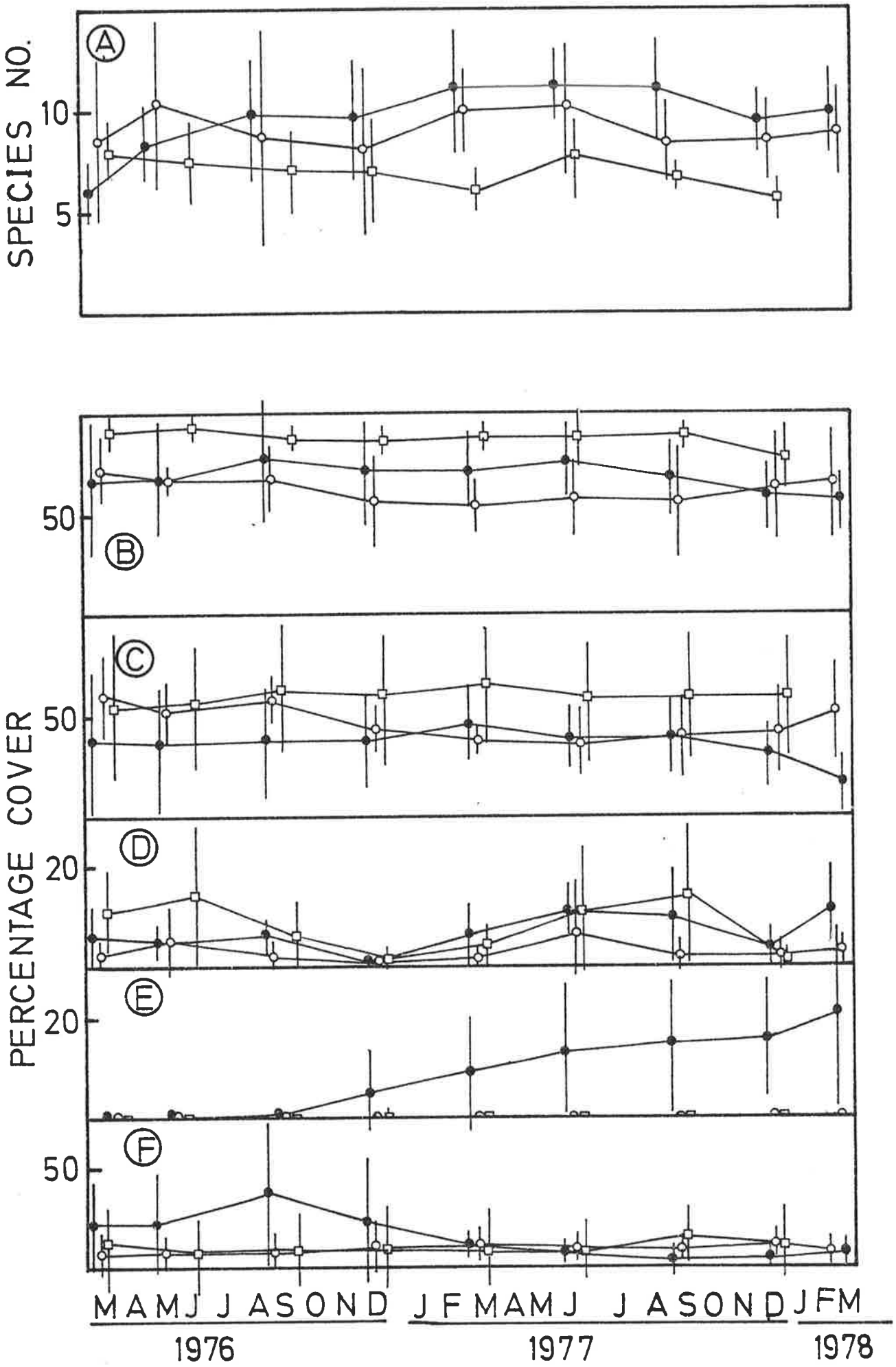

SPECIES NO.
A
10
5
PERCENTAGE COVER
B
50
C
50
D
20
E
20
F
50
M A M J J A S O N D J F M A M J J A S O N D J F M
1976
1977
1978

FIGURE 6.7A, B The mean and standard deviation (vertical line) of the percentage cover of

A. *Didemnum* sp.a

B. individual species of solitary tunicate

T4 *Halocynthia hispida*

T2 *Ascidia gemmata*

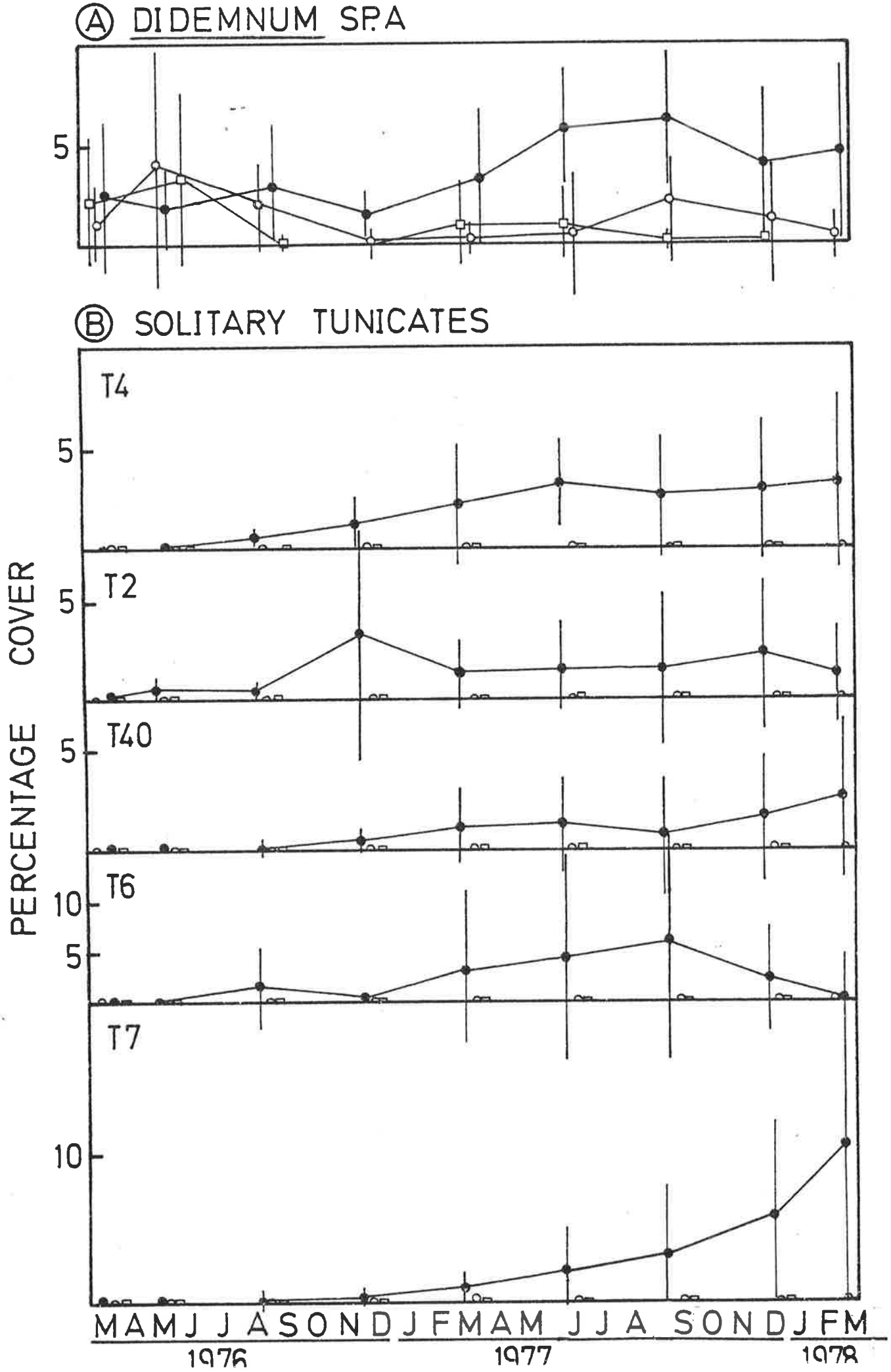
T40 *Ascidia thompsoni*

T6 *Ciona intestinalis*

T7 *Phallusia depressiuscula*

in the three experimental treatments at Edithburgh on every sample date.

See caption to Figure 6.6A for further details.


A DIDEMNUM SP.A
5
B SOLITARY TUNICATES
T4
5
T2
5
T40
5
T6
10
5
T7
10
PERCENTAGE COVER
M A M J J A S O N D J F M A M J J A S O N D J F M
1976
1977
1978

7.0 FINAL DISCUSSION: LONGEVITY AND THE STABILITY OF COMMUNITY STRUCTURE

The purpose of this section is to discuss particular aspects of the results which bear on the generalizations about "fouling communities" and to suggest work which is necessary to test further any conclusions that I make from this discussion. The other aspects of the results have been dealt with in the discussion sections of Chapters 2, 3, 4, 5 and 6.

The evidence presented in Section 2.4.3 demonstrated that the number of species, the list of species and the abundances of most species did not show continuous or drastic changes in the sessile guilds at Rapid Bay and Edithburgh. This pattern of community structure and dynamics is different from that observed by Sutherland (1976) and Sutherland and Karlson (1977) in the fouling community at Beaufort, North Carolina and from that observed by a number of other authors in fouling communities in various temperate and subtropical localities (for references see Sutherland and Karlson 1977). The primary reason for this difference is that the majority of species in these fouling communities had short life spans of a year or less (Sutherland and Karlson 1977) whereas the majority of species in the sessile guilds at Rapid Bay and Edithburgh had life spans in excess of two years (see Tables 3.4 and 3.5 in Section 3.3).

In the communities studied at Beaufort and at other temperate and subtropical localities the abundances of many species show large fluctuations due to the following interaction between short life span and variable and unpredictable larval recruitment. The species with life spans of a year or less free a large proportion

of the substratum each year for new recruits because they senesce and slough off the substratum annually. The identity and abundance of these new recruits may be different from year to year because larval recruitment may often vary dramatically between and within years (Sutherland and Karlson 1977). Thus the abundances of many species show large and unpredictable fluctuations over time. This interaction may also cause the identity of species and the number of species in these fouling communities to vary drastically and unpredictably over time.

Sutherland and Karlson (1977) also propose that the unequal ability of species to invade occupied substratum or to resist larval invasion will produce additional fluctuations in the abundances of species over time.

In summary, in certain temperate and subtropical fouling communities short annual life-span, variable recruitment and the unequal ability of species to invade occupied substratum or to resist larval invasion interact to produce continuous changes in community structure, some aspects of which are unpredictable in the sense that they have the properties of random variables. However it is obvious that without the annual sloughoffs in these communities caused by the short life-spans of their constituent species the effect of the second and third factors would be vastly reduced.

During the entire period of the study at both Edithburgh and Rapid Bay there was no evidence of the simultaneous senescence of a large number of colonies belonging to any perennial species. Unoccupied substratum was not plentiful and did not

show any pronounced variation in abundance throughout a year (Section 2.4.3). Consequently, although variation in larval recruitment between years was observed in both sessile guilds (Edithburgh Section 4.3.1.2 Appendix IIIa; Rapid Bay Section 5.3.2) there was little opportunity for it to contribute to substantial variations in the abundances of species between years. This statement depends on the assumption that the resident adults were inhibiting larval invasion.

Casual observations suggested that recruitment by one species on top of another was a very rare event although a large number of recruits were recorded on unoccupied substratum in both sessile guilds (Edithburgh Section 4.3.1.2; Rapid Bay Section 5.3.2). In particular I never observed bryozoans or *Galeolaria* spp. settled on top of a live colony of sponge, tunicate or *Culicia* sp. in either sessile guild. Bryozoans and *Galeolaria* spp. were abundant colonists of unoccupied substratum in both sessile guilds. This suggests that the resident adults at both sites were resisting larval invasion, thus reducing its potential effect on variations in the composition of the sessile guilds. The results of the *Culicia* sp. removal experiment reported in Section 6.3.2.3 provide some experimental evidence for this proposition in the case of the sessile guild at Rapid Bay. However further experimentation is needed at both sites to determine whether the resident adults resisted larval invasion by all species or only by certain species groups such as bryozoans and serpulids. This could be done, for example, by submerging large numbers of small panels of bare substratum

within the study areas and comparing colonization on them with colonization on the surfaces of established colonies.

The capacity for rapid vegetative growth shown by the majority of species in the sessile guilds at Rapid Bay and Edithburgh (Section 3.3.2.1) is an additional factor which reduced the effect of variability in larval recruitment on the structure of the sessile guilds. The results of the artificial patch experiments at Edithburgh demonstrated that most of the free space available in this sessile guild will ultimately be reoccupied by the lateral expansion of established sponge colonies (Section 4.4.2). Similarly the unsuccessful *Culicia* sp. removal experiment at Rapid Bay reported in Section 6.3.2 indicated that most free space available in this sessile guild will be reoccupied by the lateral extension of established colonies of *Culicia* sp. In contrast, sessile species at Beaufort, North Carolina rarely invade unoccupied substratum by vegetative growth (Sutherland 1976). Thus, at Edithburgh and Rapid Bay larval recruitment will play a less important role in the reoccupation of free space than in fouling communities such as that at Beaufort.

In summary this study has identified two aspects of the life histories of most species in the sessile guilds at Rapid Bay and Edithburgh which are responsible for the greater stability of these guilds in comparison to other temperate and subtropical fouling communities. These are 1) perennial life-span which is at least greater than two years 2) capacity for rapid vegetative growth. I acknowledge that these factors may not be the only

ones responsible for the lack of rapid changes in the structure of these two sessile guilds. However I consider perennial life-span to be the most important factor because it prevents the occurence of catastrophic annual "slough-offs."

This conclusion leads one to ask the following question: why should a greater proportion of the species in the sessile guilds at Rapid Bay and Edithburgh be long lived than in the fouling communities at other temperate and subtropical localities? The results of other investigations and various theoretical formulations suggest three hypothesis. They are not necessarily mutually exclusive and are as follows:

1) The subtidal sessile fauna and flora found at Edithburgh and Rapid Bay have evolved under conditions which favour long lived perennials whereas the subtidal fauna and flora at other localities have evolved under conditions which favour annuals.
2) The large size of the pilings at Rapid Bay and Edithburgh biased the species sampled towards those with perennial life spans whereas the smaller artificial substrata used at other localities biased the species sampled towards those with life spans of a year or less.
3) The long period of submergence of the pilings at Rapid Bay and Edithburgh biased the species sampled towards those with perennial life-spans whereas the comparatively brief period of submergence of the artificial substrata used at other localities biased the species sampled towards those with life spans of a year or less. I shall now examine the available

evidence for each of these hypotheses in turn.

