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Community dynamics of the epifauna of the bivalve *Pinna bicolor* Gmelin

by

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Declaration

This thesis contains no material accepted for the award of any other degree or diploma in this or any other University.

To the best of my knowledge this thesis contains no material previously published or written by another person, except where due reference is made in the text.

Michael J. Keough

19.1.81

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ABSTRACT

Many habitats are non-uniform, or "patchy". One way of studying communities in such habitats is to examine events within individual patches, and then to combine results from a number of patches. A common approach to the study of patch dynamics is the equilibrium model developed by MacArthur and Wilson. This model is widely regarded as having been tested adequately, and consequently is used to solve applied problems.

There are a number of problems with this approach. Many studies regarded as tests are in fact flawed, and are not critical tests of the model. There are a number of more general problems: The concept of equilibrium is poorly defined, with little regard for chance events or differences in the life-histories of individual species.

The concept of equilibrium is here re-defined. Fluctuations in species number (S) are assumed to occur, and the concept of narrow boundedness is introduced. Fluctuations in S are narrowly bounded if (1) S has no tendency to increase indefinitely or to decline to zero with time, and (2) Fluctuations in S fall with 95% probability within a band $\overline{S} \pm \overline{S}\, w$, with $w = 0.20$.

This definition allows the equilibrium model to be tested, in this case for the sessile invertebrates associated with shells of the fanshell, *Pinna bicolor*, a sedentary bivalve widely distributed in shallow seas of the Indo Pacific region. The fluctuations in S were not narrowly bounded on most *Pinna* shells, and in order to accommodate the fluctuations on 95% of shells, a $w > 0.5$ would be required. Fluctuations of this magnitude are unacceptably large.

Recruitment onto identical patches varies considerably, indicating a large stochastic component. There is also between-seasons, between-years, and between-localities variation. Individual species

vary greatly in their patterns of recruitment, sufficient to account for most of the fluctuations in S.

There are considerable differences in the competitive abilities of different species. Some, mainly didemnid ascidians and to a lesser extent, sponges, influence dramatically the composition of any patch in which they occur. Their influence in the overall community is restricted by predatory fish, mainly the monacanthids *Eubalichthys mosaicus* and *Brachaluteres jacksonianus*, which prey upon newly metamorphosed post-larvae. No tunicate recruits onto uncaged *Pinna* shells were observed in two years, despite the settlement of larvae.

On *Pinna* shells, percent cover is low, and bryozoans and serpulids are the most widespread taxa. Sponges and tunicates occur infrequently, but when they occur have high percent covers. The discrete nature of the patches in this case means that invasion of patches must be by dispersive larvae, rather than the vegetative growth of existing colonies (cf. pier pilings). This accounts for the rarity of sponges, which invade patches almost exclusively by the latter method. Tunicates are similar although dispersive larvae play a greater role than for sponges. Tunicates are restricted by a combination of this and the action of fish.

Species composition is extremely variable. Aside from the aforementioned factors, the outcomes of competitive interactions between given pairs of species were frequently variable, and often neither species was able consistently to win. Thus, even when the species composition of a patch was known, subsequent events usually were not predictable.

The reasons for the lack of usefulness of the equilibrium model in this instance are likely to be features common to other communities, but obscured by a lack of data. It appears that equilibrium models are not of general use in the study of patchy habitats. Disturbance is unimportant in the community studied, thus "non-equilibrium" models are

inapplicable. Although these models apply to other communities, they do not have great generality.

An alternative model is developed, using life-history characteristics of species (modes of dispersion, competitive ability) to make qualitative, probabilistic predictions about the composition of patches of a given size. Species composition is assumed to be variable, due to chance factors. The model is tested using the sessile assemblage on Edithburgh pier, and its predictions supported. Examples from other habitats give hope of some general applicability, and the model is expanded to take account of variations in recruitment rates, predation and physical disturbance. The expanded version has not yet been tested. Stochastic, rather than deterministic, models are likely to prove most useful in understanding patchy habitats.