1) Short or annual life spans are thought to be selected for in high disturbance environments and longevity is thought to be selected for in low disturbance environments (Grassle and Sanders 1973, Grime 1977, Vermeij 1978, Whittaker and Goodman 1979). As pointed out in Section 1.1 the term disturbance refers to a wide range of phenomena which cause the destruction of plant or animal biomass. Some examples are extreme seasonal fluctuations in climate, the activities of herbivores and predators and natural catastrophies such as violent storms and fires.

Whether the majority of sessile species found in the subtidal zones at Edithburgh and Rapid Bay have evolved under conditions of low disturbance is impossible to prove. However it is noteworthy that there is an ample supply of large and stable natural substrata in the form of reefs and rocky drop offs from cliffs along the coastline near both sites. Consequently neither of the species assemblages has been restricted to small transient substrata such as rocks and shells that would have favoured the evolution of species with short life spans, rapid maturation and high reproductive output (Grime 1977, Sutherland and Karlson 1977, Whittaker and Goodman 1979). In contrast the natural substrata available to the species assemblages found at Beaufort are small transient substrata such as shell debris on channel bottoms (Karlson 1978).

Additionally occasional measurements made during the study period suggested that at both Edithburgh and Rapid Bay water temperatures ranged from approximately 11^{o}C-12^{o}C in Winter to 20^{o}C-

21°C in Summer and that the annual range of water salinity lay between 35‰ and 40‰ (Butler pers. comm.). This suggests that disturbances in the form of extreme fluctuations of either of these environmental parameters are not an annual event at either pier and occur rarely, if at all. Annual fluctuations in water temperature and salinity at Beaufort are at least twice as large as those estimated for the south australian sites (see Sutherland and Karlson 1977).

These observations suggest that the species assemblage at Beaufort evolved in an environment subject to more frequent disturbance than the species assemblages at Edithburgh and Rapid Bay. This is consistent with the first hypothesis.

Also it is worth noting that "stress-tolerant" organisms are also thought to be long lived (Grime 1977, Vermeij 1979). However I have no evidence indicating that the organisms in the south australian guilds have evolved in conditions of greater stress than those in other fouling communities, particularly at Beaufort, with one possible exception. Vermeij (1978, pp. 171) suggests that caves are often stressful habitats in the marine environment because of chronically low food supplies. Small caves, crevices and overhangs are common in the reefs and cliffs near the south australian sites. This is not the case, for example, at Beaufort (Karlson 1978).

In relation to the preceding considerations it should be pointed out that the majority of species at Bodega Bay, California have similar life-history characteristics to those at Beaufort even though the environmental conditions are very different

at this locality (Boyd 1972 referenced in Sutherland and Karlson 1977). This indicates that there is not a simple and direct relationship between the values, ranges and/or patterns of variation of the physical parameters of the subtidal environment and the evolution of the life history patterns of the species which inhabit it. As Whittaker and Goodman (1979) pointed out "a wide spectrum of demographies may evolve as an expression of niche differentiation in adaptive response to what is superficially a common environment."

2) Species with opportunistic life-histories characterized by short life spans, high reproductive rates and poor interference capacity have been shown to recruit preferentially onto smaller substrata when several different sized substrata are available (Jackson 1977a, Keough pers. comm.). In particular at Edithburgh relatively short lived species (18 months or less) such as some bryozoans and serpulids colonize small substrata in much higher numbers than they colonize large substrata (Keough pers. comm.). Moreover these species are at least twice as abundant on the small shells (300cm^2 in area) of *Pinna bicolor* individuals adjacent to Edithburgh pier than they are on the pilings themselves. (Kay and Keough In prep.). Long lived species such as sponges make up less than 25% of the occupied space on the *Pinna bicolor* shells.

These observations suggest that in a given locality species with short life spans will be more abundant on small substrata than large substrata. Furthermore there is likely to be more short lived species on the small substrata.

The pilings at Edithburgh and Rapid Bay are much larger than the artificial plates typically used in studies of fouling communities (e.g. see Sutherland 1974, 1975, 1976, 1978, Sutherland and Karlson 1977, Osman 1977, Anger 1978, Russ In press). This fact in combination with the preceding considerations is consistent with the second hypothesis.

3) Both Harris (1978) and Karlson (1978) have reported that the most abundant species on old pier pilings are long-lived while those on more recently submerged pier pilings are short lived. It is noteworthy that Karlson's (1978) investigation was carried out at Beaufort and one long lived species, the colonial hydroid *Hydractinia echinata*, which was rarely recorded on artificial plates covered approximately 30% of the substratum on 12 year old pilings.

Additionally both Osman (1977) and Anger (1978) report that species with opportunistic life histories are most abundant on newly submerged substrata. The monopolization of the long term panels at Rapid Bay by the comparatively short-lived members of the sessile guild on the pilings for approximately one and a half years after submergence (see Section 5.3.1) parallels these observations. *Culicia* sp. the most abundant long-lived member of this sessile guild did not colonize the panels until they had been submerged for at least one and a half years. Furthermore this species increased in abundance very slowly after initial recruitment.

These observations suggest that in a given locality species with long life spans will be more abundant on substrata which

have been submerged for a long period of time than on substrata which have been submerged for a relatively short period of time. The pilings at Edithburgh and Rapid Bay have been submerged for at least 15 years whereas the artificial plates typically used in studies of fouling communities have not been submerged for longer than four years (e.g. see Sutherland 1974, 1975, 1976, 1978, Sutherland and Karlson 1977, Osman 1977, Anger 1978, Russ In press). The preceding facts and observations are consistent with the third hypothesis.

Finally it is worth noting that the catastrophic slough off from the long term panels at Rapid Bay was caused by the death of the colonial tunicate *Pycnoclavella diminuta* which was very abundant on the panels (see Section 5.3.1). A similar slough off from the pilings was not observed because this short lived species was comparatively rare in the established guild on the pilings (see Appendix Ib, T19).

Given the available evidence the most likely explanation for the preponderance of perennial species in the sessile guilds at Edithburgh and Rapid Bay is a combination of hypotheses two and three. Clearly there are a number of short lived species in the species assemblages at Edithburgh and Rapid Bay which are more abundant on small substrata or recently submerged substrata respectively than on pier pilings. These species may have evolved in disturbed environments provided by small and transient substrata such as small rocks and shell debris on the ocean floor. Whatever the evolutionary history of the species assemblages at Edithburgh and Rapid Bay the evidence strongly suggests that the

large size and the long period of submergence of the pier pilings has biased the species sampled towards those with perennial life spans.

Further experimentation and observations are required to provide clear disproof of hypothesis one and to determine more accurately the effect of substratum size and age on the structure and organization of the sessile guilds at Edithburgh and Rapid Bay. Comparison of the structure and dynamics of the sessile guilds on substrata of different ages and sizes at both sites would be essential to resolve these questions. A more thorough knowledge of the life histories and natural habitats of the sessile species in these areas would also be necessary.

APPENDIX Ia The mean and standard deviation (parenthesis) of the percentage cover of (1) each species
(2) the following three phyletic groups: sponges, tunicates and bryozoans
(3) all species present (total cover)
(4) total space unoccupied
calculated from the 16 permanent quadrats at Edithburgh pier for all quarterly sample dates. The code numbers given for individual species are the same as those used in Table 2.1.

	16/12/75	14/03/76	20/06/76	25/09/76	06/12/76	18/03/77	11/06/77	26/09/77	27/12/77
Sponges SP1	4.87 (8.77)	4.59 (10.65)	5.24 (12.27)	6.77 (13.84)	7.85 (14.72)	8.18 (15.25)	7.32 (13.92)	8.88 (11.26)	8.00 (10.40)
SP2	2.83 (7.14)	3.13 (6.55)	3.99 (7.82)	4.36 (8.00)	4.21 (7.81)	4.23 (8.31)	4.13 (7.84)	4.01 (7.69)	3.01 (5.45)
SP14	0.01 (0.39)	0.50 (2.0)	0.52 (2.07)	0.63 (2.50)	0.64 (2.58)	0.86 (3.42)	0.89 (3.57)	1.07 (4.06)	0.95 (3.80)
SP30	24.82 (28.22)	22.77 (27.76)	20.57 (25.73)	23.07 (27.89)	21.10 (25.10)	20.39 (22.57)	20.40 (24.39)	21.69 (25.08)	23.60 (25.85)
SP20	4.34 (14.58)	3.48 (9.36)	3.88 (9.44)	6.72 (15.99)	9.93 (22.12)	8.21 (21.49)	6.51 (12.91)	9.20 (20.03)	11.66 (23.97)
SP47	2.25 (3.37)	2.51 (4.65)	3.50 (5.47)	4.04 (5.98)	4.41 (6.51)	4.72 (8.16)	3.07 (5.66)	2.71 (5.78)	2.95 (5.74)
SP13	2.62 (3.91)	3.08 (5.03)	4.16 (6.09)	3.68 (5.40)	2.95 (5.30)	4.17 (8.07)	3.41 (5.99)	3.77 (5.24)	3.70 (5.69)

	SAMPLE DATES								
	16/12/75	14/03/76	20/06/76	25/09/76	06/12/76	18/03/77	11/06/77	26/09/77	27/12/77
Sponges SP49	0.25 (0.84)	0.12 (0.36)	0.42 (1.20)	0.48 (1.72)	0.37 (1.14)	1.46 (5.14)	2.00 (3.67)	1.48 (5.50)	2.29 (8.74)
SP50	0.0 (0.0)	0.17 (0.67)	0.0 (0.0)	0.0 (0.0)	0.39 (1.56)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
SP51	0.29 (1.16)	0.11 (0.43)	0.14 (0.56)	0.17 (0.67)	0.12 (0.47)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.04 (0.18)
SP18	0.30 (0.97)	0.44 (1.74)	0.20 (0.69)	0.46 (1.44)	0.44 (1.54)	0.31 (1.21)	0.59 (2.36)	0.20 (0.82)	0.25 (0.98)
SP46	0.10 (0.40)	0.0 (0.0)	0.29 (0.84)	0.0 (0.0)	0.03 (0.13)	0.01 (0.04)	0.03 (0.11)	0.0 (0.0)	0.0 (0.0)
SP5	1.67 (2.54)	6.24 (8.78)	5.98 (9.25)	3.70 (5.67)	4.29 (10.23)	4.52 (9.57)	3.45 (6.02)	2.97 (5.33)	3.74 (7.21)
SP55	0.26 (1.05)	0.55 (2.18)	0.55 (2.21)	0.89 (3.56)	1.25 (4.99)	0.84 (3.35)	1.06 (4.25)	0.79 (3.18)	0.70 (2.81)
SP57	0.32 (1.29)	0.39 (1.57)	0.10 (0.40)	0.36 (1.42)	0.49 (1.97)	0.66 (2.66)	0.53 (2.11)	0.46 (1.83)	0.46 (1.84)
SP58	0.14 (0.56)	0.49 (1.96)	0.26 (1.05)	0.30 (1.18)	0.25 (1.01)	0.25 (1.00)	0.58 (1.62)	0.77 (2.26)	0.82 (2.29)
SP62	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.05 (0.15)	0.13 (0.35)	0.10 (0.41)	0.0 (0.0)	0.25 (0.77)	0.35 (1.41)
SP63	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.45 (1.36)	0.09 (0.26)	0.25 (0.94)	0.66 (2.48)	0.46 (1.50)	0.04 (0.13)
TOTAL	45.17 (32.48)	48.55 (31.64)	49.80 (30.69)	56.11 (25.50)	58.93 (27.15)	59.15 (26.63)	56.63 (26.12)	58.67 (24.15)	62.70 (24.34)

	SAMPLE DATES								
	16/12/75	14/03/76	20/06/76	25/09/76	06/12/76	18/03/77	11/06/77	26/09/77	27/12/77
Bryozoans B1	5.81 (10.41)	4.66 (10.27)	4.45 (9.39)	4.47 (9.02)	5.41 (11.36)	5.17 (9.50)	4.58 (8.60)	4.54 (7.97)	4.75 (9.05)
B2	4.31 (5.84)	3.86 (4.73)	2.94 (4.09)	3.39 (4.43)	2.01 (2.92)	2.17 (2.82)	2.61 (3.98)	2.80 (5.06)	4.45 (7.77)
B3	1.85 (2.88)	2.00 (2.89)	1.63 (3.95)	2.61 (4.87)	2.15 (4.82)	0.59 (1.06)	0.47 (0.69)	0.88 (1.26)	0.65 (1.08)
B4	0.22 (0.80)	0.29 (1.08)	0.55 (1.42)	0.26 (0.64)	0.17 (0.44)	0.05 (0.12)	0.14 (0.34)	0.16 (0.26)	0.15 (0.36)
B5	0.22 (0.88)	0.37 (1.46)	0.36 (1.35)	0.34 (1.36)	0.0 (0.0)	0.05 (0.22)	0.14 (0.55)	0.18 (0.71)	0.11 (0.46)
B6	0.30 (1.00)	0.31 (1.00)	1.30 (4.19)	0.10 (0.41	0.72 (1.64)	0.05 (0.19)	0.03 (0.10)	0.07 (0.29	0.0 (0.0)
B7	1.03 (3.09)	1.09 (2.97)	0.92 (2.00)	1.08 (2.28)	0.96 (2.12)	0.83 (1.84)	0.62 (1.43)	1.15 (2.21)	1.14 (2.02)
TOTAL	13.74 (14.74)	12.58 (13.66)	12.15 (13.47)	12.24 (13.26)	11.41 (13.48)	8.90 (11.25)	8.59 (10.33)	9.79 (10.80)	11.25 (12.01)
Tunicates T10	0.0 (0.0)	0.03 (0.12)	0.03 (0.12)	0.03 (0.12)	0.03 (0.12)	0.03 (0.12)	0.03 (0.12)	0.03 (0.12)	0.03 (0.12)
T11	0.10 (0.31)	1.86 (5.67)	2.07 (7.14)	6.89 (21.91)	0.03 (0.14)	2.63 (7.88)	1.99 (7.95)	2.15 (8.28)	0.0 (0.0)
T5	0.01 (0.02)	0.0 (0.0)	0.07 (0.11)	0.06 (0.09)	0.04 (0.09)	0.09 (0.12)	0.08 (0.11)	0.08 (0.10)	0.09 (0.13)