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1. INTRODUCTION

1.1 Patchy habitats

Natural habitats have long been recognised as being distributed in a non-homogeneous, or "patchy" manner. It has similarly been acknowledged that this partly explains the non-uniform distribution of most animal species (e.g. see Andrewartha and Birch 1954). Patchiness occurs in almost all habitats, and on a wide range of spatial scales. Whittaker and Levin (1977) give a comprehensive review of the phenomenon, and obvious examples abound, such as host plants for insects (Andrewartha and Birch (1954) give numerous examples), patch reefs for coral reef fish (Sale 1977), and lakes and streams for freshwater invertebrates (e.g. Cairns *et al.* 1969; Keddy 1976).

Whittaker and Levin (1977) suggested that it is appropriate to view natural communities as mosaics of small, interconnected patches against a relatively homogeneous reference background. This background may be either biotic, such as a bed of mussels within which patches are cleared, or abiotic, such as the land between lakes. In such a case, it seems intuitively reasonable to study the events within individual patches and to make formulations about the abundance of species on wider scales by combining the results for a number of patches.

The most extreme form of habitat patchiness is of course oceanic islands. They have stimulated the interest of naturalists as far back as the early and mid-nineteenth century (de Candolle 1855, cited by Connor and Simberloff (1978)), and the influence of the Galapagos Islands on the thinking of Darwin (1859) is probably the best example of this. Interest in island biotas was maintained, but the approach to the composition of island biotas remained largely descriptive and anecdotal, until the publication of "The Theory of Island Biogeography" by Robert MacArthur and Edward Wilson in 1967, although it was preceded by three

earlier works (MacArthur and Wilson 1963; Preston 1960, 1962).

MacArthur and Wilson proposed that the biota of an island can be viewed as an equilibrium between the arrival of new species and the extinction of already present ones. The immigration rate (I) is postulated to be higher for islands closer to the source of colonists. It is implicitly assumed that there is a point source for colonists. Immigration rate falls with time, since fewer species are left to colonise, and MacArthur and Wilson proposed that the curve of Immigration rate against number of species present (S) should be concave (Figure 1.1), since the better colonisers will establish first, and slower colonisers should be increasingly less likely to colonise an island.

Similarly, extinction rate (E) rises with the number of species, since the probability of deleterious interactions with other species is increased. In addition, with a larger number of species and assuming a constant probability of extinction per unit time for each species, the expected number of extinctions should increase with S in a curvilinear manner. Extinction rate should then be higher on larger islands than small. MacArthur and Wilson arbitrarily assigned exponential shapes to their curves of I and E against S (Figure 1.1), but stressed that it was only necessary for the curves to be monotonic.

The point of intersection of the two curves for a given island determines the equilibrium number of species, $\hat{S}$. This value should be approached asymptotically with time, and the effect of island size on extinction rate should produce a monotonically increasing curve of species number versus area. This has become known as a species-area curve, and is usually expressed as $\log \hat{S} = \log c + z \log A$, or $S = c A^z$, where S is the number of species, A the area of the island, and z and c are constants. The increase in species number with area had been recognised for many years, but the MacArthur and Wilson model surrounded it with this semi-rigorous framework.

After $\hat{S}$ is reached, extinctions continue, with replacement of species by new immigrants. Thus, it is only the number of species which reaches an equilibrium; the actual species composition is continually changing. This became known as species turnover. There are thus two clear predictions from the equilibrium model.

(1) The number of species on an island should increase with the area of the island, and

(2) The number of species should remain constant or nearly constant, but there should be continuous turnover of species.

It is of course not sufficient for a model to apply only to the extremes of a class of situations; if a model is to be of general use, it should be applicable to the whole class of situations with as little modification as possible. MacArthur and Wilson were certainly aware of this, and clearly viewed their equilibrium model as being applicable to a variety of other patchy habitats. This is stated explicitly in the introductory chapter (MacArthur and Wilson 1967, pp3-5), and further evidence comes from their use of data from so-called "habitat islands", such as diatoms on glass slides in streams (Patrick 1975).

These predictions have been treated extensively in the literature, and Simberloff (1974) gives a comprehensive review of much of this work. Recently, many of these studies have been criticised heavily, and in many cases it appears that researchers ignored the *caveats* of MacArthur and Wilson. Many sections of their book clearly imply that the work is intended to be a stimulus for further and rigorous investigations, rather than a definitive treatment of the biotas of islands.

In the following sections, I shall first try to give a workable definition of "equilibrium", and then to review briefly the "tests" and expansions of the MacArthur-Wilson model. Then I shall give an account of various criticisms of these tests.

Finally, I shall describe briefly alternative approaches to the

study of patchy habitats and describe what is known of marine habitats of this type, since all of the experimental data to be presented in this thesis will be drawn from one such habitat.

1.2 An operational definition of equilibrium

The use of the term "equilibrium" implies some kind of "steady-state". In practice, of course, species number will never be constant. Trivially, species will never be gained and lost simultaneously, and sometimes successive immigrations will occur by chance before corresponding extinctions occur, and *vice versa*.

For this and other reasons which will become apparent in the following sections, we should expect S to fluctuate about $\hat{S}$ with time. Correspondingly, for a given set of islands surveyed simultaneously, we would expect to find a range of S values, since there is no reason to expect that the fluctuations in S for individual islands will be synchronised.

MacArthur and Wilson recognised this, and developed a simple model to predict the variance of S for a set of identical islands. Subsequent workers have largely ignored this, and it has been assumed that equilibrium means a constant value for S.

When it is acknowledged that S varies, it is clear that "equilibrium" must mean that the variance of S is relatively small. The alternative view is that a situation may be "non-equilibrium" (e.g. Connell 1978, 1979), i.e. few patches have attained this steady-state, and most have been disturbed so that they are not near equilibrium. This statement means simply that the variance of S is relatively large. The terms "large" and "small" are arbitrarily defined, but the decision about the variance of S is important. If the variance of S is large, then it may not be useful to talk about an equilibrium, since at a given time most patches will not have $\hat{S}$ species.

It follows that the existence of an equilibrium is not disprovable unless we define *a priori* the level of variation in S below which it is considered useful to employ the concept of equilibrium. In practice, this is rarely, if ever, done and the decision about whether an equilibrium exists appears to have been made by subjective, visual inspection.

We can approach the question of equilibrium in a slightly less arbitrary manner. If we acknowledge that S will fluctuate in some way, we can specify the limits to the fluctuations, without assuming anything about the distribution of S. The same approach has been adopted by Chesson (1978) for the case of a stochastic population model which can not usefully be thought of as "stable", but where the populations have a limiting average density as time increases and where we can consider the populations unlikely to decline to zero or increase in an unbounded way. This likelihood can be expressed as "stochastic boundedness".

To paraphrase the definition given by Chesson (1978, p 344), let S(t) be the value of S at time t. S will be stochastically bounded in the local sense, if for every positive probability ξ there is a number $U_\xi < \infty$ such that for any t, S (t) is less than U_ξ with probability at least $1-\xi$, and a number $L_\xi > 0$ such that for some $\xi < 1$, S(t) is greater than L_ξ with probability at least $1-\xi$.

Now, the MacArthur-Wilson theory predicts that S will be stochastically bounded in just this sense. However we are concerned not only with whether or not S remains within some bounds, but also with whether the boundaries are so far apart that the fluctuations become of more interest than the central location of the data.

We can then define narrow boundedness by the following:

S(t) is narrowly bounded if

(1) S(t) is stochastically bounded (as defined above) for $\xi = 0{,}025$ (i.e. there exists an envelope such that the probability of S being

outside its boundaries at any t is 0.05).

(2) The width of that envelope is sufficiently small relative to the mean, $\bar{S}$.

It is necessary to define "sufficiently small" arbitrarily, and we can gain some idea of useful magnitudes as follows.