	SAMPLE DATES								
	16/12/75	14/03/76	20/06/76	25/09/76	06/12/76	18/03/77	11/06/77	26/09/77	27/12/77
Tunicates T9	0.53 (1.60)	3.86 (7.05)	5.06 (10.18)	1.42 (4.26)	0.16 (0.34)	0.67 (1.41)	2.38 (4.95)	3.25 (6.98)	0.15 (0.34)
T18	3.79 (7.32)	5.52 (7.46)	6.91 (5.39)	3.24 (4.78)	3.38 (4.38)	1.66 (2.78)	3.88 (5.20)	1.85 (2.92)	0.80 (2.01)
TOTAL	4.43 (8.03)	11.28 (9.32)	14.13 (10.44)	11.65 (21.11)	3.64 (4.26)	5.08 (8.93)	8.35 (8.49)	7.35 (9.56)	1.06 (1.95)
OTHER M18	0.09 (0.13)	0.09 (0.12)	0.05 (0.08)	0.03 (0.04)	0.04 (0.06)	0.04 (0.07)	0.05 (0.08)	0.06 (0.12)	0.02 (0.06)
J5	5.08 (18.83)	4.75 (18.85)	4.35 (17.34)	3.60 (14.32)	4.00 (16.21)	3.80 (14.98)	3.05 (12.04)	3.51 (13.51)	2.59 (9.66)
TW3/4	0.12 (0.31)	0.12 (0.27)	0.01 (0.05)	0.14 (0.29)	0.20 (0.53)	0.0 (0.0)	0.17 (0.40)	0.08 (0.27)	0.15 (0.40)
Total Cover	68.62 (29.69)	77.36 (22.80)	80.50 (17.65)	83.76 (11.92)	78.22 (21.30)	76.97 (15.71)	76.83 (16.92)	79.46 (14.85)	77.77 (14.27)
Total space unoccupied	31.38 (29.69)	22.64 (22.80)	19.50 (17.65)	16.24 (11.92)	21.78 (21.30)	23.03 (15.71)	23.17 (16.92)	20.54 (14.85)	22.23 (14.27)

APPENDIX Ib The mean and standard deviation (parenthesis) of the percentage cover of (1) each species
(2) the following three phyletic groups: sponges, tunicates and bryozoans
(3) all species present (total cover)
(4) skeletal remains of *Culicia* sp.
(5) bare piling
(6) total space unoccupied

calculated from the 16 permanent quadrats at Rapid Bay pier for all quarterly sample dates. The code numbers given for individual species are the same as those used in Table 2.1.

	SAMPLE DATES							
	14/06/76	04/09/76	28/12/76	29/03/77	20/06/77	29/09/77	04/12/77	01/03/78
Sponges SP1	4.06 (7.73)	2.09 (5.93)	3.87 (8.09)	3.70 (6.23)	2.54 (3.37)	2.19 (3.75)	2.15 (3.63)	2.93 (4.34)
SP2	0.18 (0.38)	0.28 (0.52)	0.14 (0.37)	0.71 (2.17)	0.28 (0.44)	0.50 (1.08)	0.48 (1.35)	0.04 (0.17)
SP14	0.01 (0.02)	0.01 (0.02)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
SP30	0.89 (2.67)	0.98 (3.39)	1.19 (4.77)	1.37 (5.50)	0.81 (3.26)	0.65 (2.60)	0.92 (3.67)	0.82 (2.62)
SP20	0.15 (0.44)	0.28 (0.77)	0.10 (0.28)	0.24 (0.97)	0.26 (0.94)	0.36 (1.05)	0.24 (0.69)	0.07 (0.29)

	SAMPLE DATES							
	14/06/76	04/09/76	28/12/76	29/03/77	20/06/77	29/09/77	04/12/77	01/03/78
Sponges SP13	1.00 (4.14)	1.55 (3.60)	0.94 (1.48)	0.94 (1.25)	1.37 (2.15)	1.51 (2.26)	0.86 (1.70)	0.14 (0.14)
SP49	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.07 (0.26)	0.08 (0.31)	0.0 (0.0)
SP18	0.21 (0.82)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
SP33	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.02 (0.09)	0.12 (0.49)	0.01 (0.27)	0.24 (0.96)
SP54	0.10 (0.31)	0.14 (0.26)	0.05 (0.21)	0.19 (0.46)	0.02 (0.07)	0.01 (0.05)	0.03 (0.12)	0.0 (0.0)
SP46	0.12 (0.47)	0.04 (0.15)	0.24 (0.87)	0.17 (0.57)	0.16 (0.65)	0.16 (0.63)	0.06 (0.24)	0.0 (0.0)
SP5	1.34 (1.19)	1.11 (0.88)	0.82 (1.00)	1.34 (1.74)	1.33 (1.51)	1.07 (1.13)	0.95 (1.32)	2.39 (2.86)
SP36	0.73 (1.66)	0.10 (0.28)	0.10 (0.41)	0.17 (0.70)	0.0 (0.0)	0.12 (0.32)	0.25 (0.79)	0.10 (0.40)
SP4	4.70 (5.04)	5.28 (5.98)	3.55 (3.12)	2.20 (2.54)	1.96 (2.43)	3.17 (4.16)	3.33 (3.68)	3.55 (6.84)
SP8	0.39 (1.22)	0.80 (1.73)	0.62 (1.82)	0.47 (1.88)	0.69 (2.49)	0.92 (2.99)	0.82 (3.20)	0.86 (3.13)
SP56	0.09 (0.37)	1.34 (2.55)	0.14 (0.58)	0.82 (1.84)	0.37 (1.18)	0.36 (1.06)	0.77 (2.44)	0.34 (1.04)

	SAMPLE DATES							
	14/06/76	04/09/76	28/12/76	29/03/77	20/06/77	29/09/77	04/12/77	01/03/78
Sponges								
SP7	1.38 (5.15)	0.90 (3.39)	0.74 (2.85)	0.68 (2.47)	1.06 (3.64)	0.94 (3.24)	0.99 (3.27)	0.75 (2.35)
SP57	0.0 (0.0)	0.0 (0.0)	0.04 (0.15)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.05 (0.19)	0.05 (0.21)
SP58	0.04 (0.16)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.02)	0.0 (0.0)	0.0 (0.0)	0.78 (3.14)
SP59	0.09 (0.36)	0.18 (0.72)	0.28 (1.12)	0.31 (1.26)	0.67 (2.69)	0.45 (1.80)	0.56 (2.22)	0.42 (1.68)
SP63	0.27 (1.10)	0.0 (0.0)	0.11 (0.45)	0.11 (0.44)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
SP64	0.09 (0.29)	0.02 (0.08)	0.0 (0.0)	0.0 (0.0)	0.12 (0.30)	0.11 (0.26)	0.10 (0.28)	0.13 (0.40)
TOTAL	16.82 (8.50)	15.92 (8.94)	12.94 (9.48)	13.43 (8.28)	11.69 (6.70)	12.70 (8.42)	12.69 (6.56)	13.61 (10.81)
Tunicates								
T28	1.74 (3.40)	2.65 (5.28)	2.46 (5.89)	2.50 (6.23)	2.14 (5.07)	1.38 (4.99)	1.38 (4.99)	1.38 (4.99)
T40	0.29 (1.16)	0.91 (1.93)	0.92 (2.09)	1.07 (2.58)	1.08 (2.45)	0.89 (2.05)	0.89 (2.05)	0.58 (1.30)
T11	1.51 (3.30)	2.85 (5.14)	0.05 (0.07)	0.38 (1.03)	0.36 (0.93)	1.12 (2.04)	0.18 (0.42)	0.78 (1.66)
T13	0.51 (0.80)	2.35 (3.21)	2.52 (5.26)	0.38 (0.69)	0.23 (0.38)	0.55 (1.13)	1.12 (1.70)	0.36 (0.51)

	SAMPLE DATES							
	14/06/76	04/09/76	28/12/76	29/03/77	20/06/77	29/09/77	04/12/77	01/03/78
Tunicates T5	0.07 (0.10)	0.06 (0.09)	0.06 (0.09)	0.03 (0.05)	0.05 (0.07)	0.08 (0.10)	0.02 (0.04)	0.05 (0.07)
T19	2.67 (4.72)	1.62 (4.72)	0.10 (0.27)	1.30 (2.20)	2.89 (4.62)	3.28 (5.69)	1.41 (5.62)	0.0 (0.0)
T34	0.04 (0.14)	0.07 (0.28)	0.03 (0.11)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
T12	2.68 (10.72)	2.79 (10.02)	1.79 (6.76)	2.17 (7.91)	1.22 (4.38)	0.33 (0.98)	0.03 (0.13)	0.18 (0.74)
T9	2.25 (3.25)	1.28 (1.31)	1.23 (1.47)	0.73 (1.09)	0.46 (1.06)	1.50 (1.90)	0.81 (1.16)	0.49 (0.74)
T18	0.29 (0.99)	0.30 (1.12)	0.22 (0.59)	0.12 (0.50)	0.55 (1.28)	0.47 (1.86)	0.0 (0.0)	0.02 (0.06)
T32	0.39 (1.38)	0.68 (2.17)	1.32 (3.68)	1.07 (4.12)	1.88 (7.52)	1.91 (7.43)	1.83 (7.31)	0.74 (1.45)
T25	0.81 (2.00)	2.22 (3.68)	2.28 (3.64)	0.32 (0.82)	0.58 (0.98)	0.80 (1.61)	0.47 (0.84)	0.22 (0.51)
T8	0.21 (0.82)	0.07 (0.28)	0.0 (0.0)	0.32 (0.96)	0.12 (0.48)	0.0 (0.0)	0.0 (0.0)	0.50 (1.99)
T37	0.0 (0.0)	0.05 (0.19)	0.12 (0.48)	0.03 (0.13)	0.0 (0.0)	0.13 (0.36)	0.14 (0.44)	0.0 (0.0)
T23	3.34 (8.45)	2.66 (5.89)	3.13 (8.47)	4.86 (10.77)	1.28 (3.49)	0.47 (1.24)	0.85 (2.76)	0.0 (0.0)
TOTAL	16.78 (11.72)	20.54 (13.40)	16.20 (14.56)	15.26 (15.22)	12.85 (13.70)	12.89 (14.52)	9.11 (13.51)	5.30 (6.56)

	SAMPLE DATES							
	14/06/76	04/09/76	28/12/76	29/03/77	20/06/77	29/09/77	04/12/77	01/03/78
Bryozoans B1	0.27 (0.52)	0.25 (0.47)	0.10 (0.21)	0.04 (0.16)	0.03 (0.13)	0.08 (0.31)	0.04 (0.14)	0.0 (0.0)
B2	0.06 (0.25)	0.06 (0.24)	0.0 (0.0)	0.19 (0.77)	0.05 (0.19)	0.0 (0.0)	0.0 (0.0)	0.01 (0.03)
B3	0.06 (0.25)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
B4	0.88 (1.95)	0.60 (1.14)	1.01 (2.06)	0.33 (1.03)	0.67 (1.33)	0.82 (1.87)	0.33 (0.93)	0.18 (0.57)
B6	0.0 (0.0)	0.09 (0.34)	0.12 (0.48)	0.12 (0.48)	0.12 (0.48)	0.06 (0.22)	0.0 (0.0)	0.0 (0.0)
B7	0.0 (0.0)	0.0 (0.0)	0.02 (0.07)	0.0 (0.0)	0.0 (0.0)	0.05 (0.20)	0.11 (0.33)	0.0 (0.0)
TOTAL	1.27 (2.34)	0.99 (1.21)	1.24 (2.20)	0.69 (1.54)	0.87 (1.55)	1.00 (1.83)	0.48 (0.94)	0.19 (0.58)
Other J5	61.0 (18.17)	56.76 (20.53)	61.95 (24.67)	66.04 (21.74)	68.54 (22.31)	67.13 (21.74)	70.27 (23.95)	74.05 (25.38)
M18	0.01 (0.02)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
TW3/4	0.07 (0.10)	0.04 (0.07)	0.05 (0.08)	0.06 (0.11)	0.04 (0.09)	0.02 (0.08)	0.01 (0.02)	0.01 (0.02)
TW2	0.04 (0.15)	0.0 (0.0)	0.16 (0.65)	0.0 (0.0)	0.0 (0.0)	0.02 (0.09)	0.30 (1.18)	0.11 (0.44)

	SAMPLE DATES							
	14/06/76	04/09/76	28/12/76	29/03/77	20/06/77	29/09/77	04/12/77	01/03/78
Other A14	0.0 (0.0)	0.0 (0.0)	0.01 (0.02)	0.0 (0.0)	0.0 (0.03)	0.02 (0.03)	0.01 (0.03)	0.01 (0.02)
A17	0.0 (0.0)	0.0 (0.0)	0.01 (0.02)	0.01 (0.02)	0.01 (0.02)	0.34 (1.32)	0.0 (0.0)	0.0 (0.0)
A16	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.01 (0.03)
Skeletal remains of *Culicia* sp.	3.31 (6.57)	5.58 (11.02)	7.14 (17.34)	4.29 (11.94)	5.86 (9.16)	5.52 (12.07)	7.12 (16.34)	6.73 (16.45)
bare piling	0.72 (1.52)	0.17 (0.69)	0.32 (1.26)	0.23 (0.73)	0.15 (0.50)	0.37 (0.85)	0.03 (0.14)	0.0 (0.0)
total space unoccupied	4.03 (6.35)	5.75 (11.10)	7.46 (17.24)	4.52 (11.87)	6.01 (9.22)	5.89 (12.04)	7.15 (16.33)	6.73 (16.45)
Total Cover	95.97 (6.35)	94.25 (11.10)	92.54 (17.24)	95.48 (11.87)	93.99 (9.22)	94.11 (12.04)	92.85 (16.33)	93.27 (16.45)

APPENDIX Ic The distributions of species abundances at Edithburgh and Rapid Bay on the seven sample dates common to both sites. The number of species found within individual 1% class intervals are given in the Table. The column headed L.L. refers to the Lower Limit of the largest 1% class interval represented on the given sample date. The column headed No. sp. refers to the number of species found within that largest class interval.