MacArthur and Wilson used immigration and extinction probabilities to generate an expected distribution of S around $\bar{S}$ ($\hat{S}$). This distribution was approximately normal (see their Figure 19). For a normal distribution, 95% of S values fall within the region $\mu_S \pm 1.96\ \sigma_S$.

Now, if the concept of equilibrium is to be useful, this region must be small. Define a coefficient w, where $0 \leqslant w \leqslant 1$ with w chosen, so that $\bar{S} \pm w\ \bar{S}$ defines the region of "sufficiently narrow" variation. Then, the observed fluctuations will be sufficiently narrow if

$$1.96\ s_S < w\ \bar{S}\ , \quad \text{or}$$

$$s_S\ /\ \bar{S}\ < w\ /\ 1.96$$

The selection of w is then the arbitrary stage, but once a value for w has been chosen, there is an objective test for the existence of narrow bounds for the observed fluctuations of S. If we accept that the normal distribution is a simplified approximation for the distribution of S, the test is simply to obtain the observed coefficient of variation in S (c.v.) from a series of censuses on one patch and test the null hypothesis H_o : c.v. = w/1.96 against H_1 : c.v. > w/1.96.

In order to try and represent the criteria graphically, I selected S values randomly with the constraint that the probability of a value falling outside the bounds is 0.05. S values were plotted against time, in the order that they occurred. The result was a random sequence of S values which nevertheless fitted the test criteria in question, i.e. would be classified as equilibrial. I performed this simulation for three values of w; 0.1, 0.2, and 0.5. The results are shown on Figure 1.2.

The graph for w = 0.1 shows the kind of fluctuations which would be likely to be called "equilibrium" in the literature. For w = 0.2 the fluctuations are moderate, and to allow S to fluctuate 20% either side of the mean seems a generous criterion for a steady state. For w = 0.5 the fluctuations appear wide and the terms "equilibrium" or "steady state" appears inappropriate.

If we accept w = 0.2 as defining sufficiently narrow bounds, the critical coefficient of variation is 10.2%. Clearly, if we are to test for an equilibrium, a relatively large number of censuses is necessary to minimise the likelihood of Type II errors.

The literature shows very few examples of such studies. Indeed, the life spans of many vertebrates, and the consequent scale of population fluctuations make it unlikely that such censuses could be obtained within the lifetime of a researcher, without sampling at intervals which are too short to be of any value. Of the other studies, most stopped after S reached an asymptote. It is clear, however, that since the species pool is finite, the curve of S vs time must at least reach an asymptote. It is the behaviour of the curve after the initial point of inflexion is reached that is of interest. It is thus unlikely that the existence of an "equilibrium" can be tested using the published literature.

For the remainder of this chapter, I shall continue to use the term equilibrium in the context of the MacArthur-Wilson model, but it will mean that species number is bounded as specified on page 5 . Elsewhere, the term "narrowly bounded" will be used.

1.3 Tests of the equilibrium model

The two main predictions of the equilibrium model have generally been investigated independently, and studies examining both are relatively rare (Simberloff 1974). Connor and Simberloff (1978) found it convenient to divide the published investigations into two categories of approach, which they termed "regression" and "experimental". Connell (1975) gives a good review of the advantages and disadvantages of each. The regression approach involves the use of naturally occurring islands, on which measurements are made of area, elevation, distance to source and/or nearest neighbour, habitat diversity, etc. Species number is also measured, generally for a single taxon, such as birds, lizards, or insects. Regression equations are then calculated using species number as the dependent variable and either area (a simple linear regression), or all of the measured variables as independent variables (multiple linear regression). The latter allows a relative importance to be assigned to each of the independent variables. Similarly, turnover and species equilibrium is assessed simply by revisiting islands and comparing species counts. This approach has obvious defects; a regression equation cannot show causality, and the independent variables used may only be significantly related to the dependent variable because they are themselves correlated with more subtle, but more important variables. The use of naturally occurring islands frequently places restrictions on the number of replicates available, and also the total sample size. True replicates are often unavailable, since there will be at least subtle differences between any pair of similar islands. Nevertheless, such experiments are sometimes labelled "natural experiments" (Diamond 1973).