A. Edithburgh: abundances expressed as a percentage of the total available substratum

B. Rapid Bay: abundances expressed as a percentage of the total available substratum

C. Edithburgh: abundances expressed as a percentage of the occupied substratum

D. Rapid Bay: abundances expressed as a percentage of the occupied substratum

Sample Date	LOWER LIMITS OF 1% Class Intervals																
	0.00	1.00	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0	No. sp.	L.L.
A.																	
20/06/76	16	2	2	3	3	3	1									1	20.0
25/09/76	16	2	1	5	3		3									1	23.0
06/12/76	19	1	3	1	4	1		1		1						1	21.0
18/03/77	17	2	2	1	4	1			2							1	20.0
11/06/77	15	2	3	5	2		1			1						1	20.0
26/09/77	14	4	4	4	1				1	1						1	21.0
27/12/77	17	2	4	3					1			1				1	23.0
B.																	
14/06/76	31	4	3	1	1											1	61.0
04/09/76	23	5	7			1										1	56.0
28/12/76	24	4	3	3												1	61.0
29/03/77	25	5	3	1	1											1	66.0
20/06/77	23	8	3													1	67.0
29/09/77	30	6	1	2												1	70.0
04/12/77	30	4	1	1												1	70.0

Sample Date	LOWER LIMITS OF 1% Class Intervals															No. sp.	L.L.
	0.00	1.00	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0	10.0	11.0	12.0	13.0	14.0		
C.																	
20/06/79	14	2	2	1	3	3	2	1	1						1	1	25.0
25/09/76	15	3	0	2	5	2			3							1	27.0
06/12/76	18	2	2	1	1	5					1		1			1	26.0
18/03/77	14	4	2	1	1	3	2				2					1	26.0
11/06/77	15	2	2	3	4	1			1				1			1	26.0
26/09/77	15	2	3	2	4	1						2				1	27.0
27/12/77	14	4	1	3	2	1	1				1			1		1	30.0
D.																	
14/06/76	29	4	4	1	2											1	63.0
04/09/76	23	6	4	2		1										1	58.0
28/12/76	23	6	4	1												1	73.0
29/03/77	25	5	3	1		1										1	69.0
20/06/77	23	6	4	1												1	71.0
29/09/77	29	6	2	2												1	75.0
04/12/77	28	6	1	1												1	79.0

Appendix Id Community flux at Edithburgh and Rapid Bay. All values have been calculated for standard 90-day intervals. For all sample intervals at each site, the following has been tabulated:

(1) Community flux for each permanent quadrat

(2) The mean and standard deviation of community flux calculated for each permanent quadrat

(3) Community flux calculated using the arithmetic means of percentage cover from the 16 permanent quadrats

Edithburgh

SAMPLE INTERVALS

Quadrat	16/12/75 to 14/03/76	14/03/76 to 20/06/76	20/06/76 to 25/09/76	25/09/76 to 06/12/76	06/12/76 to 18/03/77	18/03/77 to 11/06/77	11/06/77 to 26/09/77	26/09/77 to 27/12/77
1	72.23	21.15	37.36	57.66	36.99	27.18	16.39	26.18
2	62.17	30.31	25.95	24.89	28.32	35.21	18.55	45.51
3	15.97	23.92	27.18	32.96	20.77	13.02	5.34	25.67
4	24.42	16.32	6.29	19.13	25.47	18.35	18.84	21.97
5	19.09	20.57	27.30	14.55	30.47	24.86	29.56	13.26
6	28.12	20.92	17.71	25.43	19.50	30.40	13.68	15.29
7	40.78	16.92	14.00	16.71	17.44	29.68	14.93	31.15
8	29.75	26.86	49.35	14.77	34.06	53.66	22.83	41.56
9	42.15	16.84	14.53	15.24	16.30	20.75	30.36	29.16
10	50.23	26.41	59.54	40.68	12.23	47.77	26.38	25.05
11	91.51	20.47	44.12	42.00	48.29	64.19	26.88	54.13
12	22.49	24.39	21.78	30.81	49.38	27.85	30.84	47.52
13	36.35	44.35	47.21	63.91	20.20	22.58	34.10	20.09
14	51.54	40.52	38.04	71.39	43.93	31.22	17.35	23.91
15	14.82	16.82	33.32	33.82	18.58	19.46	12.94	26.08
16	24.56	20.54	26.87	39.19	35.86	41.83	12.73	44.11
Mean	39.14	24.21	30.66	37.07	28.61	31.75	20.11	30.67
(S.D.)	(21.77)	(8.91)	(14.57)	(20.92)	(11.77)	(13.85)	(7.86)	(12.18)
Calculated from Means	20.97	13.21	26.51	28.44	13.63	16.49	10.64	20.35

Rapid Bay

SAMPLE INTERVALS

Quadrat ARM	FACE	14/06/76 to 04/09/76	04/09/76 to 28/12/76	28/12/76 to 29/03/77	29/03/77 to 20/06/77	20/06/77 to 29/09/77	29/09/77 to 04/12/77	04/12/77 to 01/03/78
E	1	32.02	34.55	22.47	13.50	15.69	23.54	10.74
E	1	15.82	8.48	30.17	18.41	16.22	36.96	30.50
E	2	39.90	35.46	38.32	48.77	41.39	40.80	31.31
E	2	45.61	26.00	38.74	42.40	18.45	21.58	24.21
E	3	18.63	22.14	11.78	35.80	12.99	16.76	24.19
E	3	43.55	34.68	27.32	53.06	11.74	40.92	96.04
E	4	37.38	21.64	20.45	27.38	21.99	38.52	19.32
E	4	64.42	48.94	18.75	27.03	32.40	55.64	33.60
W	1	11.64	6.72	21.01	3.86	3.36	5.86	10.64
W	1	44.77	35.16	19.13	25.03	10.29	20.26	11.62
W	2	36.34	18.96	25.01	4.38	38.54	32.76	28.70
W	2	47.69	37.90	30.08	29.46	11.21	11.57	19.17
W	3	22.75	17.96	5.06	6.93	6.88	16.25	24.60
W	3	54.70	56.88	14.62	12.96	23.88	53.52	26.94
W	4	68.54	44.56	26.87	73.01	28.46	51.16	31.95
W	4	28.97	9.46	20.37	37.95	32.58	24.02	20.89
	Mean	38.30	28.72	23.14	28.78	20.38	30.63	27.78
	(S.D.)	(16.44)	(14.76)	(8.91)	(19.27)	(11.47)	(15.38)	(19.67)
Calculated from means		25.66	19.53	18.45	17.52	9.26	21.05	14.76

APPENDIX IIa: Overgrowth (the amount of live tissue overgrown during a period of 90 days, expressed as a percentage of quadrat) for each permanent quadrat for all sample intervals at Edithburgh and Rapid Bay.

Edithburgh

SIXTEEN PERMANENT QUADRATS

Sample Interval	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
16/12/75 14/03/76	8.36	1.58	2.14	3.56	5.42	8.01	1.17	1.22	3.97	0.13	14.19	7.76	0.63	21.86	3.48	3.82
14/03/76 20/06/76	11.51	5.29	7.74	7.63	2.73	4.16	8.44	1.10	1.89	2.29	9.96	9.74	12.74	5.92	2.97	10.16
20/06/76 25/09/76	22.91	4.63	4.25	3.65	1.13	0.90	3.32	20.75	2.61	8.07	1.26	4.81	4.10	8.69	2.75	4.45
25/09/76 06/12/76	6.85	3.39	6.18	5.70	1.34	9.84	5.22	0.0	3.10	3.94	1.31	6.08	1.55	10.24	9.92	4.05
06/12/76 18/03/77	7.77	4.71	1.96	0.56	0.74	0.82	3.69	0.69	5.20	5.24	2.48	1.26	1.19	10.39	4.07	9.82
18/03/77 11/06/77	13.44	7.97	6.65	5.60	0.91	2.27	2.46	0.29	1.71	2.25	17.09	11.37	5.53	8.82	2.80	18.61
11/06/77 26/09/77	1.69	1.49	0.32	0.93	2.10	3.81	3.73	1.13	2.38	0.0	11.37	10.40	0.36	3.48	3.75	1.81
26/09/77 27/12/77	4.06	3.23	0.45	5.56	0.0	2.68	5.64	4.28	5.42	1.86	0.21	4.57	6.03	7.98	1.10	0.0

Rapid Bay

SIXTEEN PERMANENT QUADRATS

Sample Interval	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
14/06/76 04/09/76	2.13	3.92	1.65	1.89	4.65	4.74	4.46	6.12	3.37	7.03	0.04	5.21	1.66	14.00	7.94	2.67
04/09/76 28/12/76	5.54	1.96	1.79	0.43	0.0	0.0	0.62	1.06	2.42	0.74	4.29	2.37	0.50	0.0	6.90	2.27
28/12/76 29/03/77	1.98	0.0	2.88	7.20	0.57	0.66	1.61	1.42	0.42	6.56	0.0	1.03	1.75	1.57	1.10	1.68
29/03/77 20/06/77	4.16	0.0	0.24	0.73	0.42	4.21	1.25	0.33	0.0	0.0	1.49	1.12	1.49	1.99	2.78	0.0
20/06/77 29/09/77	2.96	1.58	0.45	0.0	1.43	1.94	0.61	1.57	1.42	0.0	1.81	1.81	1.60	9.00	2.97	1.20
29/09/77 04/12/77	1.88	3.22	0.0	3.10	2.30	1.93	0.0	0.0	0.11	0.0	8.00	2.39	3.58	3.16	5.48	2.07
04/12/77 01/03/78	1.98	0.0	0.06	0.35	2.85	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.05	1.10	0.0	0.0

APPENDIX IIb. Growth rates (mm/day) of individual colonies at Edithburgh and Rapid Bay

Species		Growth Rate of individual colonies mm/day Edithburgh	Rapid Bay
Sponges			
SP1	*Aplysilla rosea*	0.16, 0.18, 0.26, 0.11, 0.33 0.30, 0.54, 0.23, 0.40	0.44, 0.17, 0.08, 0.14
SP2	*Aplysilla sulphurea*	0.47, 0.50	
SP30	*Crella* sp.	0.57, 0.39, 1.09, 0.47, 0.38 1.11, 0.72, 0.24, 0.58, 1.06 0.57, 0.49, 0.97	0.24, 0.30
SP20	*Mycale* sp.	0.66, 0.27, 2.11 0.58, 1.79 0.90 2.14 0.97	
SP13	*Callyspongia* sp.	0.70, 0.79, 0.56	0.56, 0.36
SP47	*Chondropsis* sp.	0.48, 0.72, 0.84, 0.38	
SP49	*Lissodendoryx* sp.	0.71, 0.54	
SP5	Red encrusting sponge	0.61, 0.60, 0.72, 0.72, 0.48 0.77, 0.56, 0.92	0.22, 0.31, 0.61, 0.44
SP4	Green encrusting sponge		0.39, 0.56, 0.33, 0.44, 0.50, 0.62
Tunicates			
T11	*Botrylloides leachii*	0.86, 1.32, 0.36, 0.97, 1.94 1.19	0.39, 0.67, 0.22, 0.33, 0.56, 0.33
T9	*Didemnum* sp.a	0.80, 0.63, 0.89, 0.71, 0.55 1.79	0.28, 0.78, 0.44, 0.52
T18	*Didemnum* sp.b	1.19, 1.96, 0.96, 2.00, 1.53 1.05	
T25	*Atapazoa fantasiana*		0.17, 0.33, 0.17, 0.19 0.20
T19	*Pycnoclavella diminuta*		0.64, 0.60, 0.39, 0.28 0.96, 0.72, 0.44, 0.71 0.78
T23	Chestnut encrusting tunicate		0.78, 0.56, 0.59, 0.28

Species		Growth Rate of individual colonies mm/day Edithburgh	Rapid Bay
Bryozoans			
B1	*Celleporaria fusca*	0.18, 0.23, 0.27, 0.12, 0.17 0.08, 0.16	
B2	*Celleporaria valligera*	0.18, 0.20, 0.13, 0.11, 0.14 0.09, 0.10, 0.10, 0.06, 0.05 0.04	
B3	*Celleporaria pigmentaria*	0.18, 0.19, 0.11, 0.06, 0.06 0.21, 0.14, 0.18	
B4	*Smittina raigii*	0.18, 0.25, 0.22, 0.32, 0.13 0.13, 0.12 0.10, 0.18	
B6	*Biflustra perfragillis*	0.20, 0.17, 0.16, 0.32, 0.12 0.07, 0.07, 0.29	0.08, 0.19, 0.22
B7	Mustard encrusting bryozoan	0.09, 0.06, 0.18, 0.08, 0.05 0.04	0.09, 0.11, 0.17
J5	*Culicia* sp.	0.19, 0.31, 0.40	0.50, 0.88, 1.11, 0.73 1.22, 1.00, 1.67, 1.56 0.78

Appendix IIIa The mean and standard deviation (parenthesis) of the colonization rate (number of colonists/600cm^2/30 days) of individual species on each sample interval for each of the four groups of patches in Experiment I at Edithburgh. Sample size=5 for all species on all groups on all sample intervals with the following exceptions

February group	06/12/76-11/01/77 11/01/77-08/02/77	sample size = 4
August group	25/09/76-30/10/76 11/06/77-20/08/77	sample size = 4

February group

SAMPLE INTERVALS

	26/02/76 to 14/03/76	14/03/76 to 17/04/76	17/04/76 to 15/05/76	15/05/76 to 20/06/76	20/06/76 to 17/07/76	17/07/76 to 24/08/76	24/08/76 to 25/09/76	25/09/76 to 30/10/76	30/10/76 to 06/12/76	06/12/76 to 11/01/77	11/01/77 to 08/02/77
Sponges SP1	7.68 (17.19)	1.94 (2.28)	2.33 (4.69)	1.32 (2.39)	1.33 (2.97)	0.75 (1.06)	0.40 (0.55)	1.20 (2.69)	1.99 (4.46)	0.62 (1.25)	0.8 (1.61)
SP30	2.00 (4.48)	0.18 (0.40)	0.0	0.66 (0.98)	0.44 (0.61)	0.75 (1.97)	0.20 (0.45)	0.69 (1.12)	0.62 (0.80)	0.83 (1.17)	1.07 (1.51)
SP47	0.67 (0.67)	0.18 (0.18)	0.97 (0.97)	1.32 (2.39)	0.44 (0.99)	0.60 (0.83)	0.0	0.34 (0.77)	0.21 (0.42)	0.21 (0.42)	0.27 (0.54)
SP20	0.0	3.17 (2.53)	0.0	1.32 (1.80)	0.67 (0.99)	0.15 (0.34)	0.80 (1.10)	0.52 (2.20)	0.17 (0.37)	1.00 (1.82)	0.54 (1.07)
SP5	0.33 (0.75)	1.23 (1.34)	0.78 (0.81)	0.0	0.22 (0.50)	0.15 (0.34)	1.00 (2.24)	0.52 (2.20)	0.17 (0.37)	0.21 (0.42)	0.54 (1.01)
SP49	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.27 (0.48)