The experimental approach involves manipulation of species composition (Crowell 1973; Paine 1966) or modifications of the islands themselves (Simberloff and Wilson 1969). This approach has been employed mostly for invertebrate taxa, and its use for studies on vertebrates has been restricted for mainly ethical reasons, although logistic reasons may also be important. Abbott (1979), however, has recently put forward a strong case for experimental removal or addition of bird species, claiming that this is the only way to test critically hypotheses about the role of competition in producing morphological changes in bird species on islands. Controlled experiments have the advantage of being able to assign causes to effects with minimal equivocation, but the main disadvantage is the possibility that the experimental procedure itself may have an effect. These effects may sometimes be difficult to control for. Chapter 4 provides examples of this problem.

Most workers have been able to show significant regression of log S on log A. Connor and McCoy (1979, see their appendix) give a comprehensive account of such investigations. The number of such studies since then is very small, and they do not affect the essential conclusion that species number generally increases with area, and frequently in such a way as to be fitted by a log S/log A curve. This has been shown for a wide range of taxa from nematodes on plant roots (Bowen and Rovira 1976) to protozoa in the guts of primates, regarding social troups as islands (Freeland 1979), through various marine and freshwater habitats to the vast number of studies on birds (see Abbott 1979), and mammals (Brown 1971; Crowell 1973).

Although most regression studies have used Area as an independent variable, there is no agreement as to what this actually represents ecologically. Area itself may be important, firstly by its effect on extinction rates. This was the view of MacArthur and Wilson

(1967). Secondly, a large island "samples" more of the medium in which the colonists disperse, and so on probabilistic grounds, we would expect more species to be "collected" by the larger island. Thirdly, larger islands tend to have a greater diversity of habitats, allowing greater niche specialisation and hence more species to coexist.

There is some evidence for each of these possibilities. Simberloff (1976) showed, for invertebrates on mangrove islands, that area alone was sufficient to account for changes in species number by changing population size and thus altering probabilities of extinction. Abele and Patton (1976) and Austin *et al.* (1980) both found that the size of coral heads *per se* influenced the number of species of decapods, although they did not determine whether or not this occurred by modification of extinction rates.

The sampling effect accounted for a large amount of variation in species number in the marine epifaunal community studied by Osman (1977, 1978).

Harger and Harper (1976) found that the number of soil types influenced strongly the number of plant species, and Abele (1976) demonstrated a similar result for crustaceans in coral heads.

Many other examples may be found in the literature, and it seems likely that all three must apply in some, and probably many, cases of patchy habitats. It may often be almost impossible to disentangle their effects, due to lack of true replicates, small sample sizes, etc.

1.3.1 Turnover rates and equilibrium

These are clearly more difficult to measure than species-area relationships, since repeated censuses are required, rather than a single, often brief visit to each island. Such studies are correspondingly fewer. Diamond (1971) examined historical records and conducted his own surveys of birds in the Channel Islands in Southern California,

and concluded that species numbers had changed very little, but that species compositions differed markedly. It should be noted that Johnson (1972) has criticised Diamond's study on the grounds of deficient censuses.

Simberloff and Wilson (1969) defaunated mangrove islets and observed an approach to the species number for unmanipulated control islets. Further, rapid turnover of insect species was observed (0.5-1.0 species.day^{-1}).

Abbott (1978; Abbott and Grant 1976) examined bird species censuses for offshore islands of southern Australia, and reported some turnover of species. The number of non-passerine bird species was generally very similar between surveys separated by intervals of 59-184 years. For passerine birds, however, species number was generally higher at the last published survey than at the first. Abbott and Grant (1976) postulated that the passerine fauna is not in equilibrium.