February group
SAMPLE INTERVALS

	26/02/76 to 14/03/76	14/03/76 to 17/04/76	17/04/76 to 15/05/76	15/05/76 to 20/06/76	20/06/76 to 17/07/76	17/07/76 to 24/08/76	24/08/76 to 25/09/76	25/09/76 to 30/10/76	30/10/76 to 06/12/76	06/12/76 to 11/01/77	11/01/77 to 08/02/77
Tunicates											
T5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.66 (1.65)	0.0	0.27 (0.54)
T18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.86 (1.93)	0.17 (0.37)	0.21 (0.42)	1.07 (2.14)
T9	8.02 (13.33)	1.76 (2.41)	3.77 (5.55)	2.64 (5.91)	4.22 (7.04)	2.85 (6.38)	2.80 (6.26)	0.17 (1.31)	2.82 (4.37)	7.06 (14.11)	5.62 (11.24)
Bryozoans											
B1	0.0	0.0	0.19 (0.44)	0.44 (0.98)	0.0	0.45 (0.67)	0.0	0.34 (0.41)	0.33 (0.46)	0.21 (0.42)	0.0
B2	0.67 (1.49)	0.53 (0.78)	0.19 (0.44)	1.54 (0.98)	1.11 (0.79)	0.60 (0.63)	0.80 (1.30)	0.34 (0.77)	0.66 (0.70)	0.21 (0.42)	0.0
B3	0.0	0.0	0.0	0.66 (1.47)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
B4	0.0	0.18 (0.40)	2.72 (1.99)	1.54 (1.84)	0.89 (0.93)	0.15 (0.34)	1.00 (1.22)	5.20 (1.15)	0.50 (1.10)	2.08 (2.49)	0.0
B5	0.0	0.0	0.0	0.22 (0.50)	0.0	0.0	0.0	0.0	0.33 (0.74)	0.0	0.0
B6	0.0	0.67 (1.49)	0.78 (1.74)	0.0	0.22 (0.50)	0.0	0.20 (0.45)	0.0	0.33 (0.46)	0.0	0.0
B7	0.67 (1.49)	0.0	0.58 (0.86)	0.22 (0.50)	0.44 (0.99)	0.30 (0.41)	0.20 (0.45)	0.0	0.0	0.0	0.0
Other											
J5	5.01 (11.21)	0.70 (1.58)	0.78 (1.74)	0.66 (1.47)	0.22 (0.50)	0.15 (0.34)	0.20 (0.45)	1.03 (2.30)	1.33 (2.97)	0.17 (0.37)	2.57 (5.75)

May group
SAMPLE INTERVALS

	18/05/76 to 20/06/76	20/06/76 to 17/07/76	17/07/76 to 24/08/76	24/08/76 to 25/09/76	25/09/76 to 30/10/76	30/10/76 to 06/12/76	06/12/76 to 11/01/77	11/01/77 to 08/02/77	08/02/77 to 18/03/77	18/03/77 to 18/04/77	18/04/77 to 15/05/77
Sponges											
SP1	0.28 (0.55)	4.22 (9.44)	1.35 (3.02)	2.20 (4.92)	0.0	0.0	0.66 (1.49)	0.0	0.0	0.0	0.92 (2.06)
SP30	0.0	0.0	0.0	0.60 (1.34)	0.69 (1.54)	0.0	0.0	0.21 (0.48)	0.0	0.19 (0.44)	0.0
SP13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.19 (0.44)	0.23 (0.52)
SP47	0.83 (1.65)	0.0	0.15 (0.34)	0.0	0.0	0.0	0.33 (0.74)	0.0	0.0	0.0	0.0
SP20	1.10 (2.20)	0.0	0.15 (0.34)	0.0	0.0	0.0	0.17 (0.37)	1.93 (4.30)	0.21 (0.48)	0.78 (1.74)	0.46 (0.02)
SP5	1.65 (2.10)	0.0	0.30 (0.41)	0.0	0.17 (0.39)	(0.83 (1.86)	0.0	0.0	0.0	0.0	0.0
SP49	0.0	0.0	0.0	0.0	0.0	0.0	0.17 (0.37)	0.0	0.0	0.0	0.0
Tunicates											
T5	0.0	0.0	0.0	0.0	0.0	0.0	0.83 (1.44)	0.0	0.43 (0.95)	0.0	0.0
T11	0.0	0.0	0.0	0.0	0.0	0.0	0.66 (1.49)	0.0	0.0	0.19 (0.44)	2.30 (5.14)
T18	0.0	0.0	0.15 (0.34)	0.0	0.0	0.66 (1.08)	0.0	0.0	1.50 (1.43)	1.36 (1.89)	1.84 (3.51)
T9	0.28 (0.55)	1.55 (3.47)	0.0	0.20 (3.94)	0.17 (0.39)	3.44 (7.42)	3.32 (4.23)	1.93 (2.19)	1.71 (2.46)	0.97 (2.17)	0.46 (1.02)

May group

	SAMPLE INTERVALS										
	18/05/76 to 20/06/76	20/06/76 to 17/07/76	17/07/76 to 24/08/76	24/08/76 to 25/09/76	25/09/76 to 30/10/76	30/10/76 to 06/12/76	06/12/76 to 11/01/77	11/01/77 to 08/02/77	08/02/77 to 18/03/77	18/03/77 to 18/04/77	18/04/77 to 15/05/77
Bryozoans B1	0.0	0.0	0.0	1.20 (2.17)	1.03 (1.12)	1.83 (1.80)	1.99 (1.26)	0.43 (0.95)	0.21 (0.48)	0.39 (0.86)	0.0
B2	0.83 (1.06)	1.78 (3.39)	0.60 (0.98)	0.0	0.69 (1.12)	0.66 (0.70)	3.82 (4.69)	3.32 (5.81)	2.35 (2.96)	1.55 (2.12)	0.92 (1.50)
B3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.21 (0.48)	0.0	0.0
B4	0.83 (1.65)	1.11 (2.49)	0.15 (0.34)	0.20 (0.45)	0.17 (0.39)	0.17 (0.37)	0.50 (0.74)	0.21 (0.48)	0.0	0.0	0.0
B6	0.0	0.0	0.0	0.0	0.52 (1.15)	0.83 (1.86)	0.66 (1.08)	0.0	0.0	0.0	0.0
B7	0.28 (0.55)	0.0	0.15 (0.34)	0.0	0.0	0.17 (0.37)	0.0	0.43 (0.95)	0.0	0.39 (0.86)	0.0
Other Tw3/4	1.38 (1.06)	0.44 (0.99)	0.30 (0.67)	0.60 (0.89)	0.34 (0.47)	0.0	0.17 (0.37)	0.0	0.0	0.0	0.0

August group
SAMPLE INTERVALS

	26/08/76 to 25/09/76	25/09/76 to 30/10/76	30/10/76 to 06/12/76	06/12/76 to 11/01/77	11/01/77 to 08/02/77	08/02/77 to 18/03/77	18/03/77 to 18/04/77	18/04/77 to 15/05/77	15/05/77 to 11/06/77	11/06/77 to 20/08/77
Sponges										
SP1	0.02 (0.45)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SP30	0.0	0.0	0.0	0.0	0.86 (1.92)	0.21 (0.48)	0.0	1.38 (1.89)	0.0	0.0
SP13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.43 (0.95)	0.0
SP47	0.0	0.0	0.0	0.0	0.0	0.0	0.19 (0.44)	0.0	0.0	0.0
SP20	0.0	0.0	0.0	0.0	0.0	0.43 (0.95)	0.0	0.0	0.0	0.0
SP49	0.0	0.0	0.0	0.0	0.0	0.0	0.78 (1.74)	0.23 (0.52)	0.64 (1.43)	0.0
SP60	0.0	0.0	0.0	1.99 (3.60)	1.93 (3.24)	0.64 (1.43)	0.0	0.0	0.0	0.0
Tunicates										
T5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.11 (0.22)
T18	0.0	0.0	0.17 (0.37)	0.33 (0.74)	1.50 (3.35)	0.43 (0.95)	0.39 (0.86)	0.0	0.21 (0.48)	0.11 (0.19)
T9	0.0	0.86 (1.49)	5.15 (8.99)	8.80 (6.45)	17.55 (22.05)	4.07 (4.17)	1.16 (1.59)	0.46 (1.02)	1.71 (3.83)	0.54 (0.54)

August group
SAMPLE INTERVALS

	26/08/76 to 25/09/76	25/09/76 to 30/10/76	30/10/76 to 06/12/76	06/12/76 to 11/01/77	11/01/77 to 08/02/77	08/02/77 to 18/03/77	18/03/77 to 18/04/77	18/04/77 to 15/05/77	15/05/77 to 11/06/77	11/06/77 to 20/08/77
Bryozoans B1	0.0	0.69 (1.54)	1.66 (2.87)	1.99 (2.79)	1.93 (4.30)	0.64 (0.59)	0.39 (0.86)	0.23 (0.52)	0.0	0.0
B2	0.0	0.0	0.33 (0.74)	1.00 (1.49)	0.64 (0.95)	1.50 (1.63)	0.78 (1.26)	0.23 (0.52)	0.0	0.09 (0.19)
B3	0.0	0.0	0.0	0.33 (0.46)	0.64 (1.43)	1.07 (1.01)	0.0	0.0	0.0	0.0
B4	0.0	0.17 (0.39)	0.33 (0.46)	2.99 (4.26)	1.28 (2.32)	0.86 (1.92)	0.0	0.0	1.01 (2.26)	0.0
B5	0.20 (0.45)	0.0	0.17 (0.37)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
B6	0.60 (1.34)	0.0	0.66 (0.91)	0.50 (1.11)	0.21 (0.48)	0.0	0.0	0.0	0.0	0.0
Other TW3/4	0.0	1.55 (2.14)	1.16 (1.82)	0.33 (0.46)	3.64 (4.52)	0.0	0.58 (1.30)	0.0	0.0	0.0

December group
SAMPLE INTERVALS

	06/12/76 to 11/01/77	11/01/77 to 08/02/77	08/02/77 to 18/03/77	18/03/77 to 18/04/77	18/04/77 to 14/05/77	14/05/77 to 11/06/77	11/06/77 to 20/08/77	20/08/77 to 26/09/77	26/09/77 to 22/10/77	22/10/77 to 27/11/77
Sponges SP1	1.49 (2.90)	0.0	0.0	0.39 (0.53)	0.23 (0.52)	0.0	0.0	0.16 (0.36)	0.0	0.23 (0.52)
SP2	0.0	0.36 (0.95)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SP20	0.0	0.21 (0.05)	0.21 (0.05)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SP49	0.0	0.0	0.0	0.39 (0.86)	0.0	0.0	0.0	0.0	0.0	0.0
Tunicates T5	0.0	0.43 (0.95)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
T18	0.0	0.0	0.0	0.39 (0.86)	0.0	0.0	0.0	0.16 (0.36)	0.46 (0.63)	0.23 (0.52)
T19	1.00 (2.22)	2.57 (3.60)	5.56 (3.33)	1.94 (1.94)	0.92 (0.97)	3.21 (4.78)	1.55 (2.33)	0.49 (0.72)	0.0	0.0
Bryozoans B1	0.50 (1.11)	0.64 (0.95)	0.21 (0.48)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
B2	0.0	10.49 (19.37)	4.71 (6.44)	3.10 (3.17)	2.53 (2.06)	2.35 (3.73)	0.60 (0.94)	0.69 (0.68)	0.46 (0.63)	0.23 (0.52)
B3	0.0	0.0	0.21 (0.48)	1.36 (3.04)	0.92 (2.06)	0.64 (1.43)	0.09 (0.19)	0.0	0.0	0.0

December group
SAMPLE INTERVALS

	06/12/76 to 11/01/77	11/01/77 to 08/02/77	08/02/77 to 18/03/77	18/03/77 to 18/04/77	18/04/77 to 14/05/77	14/05/77 to 11/06/77	11/06/77 to 20/08/77	20/08/77 to 26/09/77	26/09/77 to 22/10/77	22/10/77 to 27/11/77
Bryozoans B4	0.0	1.93 (3.73)	0.43 (0.59)	0.58 (0.86)	0.23 (0.52)	0.86 (0.09)	0.09 (0.19)	0.0	0.0	0.0
B5	0.0	0.21 (0.48)	0.21 (0.48)	0.19 (0.44)	0.0	0.21 (0.48)	0.0	0.0	0.69 (1.54)	0.0
B6	0.0	0.0	0.43 (0.95)	0.0	0.23 (0.52)	0.0	0.0	0.0	0.0	0.0
Other J5	0.0	0.0	0.0	0.0	0.0	1.07 (2.40)	0.0	0.0	0.0	0.0
TW3/4	3.32 (7.42)	16.69 (19.54)	0.21 (0.05)	0.0	0.23 (0.52)	0.0	0.0	0.0	0.46 (1.02)	0.0

Appendix IIIb The coefficents of determination (r^2) of the power curves fitted to the percentage cover data from Experiment II at Edithburgh and the number of days for the patches used in Experiment II at Edithburgh to be half covered by sponge.