Vaisanen and Jarvinen (1977) surveyed four islands and compared bird species number with earlier censuses. They found that turnover was occurring, but did not show constancy of species number. The number of species had increased with time, and this was interpreted as the result of the islands' being protected. Terns and Gulls had increased greatly, excluding other species, and tending to lower diversity. This effect was swamped by the general increase in population sizes of most species (i.e. lower extinction rates), and successful colonisation by other species.

Hunt and Hunt (1974), Diamond (1969), Diamond and Marshall (1977), and Jones and Diamond (1976) have all demonstrated turnover of avifaunas in various areas, mainly California, New Guinea, and the New Hebrides. In all cases the comparisons were between early surveys and recent investigations.

Lynch and Johnson (1974) have criticised much of the literature on turnover rates. They suggest that many censuses involve unequal sampling effort; early censuses are frequently not sufficiently comprehensive to serve as baselines. Further, the criteria by which species are included in the counts may vary between surveys, ranging from single sightings, migrants or vagrants, to breeding pairs. Lynch and Johnson showed that at least for the Farallon Islands in California, a number of landbird species would visit the island at various times of the year. Spot censuses would include these species as part of the fauna of a given island, and since more birds visited during summer months, species number would be differentially biased, depending on the time of year at which the census was made.

Their final criticism was that many of the extinctions recorded in the study of the Channel Islands avifauna by Diamond (1969) could be ascribed to the effects of man. Thus, not all extinctions originated from processes within the natural community, and the avifaunas must be regarded as being disturbed by an external agent, and equilibrium cannot be assumed. Abbott (1979) also stresses the potential importance of man's effects, both directly, by agriculture and industrial development, and indirectly, mainly by the introduction of domestic animals which become feral.

The MacArthur-Wilson model leads to the prediction that turnover rate (number of species. $time^{-1}$) should be higher on small islands than large, since extinctions are more frequent on small islands. Similarly, remote islands should have a lower turnover rate than near, since on near islands immigration is higher, so that at $\hat{S}$, on near islands both I and E will be higher. This question has not been addressed in any great detail, with the exception of the work of Diamond (1969, 1971), who was not able to detect any difference in turnover rate between islands of different sizes. He attributed this to the small distances

between the islands and the mainland (≤ 61 miles), so that all islands are effectively very near so that any effect due to island size is swamped. Diamond also suggested that differences in habitat type could be more important for turnover than either distance or area. It should be emphasised that these are *a posteriori* rationalisations for contradictory data.

Diamond and May (1977) investigated the relation between turnover rate and time between censuses, and showed a negative correlation between the two. This is presumably because some species go extinct and recolonise, or colonise and go extinct, between censuses. Abbott (1979) has criticised this idea, on the grounds that it is tautological. Diamond and May used turnover rate, as follows; consider two time periods, t_1 and t_2. The island in question is censused at these times, and has S_1 and S_2 species respectively. Between the two time periods, E species arrive, and I species become extinct. Turnover rate is then calculated as $(E + I)/(t(S_1 + S_2))$, where $t = t_1 - t_2$. Abbott (1979) claims that this is a function of the form A/Bt, where A,B are constants. He suggested that because of this, turnover rate must be negatively correlated with time between censuses, t. This is not true, however, because the quantities E and I are not immigration and extinction rates, but numbers of species. If we consider the probabilities of immigration and extinction as fixed, then the expected number of species either arriving or leaving will increase with time between surveys. The values A and B are thus not constants; rather, A is a function of the form A = ct. The t's cancel in the equation for turnover rate, so that it is no longer a function which must be negatively correlated with t.

Aside from the bird studies, there are few which have demonstrated stable or steady species number or turnover. This was demonstrated for rodents (Crowell 1973), arthropods (Simberloff and Wilson 1969); reptiles (Heatwole and Levins 1973), and sessile marine

invertebrates (Osman 1978).

Diamond (1972) provided an alternative method to the estimation of turnover rates. He used the deviation of an individual island from a species-area curve together with the age of the island, to calculate a "relaxation time". This is the time for the species number to reach 90% of the saturation number, i.e. $\hat{S}$. The method assumes that points which lie on the species-area curve are at equilibrium, while those not on the line are not at equilibrium. Used this way, the method appears circular, since the same data are used to fit a species-area curve as to calculate time to reach the curve for single data points which deviate from it. Abbott (1979) also suggests that the method may not be useful because of past differences in mainland species pools, post-glacial changes in island areas, etc. The assumption that the empirical curve represents equilibrium values would seem to be doubtful at best. The assumption would only be reasonable if area were the sole determinant of species number for a group of approximately similar, equi-distant islands. In view of the doubt about the mechanisms underlying species-area curves, it seems clear that various factors may be involved, and each island may be at equilibrium, but have an $\hat{S}$ value different from the fitted curve simply because of differences in habitat type, food availability, etc.. In other words, the fitted curve may be viewed as an "average" species-area relationship for a set of islands each of which is at equilibrium. It may be useful for some purposes, but the deviation of a single island from it does <u>not</u> imply that that island is not in equilibrium.

Terborgh (1974), however, used this method for the avifauna of Barro Colorado Island, and obtained good fit between observed and predicted numbers of extinctions. Abbott (1979) interpreted this as evidence that the relaxation method is robust. It may be that the species-area curve in this case has only one underlying mechanism, and a

major objection is removed. However, if a model can be shown to have assumptions violated, but still gives a good fit to observed data, a credible other explanation is that this is an example of making the right prediction for the wrong reason (Dayton 1973).

Heatwole and Levins (1972, 1973) have suggested that lizard communities on some Puerto Rican islands showed constant trophic structure. The islands were defaunated, and measurements were made of trophic structure before and after the islands were defaunated. This finding was greeted initially with enthusiasm (Simberloff 1974), but Simberloff (1976) subsequently cast doubt on this conclusion.

1.3.2 Uses of the equilibrium model

On the basis of these studies, many have regarded the equilibrium model as having been tested adequately, and as having some predictive value. An example of this comes from the concluding remarks of the much-cited review by Simberloff (1974):

> "We can therefore use island biogeography to further our understanding of a variety of evolutionary and ecological phenomena and even to aid in the preservation of the earth's biotic diversity in the face of man's ecological despoliation." (!)

The latter phrasing was taken from a manuscript by Terborgh (1973, cited by Simberloff 1974). Testing of the model has almost ceased, and those examples which provide what appears to be contradictory evidence are either ignored, or explained away with *a posteriori* hypotheses.

As mentioned above, the acceptance of the model can be gauged by the range of patchy habitats to which it has been applied.

The second indication of wide acceptance is the use of the model to solve applied problems. The major use is in the design of conservation parks.

There is little point in detailing the papers which have used

or cited the MacArthur-Wilson model. Most have either plotted species-area curves, or noted that the habitat in question was patchy, and so the equilibrium model should be applicable. Simberloff (1974), Abbott (1979), and Osman (1978), and Connor and McCoy (1979) together provide comprehensive accounts of these studies.

Conservation planners are usually interested in preserving as large a number of species as possible. This has led to the use of the species-area curve as a justification for making reserves as large as possible, since more species will be contained in the larger reserve than in a series of small reserves of equivalent area (Diamond 1975; May 1975; Miller and Harris 1977; Pickett and Thompson 1978; Soule *et al.* 1979; Sullivan and Schaffer 1975; Terborgh 1974, 1975, 1976; Wilson and Willis 1975). Diamond (1975) went further and suggested the use of "corridors" between small habitat islands, to facilitate migration between patches, thereby increasing effective population size. The probability of extinction is regarded as being inversely proportional to population size, and so expected time until extinction is increased. The idea has been investigated by McLaren (1979) for birds in scrub patches on Eyre Peninsula, South Australia. She found some evidence to suggest that these corridors were effective aids to the migration, for birds, at least.