	Coefficient of Determination (r^2)						Days for patch to be half covered					
Surrounding sp.	*Mycale* sp.			*Crella* sp.			*Mycale* sp.			*Crella* sp.		
Patch size cm	10 x 10	25 x 25	50 x 50	10 x 10	25 x 25	50 x 50	10 x 10	25 x 25	50 x 50	10 x 10	25 x 25	50 x 50
For average %	0.74	0.96	0.96	0.97	0.97	0.98						
For individual patches	0.76	0.85	0.89	0.97	0.82	0.87	15.12	19.97	66.90	31.01	109.35	284.20
	1.0	0.91	0.85	0.89	0.91	0.96	7.74	72.64	25.27	32.26	302.01	157.20
	1.0	0.88	0.94	0.83	0.93	0.95	18.44	20.17	71.67	78.48	142.95	432.99
	1.0	0.90	0.98	0.76	0.64		0.10	11.21	98.47	66.03	77.41	
	1.0	0.87		0.86	0.94		22.69	10.13		45.41	135.25	
	1.0	0.96		0.85	0.87		6.48	34.87		48.99	128.19	
	0.88	0.93		0.93	0.96		1.84	18.32		92.93	60.02	
	1.0	0.95		0.88	0.95		0.10	50.82		55.81	58.42	
	1.0	0.80		0.93	0.90		5.97	57.02		30.90	67.38	
	1.0	1.0		0.98	0.86		6.30	28.11		22.31	204.90	

Appendix IIIc The mean and standard deviation (parenthesis) of the percentage cover for individual species which colonized the patches in Experiment II at Edithburgh on each sample date after initial patch clearance. Sample dates 20/09/77 and 24/03/78 are 161 days and 329 days after initial clearance of patches respectively (see Table 4.5). There were no colonists on the 10cm x 10cm and 25cm x 25cm sized patches surrounded by *Mycale* sp.; therefore they are not included in the Appendix. Sample sizes are as follows:

4 for *Mycale* sp. 50cm x 50cm group
10 for *Crella* sp. 10cm x 10cm group
10 for *Crella* sp. 25cm x 25cm group
3 for *Crella* sp. 50cm x 50cm group

for all species on all sample dates.

Group of patches	Species	SAMPLE DATE 14/05/77	20/06/77	20/08/77	20/09/77	22/10/77	27/11/77	28/12/77	28/01/78	25/02/78	24/03/78
	Bryozoans										
Mycale sp. 50cm x 50cm	B1	0.0	0.0	0.0	0.14 (0.17)	0.37 (0.37)	0.43 (0.73)	0.42 (0.64)	0.15 (0.30)	0.0	0.0
	B4	0.0	0.0	0.0	0.02 (0.03)	1.01 (1.36)	0.16 (0.32)	0.10 (0.21)	0.0	0.0	0.0
	Serpulids										
	TW3/4	0.0	0.0	0.0	0.04 (0.05)	0.04 (0.05)	0.02 (0.02)	0.01 (0.02)	0.0	0.0	0.0

Group of patches	Species	SAMPLE DATE 14/05/77	20/06/77	20/08/77	20/09/77	22/10/77	27/11/77	28/12/77	28/01/78	25/02/78	24/03/78
	Bryozoan										
Crella sp. 10cm x 10cm	B1	0.0	0.0	0.31 (0.98)	0.56 (1.76)	0.54 (1.48)	0.0	0.0	0.0	0.0	0.0
	Sponges										
Crella sp. 25cm x 25cm	SP5	0.49 (1.56)	0.18 (0.56)	0.26 (0.82)	0.11 (0.36)	0.34 (1.08)	0.62 (1.94)	0.49 (1.55)	0.75 (2.36)	1.0 (3.01)	1.0 (3.07)
	SP13	0.0	0.04 (0.13)	0.08 (0.25)	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Tunicates										
	T5	0.0	0.0	0.0	0.0	0.0	0.07 (0.18)	0.17 (0.37)	0.27 (0.63)	0.28 (0.58)	0.12 (0.37)
	T9	0.03 (0.09)	0.06 (0.18)	0.28 (0.90)	0.15 (0.42)	0.18 (0.45)	0.16 (0.40)	0.03 (0.10)	0.50 (0.79)	1.14 (2.33)	2.03 (5.47)
	Bryozoans										
	B1	0.0	0.0	0.23 (0.29)	0.72 (0.83)	1.33 (1.63)	2.45 (3.29)	3.68 (5.28)	3.61 (5.27)	3.17 (4.69)	2.47 (4.62)
	B2	0.0	0.0	0.0	0.0	0.07 (0.23)	0.27 (0.61)	0.65 (1.40)	0.53 (0.84)	0.62 (0.95)	0.62 (1.04)
	B3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.04 (0.13)	0.12 (0.35)	0.0
	B4	0.0	0.06 (0.20)	0.31 (0.51)	0.53 (0.75)	1.18 (1.36)	2.03 (2.94)	1.42 (2.31)	1.04 (1.87)	1.14 (2.44)	0.84 (2.24)
	B5	0.0	0.0	0.01 (0.04)	0.04 (0.12)	0.06 (0.18)	0.26 (0.58)	0.26 (0.82)	0.41 (1.29)	0.50 (1.49)	0.0

Group of patches	Species	SAMPLE DATE 14/05/77	20/06/77	20/08/77	20/09/77	22/10/77	27/11/77	28/12/77	28/01/78	25/02/78	24/03/78
	Serpulids										
	TW3/4	0.0	0.0	0.02 (0.03)	0.06 (0.08)	0.04 (0.07)	0.04 (0.07)	0.03 (0.05)	0.02 (0.03)	0.0	0.0
	Sponges										
Crella sp. 50cm x 50cm	SP1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.32 (0.25)	1.13 (0.70)
	SP5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.32 (1.17	4.73 (5.33)	4.40 (3.81)
	SP13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.21 (0.37)	0.24 (0.42)
	SP20	0.0	0.0	0.0	0.0	0.49 (0.85)	0.91 (1.58)	1.05 (1.81)	0.51 (0.89)	0.88 (1.52)	1.09 (1.89)
	SP47	0.0	0.0	0.51 (0.88)	0.45 (0.77)	0.55 (0.95)	0.76 (1.31)	0.80 (1.39)	1.31 (1.35)	0.86 (0.91)	1.01 (0.90)
	SP49	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.29 (0.50)	0.37 (0.64)
	Tunicates										
	T5	0.0	0.0	0.0	0.0	0.0	0.09 (0.15)	0.24 (0.29)	0.26 (0.28)	0.19 (0.21)	0.20 (0.26)
	T9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.05 (0.08)	0.08 (0.10)	0.06 (0.11)
	T18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.72 (0.69)	0.31 (0.54)

Group of patches	Species	SAMPLE DATE 14/05/77	20/06/77	20/08/77	20/09/77	22/10/77	27/11/77	28/12/77	28/01/78	25/02/78	24/03/78
	Bryozoans										
	B1	0.0	0.04 (0.07)	0.10 (0.15)	0.34 (0.11)	1.23 (0.52)	3.31 (2.06)	4.11 (2.28)	4.94 (2.38)	4.15 (1.44)	4.05 (1.35)
	B2	0.0	0.0	0.0	0.02 (0.03)	0.0	0.07 (0.12)	0.11 (0.13)	0.27 (0.38)	0.89 (0.78)	1.02 (0.83)
	B3	0.0	0.0	0.04 (0.07)	0.11 (0.18)	0.16 (2.8)	0.23 (.39)	0.27 (0.40)	0.44 (0.39)	0.67 (0.37)	0.60 (0.27)
	B4	0.0	0.0	0.02 (0.02)	0.18 (0.08)	0.52 (0.29)	1.06 (0.47)	1.26 (0.89)	0.91 (0.37)	0.60 (0.18)	0.54 (0.19)
	B5	0.0	0.0	0.0	0.0	0.0	0.0	0.11 (0.18)	0.08 (0.14)	0.0	0.0
	B6	0.0	0.0	0.0	0.13 (0.23)	0.06 (0.11)	0.0	0.09 (0.15)	0.13 (0.16)	0.21 (0.18)	0.16 (0.28)
	Serpulids										
	TW3/4	0.0	0.0	0.08 (0.13)	0.09 (0.14)	0.10 (0.14)	0.09 (0.12)	0.06 (0.01)	0.05 (0.06)	0.0	0.01 (0.01)

Appendix IVa. The mean and standard deviation (parenthesis) of percentage cover for each species and the two categories "other bryozoans" (BO) and "coralline red algae" (CR) for the two groups of long-term panels on each sample date. Species code numbers are the same as those used in Table 5.3. Sample sizes are listed in Table 5.1

	March Group Sample Date							
Species	09/06/76	15/09/76	17/12/76	29/03/77	20/06/77	29/09/77	20/01/78	13/04/78
Sponges								
SP1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03 (0.05)
SP55	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.59 (4.48)
SP20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.51 (0.89)
SP13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.20 (0.35)
Tunicates								
T5	0.0	0.0	0.0	0.02 (0.03)	0.03 (0.03)	0.03 (0.03)	0.03 (0.03)	0.02 (0.03)
T11	0.0	0.0	0.51 (1.43)	0.0	0.97 (2.04)	0.0	0.0	0.0
T18	0.0	0.0	0.0	0.0	0.15 (0.37)	0.0	0.0	0.0
T9	0.0	0.13 (0.17)	0.39 (0.41)	2.56 (3.70)	1.02 (2.20)	0.58 (0.40)	0.34 (0.59)	1.81 (1.95)
T19	0.0	0.0	39.57 (22.83)	53.27 (28.66)	60.52 (14.25)	36.60 (32.37)	0.0	0.0
T12	0.0	0.0	0.0	0.05 (0.13)	0.14 (0.33)	0.0	0.0	0.0
T25	0.0	0.0	0.0	0.17 (0.28)	1.71 (3.60)	2.69 (3.17)	0.0	0.0
T20	0.0	0.0	1.62 (4.59)	0.0	0.0	0.0	0.0	0.0

Species	March Group Sample Date 09/06/76	15/09/76	17/12/76	29/03/77	20/06/77	29/09/77	20/01/78	13/04/78
Bryozoans								
B1	0.0	0.05 (0.14)	0.33 (0.92)	0.71 (1.93)	0.64 (0.77)	2.85 (4.87)	1.48 (2.57)	1.07 (1.22)
B2	0.0	0.0	0.07 (0.21)	0.04 (0.12)	0.65 (1.58)	0.13 (0.25)	0.09 (0.16)	0.91 (1.16)
B3	0.0	0.0	0.0	0.25 (0.47)	0.19 (0.45)	0.0	0.0	1.27 (2.21)
B4	0.0	0.15 (0.29)	5.22 (5.56)	6.33 (6.18)	2.14 (2.97)	2.32 (1.75)	1.62 (2.56)	2.52 (3.46)
B5	0.0	0.08 (0.23)	0.0	0.05 (0.13)	0.91 (1.24)	0.51 (1.02)	0.0	0.0
B6	0.0	0.0	4.88 (5.65)	17.82 (9.40)	22.11 (16.19)	23.01 (15.24)	33.26 (13.98)	28.53 (17.10)
B7	0.0	0.0	0.0	0.0	0.07 (0.18)	0.0	0.0	0.0
BO	0.0	0.25 (0.27)	0.46 (0.46)	0.0	0.47 (1.15)	0.0	0.0	0.0
Serpulids								
TW3/4	2.33 (0.94)	8.60 (13.69)	20.89 (19.70)	3.94 (6.16)	6.18 (4.71)	11.44 (11.20)	4.60 (3.13)	1.30 (1.92)
TW2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.76 (0.72)
Algae								
A14	0.0	0.0	0.0	0.03 (0.05)	0.0	0.0	0.0	0.0
CR	0.0	0.0	0.0	0.0	0.0	0.0	11.51 (19.93)	7.08 (7.03)
Cnidarians								
J5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.62 (2.49)

Species	October Group Sample Date 17/12/76	29/03/77	20/06/77	29/09/77	20/01/78	13/04/78
Sponges						
SP1	0.0	0.0	0.01 (0.01)	0.0	0.06 (0.11)	0.29 (0.39)
SP2	0.0	0.0	0.0	0.15 (0.42)	0.0	0.02 (0.04)
SP20	0.0	0.0	0.0	0.0	0.0	0.25 (0.51)
SP13	0.0	0.0	0.0	0.17 (0.47)	0.0	0.08 (0.22)
SP33	0.0	0.0	0.0	0.0	0.18 (0.49)	0.05 (0.15)
SP54	0.0	0.0	0.0	0.04 (0.11)	0.0	0.0
SP5	0.0	0.0	0.03 (0.09)	0.0	0.07 (0.19)	0.11 (0.28)
SP55	0.0	0.0	0.0	0.0	0.0	0.0
SP4	0.0	0.0	0.0	0.39 (1.09)	0.0	0.89 (1.03)
SP7	0.0	0.27 (0.75)	0.0	0.0	0.0	0.39 (1.11)
SP57	0.0	0.0	0.10 (0.28)	0.0	0.0	0.0
Tunicates						
T5	0.0	0.01 (0.02)	0.01 (0.02)	0.01 (0.02)	0.02 (0.03)	0.02 (0.03)
T11	0.0	0.36 (1.03)	0.28 (0.78)	0.37 (1.04)	0.39 (0.91)	0.20 (0.56)
T18	0.0	0.0	0.06 (0.16)	0.0	0.0	0.0
T9	0.0	2.67 (2.80)	8.85 (11.18)	4.81 (5.56)	0.55 (0.79)	5.39 (9.97)

Species	October Group Sample Date 17/12/76	29/03/77	20/06/77	29/09/77	20/01/78	13/04/78
Tunicates						
T23	0.0	0.0	0.24 (0.53)	0.0	0.32 (0.91)	0.45 (0.91)
T19	0.0	27.44 (22.16)	52.72 (31.59)	54.0 (19.79)	36.44 (41.19)	0.20 (0.56)
T37	0.0	0.0	0.0	0.25 (0.69)	0.0	0.0
T12	0.0	0.0	0.17 (0.38)	0.29 (0.61)	0.0	0.0
T13	0.0	0.08 (0.22)	0.19 (0.55)	0.70 (1.99)	0.19 (0.54)	0.0
T25	0.0	0.22 (0.63)	0.36 (1.00)	0.74 (2.09)	0.27 (0.54)	0.06 (0.11)
T39	0.0	0.0	0.0	0.0	0.0	0.01 (0.03)
T20	0.0	0.0	0.06 (0.16)	0.0	0.0	0.0
T7	0.0	0.0	0.0	0.0	0.10 (0.28)	0.0
T28	0.0	0.0	0.0	0.0	0.0	0.34 (0.97)
Bryozoans						
B1	0.0	0.32 (0.47)	0.13 (0.26)	0.26 (0.41)	1.25 (2.08)	0.58 (0.93)
B2	0.0	0.55 (0.59)	1.85 (3.35)	1.77 (2.60)	2.22 (1.62)	3.55 (3.17)
B3	0.0	0.02 (0.04)	0.82 (2.16)	0.0	0.0	0.16 (0.32)
B4	0.0	5.71 (6.92)	13.09 (16.18)	8.64 (11.71)	1.95 (1.45)	1.58 (1.36)

Species	October Group Sample Date 17/12/76	29/03/77	20/06/77	29/09/77	20/01/78	13/04/78
Bryozoans						
B5	0.0	0.04 (0.12)	0.07 (0.19)	1.41 (3.63)	0.0	0.44 (1.23)
B6	0.0	3.00 (2.58)	6.73 (7.79)	5.18 (10.67)	5.10 (4.38)	9.96 (5.72)
B7	0.0	0.0	0.07 (0.19)	0.0	1.09 (1.71)	1.17 (0.61)
BO	0.0	1.88 (2.34)	5.64 (6.75)	5.51 (8.87)	2.80 (5.20)	2.20 (2.89)
Serpulids						
TW3/4	2.39 (1.29)	2.67 (1.33)	0.71 (0.50)	0.63 (0.95)	0.34 (0.21)	0.42 (0.26)
TW2	0.0	0.86 (1.32)	0.0	0.0	0.0	0.0
Algae						
A14	0.0	0.0	0.0	0.0	0.01 (0.02)	0.0
A17	0.0	0.12 (0.18)	0.02 (0.04)	0.32 (0.37)	0.0	0.0
CR	0.0	0.0	0.0	0.0	0.30 (0.84)	15.11 (15.56)
Cnidarians						
J5	0.0	0.0	0.0	0.0	0.0	0.28 (0.54)

APPENDIX Va The means and standard deviations (parenthesis) of percentage cover for individual species in the six experimental treatments at Rapid Bay on the last two sample dates common to all six treatments. Species code numbers are the same as those used in Table 2.1. Solitary tunicates not listed in Table 2.1 are given below. All means are based on a sample size of four.

T2 *Ascidia gemmata*

T7 *Phallusia depressiuscula*

Sample Date: 29/09/77

	Culicia sp. removed			*Culicia* sp. not removed		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Sponges						
SP1	5.01 (7.88)	0.0	0.63 (1.25)	2.35 (1.86)	1.05 (1.23)	0.0
SP2	1.28 (2.56)	3.58 (5.00)	2.23 (3.18)	0.20 (0.26)	0.16 (0.32)	5.89 (5.16)
SP3	0.0	0.0	0.68 (1.36)	0.0	0.0	0.99 (1.99)
SP30	0.0	0.50 (1.00)	1.33 (2.67)	0.0	0.0	2.82 (5.64)
SP20	0.0	0.0	1.68 (3.36)	0.0	0.0	1.76 (3.52)
SP13	0.92 (0.68)	0.21 (0.26)	1.03 (1.10)	4.21 (5.17)	0.41 (0.81)	0.77 (0.70)
SP5	2.56 (2.53)	3.30 (3.48)	0.03 (0.07)	0.45 (0.52)	0.0	0.26 (0.52)
SP4	5.51 (7.56)	6.14 (4.53)	4.40 (5.38)	0.0	2.33 (3.02)	0.63 (0.97)
SP8	0.0	3.27 (6.55)	0.0	1.29 (2.58)	0.0	0.0
SP54	0.65 (1.30)	0.0	3.90 (7.79)	0.0	0.0	0.0
SP56	2.70 (5.13)	3.85 (5.23)	1.54 (1.82)	0.72 (1.45)	8.76 (6.61)	3.70 (2.51)

Sample Date: 29/09/77

Species	*Culicia* sp. removed			*Culicia* sp. not removed		
	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Sponges						
SP49	0.0	0.0	0.34 (0.69)	0.0	0.0	0.0
SP50	0.0	0.0	1.25 (1.95)	0.0	0.0	0.0
SP57	0.0	1.91 (3.83)	0.0	0.0	2.50 (5.00)	0.0
Colonial tunicates						
T8	0.0	0.0	0.0	0.20 (0.39)	0.0	0.0
T5	0.02 (0.04)	0.0	0.02 (0.04)	0.02 (0.04)	0.0	0.0
T19	9.49 (11.92)	9.50 (18.99)	9.25 (6.53)	1.07 (2.02)	2.48 (2.63)	0.0
T11	0.82 (1.63)	1.41 (2.82)	5.18 (10.03)	0.0	0.16 (0.31)	2.96 (5.09)
T15	4.93 (9.86)	0.0	0.0	0.0	0.0	0.0
T20	0.0	0.0	0.0	0.0	0.0	0.0
T13	4.52 (5.62)	0.0	0.0	0.24 (0.27)	0.0	0.37 (0.74)
T12	0.19 (0.38)	11.74 (23.35)	1.29 (0.91)	3.34 (5.82)	22.87 (43.71)	0.0
T9	4.85 (1.75)	9.45 (14.14)	3.64 (7.04)	9.07 (14.80)	0.90 (0.82)	2.09 (1.77)
T18	0.0	0.0	1.61 (3.05)	0.0	0.0	0.21 (0.42)
T25	3.84 (2.80)	0.0	0.0	0.46 (0.92)	0.0	0.0
T23	0.93 (1.77)	1.00 (1.67)	1.35 (1.56)	0.0	1.28 (2.57)	3.54 (7.09)

Sample Date: 29/09/77

	Culicia sp. removed			*Culicia* sp. not removed		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Colonial tunicates						
T37	0.0	0.0	0.0	0.37 (0.74)	0.0	0.0
T38	0.0	0.0	0.0	0.0	0.0	0.0
Solitary tunicates						
T10	0.0	0.0	0.0	0.0	0.0	0.26 (0.52)
T2	0.22 (0.45)	0.0	3.93 (4.91)	0.0	0.0	2.55 (5.11)
T40	0.0	0.0	0.0	0.0	0.0	1.68 (2.70)
T7	2.32 (4.40)	0.0	0.29 (0.59)	0.0	0.0	1.57 (1.83)
T28	0.0	0.0	5.94 (10.53)	0.0	0.98 (1.96)	3.94 (4.81)
Bryozoans						
B1	0.0	1.67 (2.73)	1.22 (2.35)	0.0	0.0	0.0
B2	0.0	0.46 (0.78)	0.26 (0.52)	0.0	0.0	0.0
B3	0.0	0.0	0.18 (0.35)	0.0	0.0	0.0
B4	1.65 (1.94)	3.28 (4.17)	0.63 (0.73)	0.11 (0.22)	0.0	0.42 (0.84)
B5	0.0	0.90 (1.79)	0.0	0.27 (0.54)	0.0	0.0
B6	4.72 (6.51)	0.0	0.0	0.0	0.15 (0.29)	0.0
B7	0.93 (1.86)	0.39 (0.77)	0.0	0.0	0.0	0.0

Sample Date: 29/09/77

	Culicia sp. removed			*Culicia* sp. not removed		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Other						
TW3/4	0.14 (0.19)	0.33 (0.28)	0.75 (0.33)	0.03 (0.06)	0.0	0.0
J5	28.52 (20.23)	19.27 (16.66)	8.99 (11.26)	73.02 (13.99)	55.48 (33.28)	45.79 (22.91)
TW2	0.0	0.0	0.0	1.70 (3.40)	0.0	0.0

Sample Date: 13/04/78

	Culicia sp. removed			*Culicia* sp. not removed		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Sponges						
SP1	3.73 (3.82)	0.0	0.73 (1.09)	1.44 (0.82)	0.0	0.0
SP2	1.75 (3.20)	4.61 (6.19)	3.39 (3.97)	0.11 (0.22)	0.0	3.19 (3.52)
SP3	0.0	0.0	0.88 (1.75)	0.0	0.0	0.0
SP30	0.45 (0.90)	0.21 (0.42)	2.36 (4.72)	0.0	0.0	4.46 (8.93)
SP20	0.0	0.0	0.0	0.0	0.35 (0.69)	4.27 (8.54)
SP13	0.0	0.30 (0.60)	2.17 (3.68)	5.18 (8.49)	0.09 (0.19)	2.08 (1.71)
SP5	6.74 (9.21)	3.22 (4.31)	0.37 (0.73)	0.58 (0.97)	0.0	1.68 (1.83)
SP4	3.67 (6.03)	9.22 (8.40)	1.55 (3.09)	0.0	2.79 (4.63)	0.16 (0.32)
SP8	0.0	1.37 (2.74)	0.0	0.55 (1.09)	0.0	0.0
SP54	1.48 (1.81)	0.0	1.51 (3.02)	0.0	0.0	0.0

Sample Date: 13/04/78

	Culicia sp. removed			*Culicia* sp. not removed		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Sponges						
SP56	0.34 (0.68	4.27 (5.70)	3.64 (2.45)	0.0	5.36 (6.81)	0.57 (0.77)
SP57	0.0	0.0	0.0	0.0	2.70 (5.40)	0.0
SP50	0.0	0.0	0.61 (1.23)	0.0	0.0	0.0
SP49	0.0	0.0	0.68 (1.37)	0.0	0.0	0.0
SP61	0.0	0.0	0.0	0.0	0.0	0.38 (0.76)
Colonial tunicates						
T34	0.0	0.0	0.81 (1.62)	0.0	0.0	0.0
T5	0.06 (0.08)	0.0	0.0	0.0	0.0	0.0
T19	5.56 (6.54)	0.0	4.33 (8.66)	0.85 (1.70)	2.95 (5.90)	2.72 (3.15)
T11	0.0	0.92 (1.19)	3.72 (7.45)	0.0	0.0	1.76 (2.92)
T15	0.0	0.49 (0.99)	0.0	0.0	0.0	0.0
T20	0.0	0.0	1.13 (2.25)	0.0	0.0	0.0
T13	2.67 (5.34)	0.01 (0.14)	0.0	0.17 (0.34)	0.14 (0.28)	0.0
T12	0.0	10.41 (20.59)	2.26 (1.90)	1.05 (2.09)	19.63 (36.98)	1.16 (2.32)
T9	0.54 (0.88)	5.63 (10.77)	0.37 (0.42)	0.98 (1.97)	0.26 (0.51)	1.81 (2.27)
T18	0.0	0.0	5.35 (6.22)	0.0	0.0	0.57 (1.40)

Sample Date: 13/04/78

Species	*Culicia* sp. removed			*Culicia* sp. not removed		
	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Colonial tunicates						
T25	1.84 (3.69)	0.0	0.0	0.0	0.0	0.0
T23	0.0	0.24 (0.47)	2.36 (2.88)	0.0	3.15 (3.18)	3.20 (6.39)
T37	0.0	0.0	0.0	0.0	0.0	0.0
T38	0.0	0.0	1.15 (2.29)	0.0	0.0	0.0
Solitary tunicates						
T10	0.0	0.0	0.0	0.0	0.0	0.48 (0.62)
T2	0.0	0.0	7.03 (6.60)	0.0	0.0	5.07 (9.59)
T40	0.0	0.0	0.0	0.0	0.0	2.04 (2.94)
T7	0.0	0.0	0.07 (0.15)	0.0	0.0	2.68 (1.86)
T28	0.0	1.39 (2.79)	11.48 (10.18)	0.0	1.39 (2.79)	5.02 (6.01)
Bryozoans						
B1	0.0	7.63 (9.77)	2.80 (2.28)	0.0	0.94 (1.88)	0.43 (0.85)
B2	0.0	0.57 (0.54)	0.40 (0.79)	0.0	0.0	0.0
B3	0.0	0.0	0.0	0.0	0.0	0.0
B4	1.25 (2.50)	2.15 (3.62)	0.62 (1.23)	0.0	0.0	0.29 (0.58)
B5	0.0	0.0	0.0	0.0	0.0	0.0
B6	2.49 (4.97)	0.77 (1.54)	0.0	0.0	0.47 (0.94)	0.0
B7	0.23 (0.45)	0.0	0.0	0.0	0.47 (0.94)	0.0

Sample Date: 13/04/78

	Culicia sp. removed			*Culicia* sp. not removed		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Other						
TW3/4	0.14 (0.13)	0.29 (0.25)	0.56 (0.44)	0.04 (0.06)	0.0	0.0
J5	48.50 (20.0)	44.71 (16.50)	15.15 (20.09)	79.16 (16.59)	55.48 (33.28)	40.17 (25.85)

APPENDIX Vb The means and standard deviations (parenthesis) of percentage cover for individual species in the three caging treatments at Edithburgh on the last two sample dates common to all three treatments. Species code numbers are the same as those used in Table 2.1. Solitary tunicates not listed in Table 2.1 are given below. All means are based on a sample size of five.

T2 *Ascidia gemmata*
T4 *Halocynthia hispida*
T6 *Ciona intestinalis*
T7 *Phallusia depressiuscula*

	24/09/77			28/12/77		
Species	Uncaged	Control	Exclusion	Uncaged	Control	Exclusion
Sponges						
SP1	6.0 (9.23)	7.68 (8.02)	1.89 (4.22)	7.37 (11.98)	9.03 (7.0)	0.39 (0.56)
SP2	0.0	5.49 (7.55)	7.38 (10.16)	0.0	4.25 (8.50)	8.07 (11.72)
SP14	0.0	1.90 (4.25)	0.0	0.0	0.27 (0.61)	0.0
SP3	0.0	0.0	0.0	0.0	0.0	0.15 (0.34)
SP20	8.02 (9.25)	3.69 (7.70)	8.46 (9.69)	8.87 (11.40)	5.56 (10.24)	11.01 (13.34)
SP30	33.11 (28.20)	19.15 (17.14)	16.66 (18.53)	29.01 (27.11)	17.77 (19.58)	10.54 (12.10)
SP13	0.98 (2.19)	0.15 (0.33)	0.36 (0.80)	1.44 (2.31)	0.0	0.82 (1.82)
SP47	3.90 (7.48)	0.76 (1.69)	0.0	1.79 (2.63)	1.30 (2.90)	0.0
SP49	4.11 (9.19)	0.22 (0.50)	0.0	6.15 (13.75)	0.0	0.0
SP5	8.43 (15.55)	1.75 (3.91)	1.07 (2.25)	2.48 (4.50)	0.37 (0.83)	1.59 (3.55)

Species	24/09/77 Uncaged	24/09/77 Control	24/09/77 Exclusion	28/12/77 Uncaged	28/12/77 Control	28/12/77 Exclusion
Sponges						
SP62	0.0	0.0	1.13 (1.79)	0.0	0.0	2.02 (2.79)
SP63	0.0	0.0	4.02 (8.98)	0.0	4.28 (9.57)	0.0
SP55	0.0	0.0	0.0	0.0	0.89 (1.99)	0.0
SP58	0.0	0.19 (0.42)	0.0	0.0	0.0	0.0
SP57	0.0	0.0	0.0	0.0	0.21 (0.48)	0.0
Colonial tunicates						
T5	0.02 (0.04)	0.0	0.02 (0.04)	0.05 (0.11)	0.0	0.02 (0.04)
T11	2.42 (5.42)	0.0	0.44 (0.97)	6.36 (14.22)	0.03 (0.08)	0.49 (1.09)
T9	0.0	2.12 (3.05)	6.16 (3.08)	0.0	1.42 (3.18)	4.08 (3.65)
T18	1.74 (2.21)	0.51 (0.70)	3.54 (6.91)	5.04 (7.97)	0.06 (0.13)	0.05 (0.10)
Solitary tunicates						
T4	0.0	0.0	2.58 (1.97)	0.0	0.0	2.93 (3.10)
T2	0.0	0.0	1.77 (2.45)	0.0	0.0	2.42 (3.65)
T40	0.0	0.0	0.72 (1.60)	0.0	0.0	2.18 (2.99)
T6	0.0	0.0	6.01 (13.43)	0.0	0.0	2.61 (5.83)
T7	0.0	0.0	3.02 (4.97)	0.0	0.0	5.69 (8.29)

Species	24/09/77 Uncaged	24/09/77 Control	24/09/77 Exclusion	28/12/77 Uncaged	28/12/77 Control	28/12/77 Exclusion
Bryozoans						
B1	7.46 (16.68)	1.97 (1.65)	0.59 (0.82)	6.81 (5.22)	2.61 (2.56)	1.19 (2.27)
B2	0.74 (1.30)	1.49 (3.02)	2.03 (3.00)	0.58 (0.81)	2.12 (2.97)	2.31 (3.18)
B3	0.13 (0.29)	4.61 (6.87)	0.0	0.39 (0.54)	4.93 (8.88)	0.0
B4	0.0	0.41 (0.56)	0.84 (1.55)	0.07 (0.15)	0.83 (1.74)	0.50 (1.11)
B5	0.0	0.26 (0.59)	0.12 (1.28)	0.0	0.18 (0.40)	0.26 (0.58)
B6	0.0	0.68 (1.54)	0.24 (0.54)	0.0	0.24 (0.54)	0.41 (0.91)
B7	0.0	1.26 (1.45)	0.0	0.0	1.59 (1.46)	0.21 (0.47)
Other						
M18	0.0	0.04 (0.11)	0.37 (0.50)	0.03 (0.04)	0.06 (0.10)	0.08 (0.10)
J5	12.0 (26.83)	2.54 (5.68)	0.03 (0.07)	9.64 (21.55)	3.24 (7.25)	0.0
TW3/4	0.0	0.24 (0.29)	0.16 (0.20)	0.29 (0.64)	0.02 (0.04)	0.26 (0.29)

APPENDIX Vc

(1) H values for Kruskal-Wallis ANOV comparing the abundances of phyletic groups and species between caging treatments for each removal treatment on the last two sample dates common to all six treatments at Rapid Bay.
Sample size=4 for all groups.

(2) U values for Mann-Whitney U-tests (one-tailed) comparing the abundances of phyletic groups and species between removal treatments for each caging treatment on the last two sample dates common to all six treatments at Rapid Bay.
Sample size=4 for all groups.

ns: not significant at the .05 significance level

*: .05>P>.01

**: .01>P>.001

Species code numbers not listed in Table 2.1 or the caption of Appendix Va are shown below.

C-J5: Total cover minus *Culicia* sp.

SP: total cover of sponges

TC: total cover of colonial tunicates

TS: total cover of solitary tunicates

B: total cover of bryozoans

(1) KRUSKAL-WALLIS one-way ANOV

(2) MANN-WHITNEY U-TEST

	Culicia sp. removed		*Culicia* sp. not removed		Uncaged		Control		Exclusion	
	29/09/77	13/04/78	29/09/77	13/04/78	29/09/77	13/04/78	29/09/77	13/04/78	29/09/77	13/04/78
C-J5	0.3 ns	4.2 ns	1.5 ns	3.8 ns	3.0 ns	7.0 ns	3.0 ns	4.0 ns	5.0 ns	4.0 ns
SP	1.2 ns	0.8 ns	0.3 ns	0.7 ns	6.0 ns	8.0 ns	4.0 ns	3.0 ns	7.0 ns	6.0 ns
TC	0.2 ns	1.1 ns	0.5 ns	5.7 ns	3.0 ns	0.0 *	7.0 ns	6.0 ns	2.0 ns	5.0 ns
TS	5.2 ns	10.4 **	8.3 **	8.3 **	2.0 ns	8.0 ns	6.0 ns	6.0 ns	7.0 ns	6.0 ns
B	3.7 ns	0.4 ns	0.1 ns	2.8 ns	7.5 ns	2.0 ns	2.5 ns	5.0 ns	3.0 ns	0.0 *
SP1	2.8 ns	4.8 ns	6.3 *	10.4 **	7.0 ns	5.0 ns	4.0 ns	8.0 ns	6.0 ns	4.0 ns
SP2	1.0 ns	0.6 ns	8.0 **	5.7 ns	7.0 ns	7.0 ns	4.0 ns	2.0 ns	4.0 ns	7.0 ns
SP3	1.9 ns	1.9 ns	1.9 ns	0.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	6.0 ns
SP30	1.1 ns	0.1 ns	1.9 ns	1.9 ns	8.0 ns	6.0 ns	6.0 ns	6.0 ns	7.5 ns	7.5 ns
SP20	1.9 ns	0.0 ns	1.9 ns	0.1 ns	6.0 ns	6.0 ns	8.0 ns	6.0 ns	6.0 ns	6.0 ns
SP13	3.1 ns	1.1 ns	0.3 ns	0.0 ns	7.0 ns	6.5 ns	7.0 ns	4.0 ns	7.5 ns	5.5 ns
SP5	3.8 ns	1.3 ns	2.1 ns	4.8 ns	2.0 ns	6.0 ns	2.0 ns	4.0 ns	7.5 ns	3.5 ns
SP4	0.1 ns	1.8 ns	2.4 ns	3.5 ns	6.0 ns	6.0 ns	5.5 ns	5.5 ns	7.0 ns	7.5 ns
SP8	1.9 ns	1.9 ns	1.9 ns	1.9 ns	6.0 ns	6.0 ns	6.0 ns	6.0 ns	8.0 ns	8.0 ns
SP54	1.1 ns	2.1 ns	0.0 ns	0.0 ns	6.0 ns	6.0 ns	8.0 ns	8.0 ns	6.0 ns	6.0 ns
SP56	0.2 ns	2.4 ns	3.8 ns	2.8 ns	6.0 ns	6.0 ns	4.0 ns	8.0 ns	3.0 ns	3.0 ns
SP49	1.9 ns	1.9 ns	0.0 ns	0.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	8.0 ns
SP50	1.9 ns	1.9 ns	0.0 ns	0.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	6.0 ns
SP57	1.9 ns	0.0 ns	1.9 ns	1.9 ns	8.0 ns	8.0 ns	7.5 ns	6.0 ns	8.0 ns	8.0 ns
SP61	0.0 ns	0.0 ns	0.0 ns	1.9 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns
T8	0.0 ns	0.0 ns	1.9 ns	1.9 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	6.0 ns

(1) KRUSKAL-WALLIS one-way ANOV

	Culicia sp. removed		*Culicia* sp. not removed	
	29/09/77	13/04/78	29/09/77	13/04/78
T5	1.1 ns	4.3 ns	1.9 ns	0.0 ns
T19	0.8 ns	2.1 ns	3.7 ns	0.8 ns
T11	2.1 ns	2.1 ns	2.8 ns	4.3 ns
T15	1.9 ns	1.9 ns	0.0 ns	0.0 ns
T20	0.0 ns	1.9 ns	0.0 ns	0.0 ns
T13	7.2 **	1.1 ns	2.1 ns	1.9 ns
T12	2.5 ns	4.0 ns	4.3 ns	0.6 ns
T9	0.0 ns	1.2 ns	1.5 ns	0.1 ns
T20	0.0 ns	1.9 ns	0.0 ns	0.0 ns
T18	1.9 ns	1.9 ns	1.9 ns	1.9 ns
T25	7.2 **	1.9 ns	1.9 ns	0.0 ns
T23	0.0 ns	2.8 ns	1.1 ns	1.8 ns
T37	0.0 ns	0.0 ns	1.9 ns	0.0 ns
T38	0.0 ns	1.9 ns	0.0 ns	0.0 ns
T10	0.0 ns	0.0 ns	1.9 ns	1.9 ns
T2	2.8 ns	7.2 **	1.9 ns	4.3 ns
T40	0.0 ns	0.0 ns	4.3 ns	4.3 ns
T7	2.4 ns	1.9 ns	4.3 ns	7.2 **
T28	4.3 ns	4.3 ns	2.8 ns	2.8 ns

(2) MANN-WHITNEY U-TEST

	Uncaged		Control		Exclusion	
	29/09/77	13/04/78	29/09/77	13/04/78	29/09/77	13/04/78
T5	8.0 ns	4.0 ns	8.0 ns	8.0 ns	6.0 ns	8.0 ns
T19	3.5 ns	2.5 ns	5.5 ns	6.0 ns	3.0 ns	7.0 ns
T11	6.0 ns	8.0 ns	7.5 ns	6.0 ns	8.0 ns	7.0 ns
T15	6.0 ns	8.0 ns	8.0 ns	6.0 ns	8.0 ns	8.0 ns
T20	6.0 ns	8.0 ns	8.0 ns	6.0 ns	8.0 ns	8.0 ns
T13	3.0 ns	6.0 ns	8.0 ns	7.5 ns	6.0 ns	8.0 ns
T12	6.0 ns	6.0 ns	4.0 ns	7.0 ns	2.0 ns	5.5 ns
T9	2.0 ns	7.0 ns	5.5 ns	6.0 ns	6.5 ns	7.0 ns
T20	8.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns
T18	8.0 ns	8.0 ns	8.0 ns	8.0 ns	7.5 ns	7.5 ns
T25	2.5 ns	6.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns
T23	2.5 ns	8.0 ns	4.0 ns	7.0 ns	7.0 ns	7.0 ns
T37	6.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns
T38	8.0 ns	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns
T10	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	4.0 ns
T2	6.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	5.5 ns
T40	4.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	2.5 ns
T7	6.0 ns	8.0 ns	8.0 ns	8.0 ns	4.0 ns	4.0 ns
T28	8.0 ns	8.0 ns	6.0 ns	6.0 ns	8.0 ns	8.0 ns

(1) KRUSKAL-WALLIS one-way ANOV

	Culicia sp. removed		*Culicia* sp. not removed	
	29/09/77	13/04/78	29/09/77	13/04/78
B1	2.6 ns	3.6 ns	0.0 ns	1.1 ns
B2	2.4 ns	1.3 ns	0.0 ns	0.0 ns
B3	1.9 ns	0.0 ns	0.0 ns	0.0 ns
B4	0.7 ns	0.6 ns	1.1 ns	1.9 ns
B5	1.9 ns	0.0 ns	1.9 ns	0.0 ns
B6	2.8 ns	4.3 ns	1.9 ns	1.9 ns
B7	1.9 ns	1.9 ns	0.0 ns	1.9 ns
TW3/4	5.6 ns	0.2 ns	1.1 ns	2.7 ns
J5	0.9 ns	5.7 *	2.6 ns	2.6 ns
TW2	0.0 ns	0.0 ns	1.9 ns	0.0 ns

(2) MANN-WHITNEY U-TEST

	Uncaged		Control		Exclusion	
	29/09/77	13/04/78	29/09/77	13/04/78	29/09/77	13/04/78
B1	8.0 ns	8.0 ns	4.0 ns	5.0 ns	4.0 ns	2.5 ns
B2	6.0 ns	6.0 ns	4.0 ns	2.0 ns	6.0 ns	6.0 ns
B3	8.0 ns	8.0 ns	8.0 ns	8.0 ns	6.0 ns	8.0 ns
B4	6.0 ns	6.0 ns	4.0 ns	4.0 ns	5.0 ns	7.5 ns
B5	6.0 ns	8.0 ns	6.0 ns	8.0 ns	8.0 ns	8.0 ns
B6	4.0 ns	6.0 ns	6.0 ns	7.5 ns	8.0 ns	8.0 ns
B7	6.0 ns	6.0 ns	6.0 ns	6.0 ns	8.0 ns	8.0 ns
TW3/4	4.0 ns	6.0 ns	2.0 ns	2.0 ns	1.0 *	3.0 ns
J5	0.0 *	0.0 *	3.0 ns	4.0 ns	1.0 *	2.0 ns
TW2	6.0 ns		8.0 ns	8.0 ns	8.0 ns	8.0 ns

Appendix Vd H values for Kruskal-Wallis ANOV comparing the abundances of phyletic groups and species between the three caging treatments on the last two sample dates common to all three treatments at Edithburgh. Only those groups and species not included in Table 6.13 are listed. Species code numbers are the same as those listed in Table 2.1 and the caption of Appendix Vb. A significance level of .05 was used.

ns: no significant heterogeneity between treatments

Sample size=5 for all groups

	24/09/77		28/12/77	
Phyletic group				
Sponges	1.0	ns	1.8	ns
Colonial tunicates	4.5	ns	3.8	ns
Bryozoans	3.0	ns	1.0	ns
Species				
SP1	1.7	ns	2.96	ns
SP2	1.5	ns	1.5	ns
SP14	2.0	ns	2.0	ns
SP3	0.0	ns	3.0	ns
SP20	0.8	ns	1.2	ns
SP30	2.8	ns	1.7	ns
SP13	1.2	ns	1.1	ns
SP47	1.1	ns	1.1	ns
SP49	1.1	ns	2.0	ns
SP5	1.0	ns	0.6	ns
SP62	4.3	ns	4.3	ns
SP63	2.0	ns	2.0	ns
SP55	0.0	ns	2.0	ns
SP58	2.0	ns	2.0	ns
SP57	0.0	ns	2.0	ns

	24/09/77		28/12/77	
T11	1.1	ns	1.1	ns
T5	2.7	ns	1.1	ns
T18	3.6	ns	3.6	ns
T2	4.3	ns	4.3	ns
T40	2.0	ns	4.3	ns
T6	2.0	ns	2.0	ns
T7	4.3	ns	4.3	ns
B1	2.9	ns	2.1	ns
B2	0.8	ns	0.8	ns
B3	4.3	ns	3.7	ns
B4	1.0	ns	0.6	ns
B5	1.1	ns	1.1	ns
B6	1.1	ns	1.1	ns
B7	2.0	ns	2.5	ns
M18	0.6	ns	4.6	ns
J5	0.2	ns	2.2	ns
TW3/4	2.2	ns	0.9	ns

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