These ideas have been criticised by Simberloff and Abele (1976), and Abele and Connor (1978; cited in Connor and McCoy 1979), for the following reasons. The comparison between a large patch and small patches of equivalent size is made by noting that the theory predicts that if the large patch has S_L species, then each small patch will have S_S species, $S_L > S_S$. It seems to be assumed that even if a large number of small patches is used, they will jointly house about S_S species, i.e. less than S_L. This implicitly assumes that each small patch has the same species list. The composition of individual small patches will

vary, however, since the identities of immigrating species will be at least partly influenced by chance in any given patch. Similarly, the extinctions will not be identical for all patches. The MacArthur-Wilson model predicts, in short, that the actual species identities will vary widely between a series of identical patches. Simberloff and Abele (1976) suggest that, under these conditions, it is quite likely that the total number of species in all small patches may be greater than S_L. A series of small patches may also offer a better buffer against extinction, since if a species becomes extinct in a small patch, it may recolonise from another patch, but if extinction occurs in the large patch, further immigration may be less likely.

The MacArthur-Wilson model is dynamic, and assumes that extinctions occur frequently, but conservation planners are frequently interested in the preservation of species *per se*, and so park design may need to consider the probability of local extinction and consider ways of compensating for this.

There are further reasons for doubting the applicability of this model to the planning of reserves, but these will be developed more fully in Chapters 4 and 5.

The preservation of large areas of relatively undisturbed land can be justified on other grounds, such as the need to maintain genetic diversity, but the MacArthur-Wilson model should not be invoked to justify this procedure.

1.4 Validity of "tests"

1.4.1 Regression Studies

Despite the general acceptance of the model, a number of criticisms can be made. These relate to the reliability and uncritical nature of some "tests" of the model, and some more general points about

the model itself.

Connor and Simberloff (1978) noted that the conclusions of two multiple regression studies on the avifauna of the Galapagos Islands differed (Johnson and Raven 1973; Hamilton *et al.* 1963). Hamilton *et al.* claimed that the number of plant species was best predicted by untransformed values for area and elevation, while Johnson and Raven (1973) concluded that the log of area was the best predictor. In order to resolve this, Connor and Simberloff (1978) reanalysed these data, including a recalculation of island areas and elevations and the use of more comprehensive present-day species numbers. They found that for a given island, the two studies differed by as much as 39% in the calculated areas, and 42% for elevations. The floral lists from individual islands also differed between the two studies. Further, Simpson (1974) claimed that species numbers for Galapagos flora are a reflection more of areas of islands during the Pleistocene than present day areas, which implies that they are not at equilibrium in present day conditions. Connor and Simberloff (1978) reanalysed her data as well. They found flaws in the regression analysis; further, her conclusions could be altered by the type of regression. When forward-stepwise regression was used, present-day conditions (area, elevation, isolation etc.) were the best predictors of species number, while if all variables were included regardless of whether they explained significant amounts of the residual variance in species number, glacial configurations were superior. The above conclusions were altered if the same analyses were repeated using log-transformed variables, or if the independent variables only were log-transformed.

A stepwise regression seems preferable in this case, since the aim is to generate an equation which predicts species number as accurately as possible, ie which maximises r^2, the coefficient of determination.

Connor and Simberloff (1978) also criticised the criteria by which species were included by Simpson, and calculated a further regression using more accurate species lists. They found that present-day island conditions were better predictors of plant species number than glacial conditions. This was true for both log-transformed and untransformed variables.

However, it is notable that, when such regressions are performed, the independent variables are usually either all untransformed or all log-transformed. No combination of the two is done, and it is possible that the value of r^2 may be altered by this procedure. In the multiple regressions of Connor and Simberloff (1978, Tables 4,5), for example, the independent variables do not enter the regression equation in the same order when untransformed as when log-transformed. This suggests strongly that some variables are better predictors when on a log scale, others on a "natural" scale. If a log-normal distribution of species abundances is assumed (Preston 1962; MacArthur and Wilson 1967), then there are *a priori* grounds for transforming area to $\log_{10}$. However, for variables such as isolation, distance to centre of archipelago, and possibly elevation, there are no *a priori* grounds for the log-transformation; if the desire is simply to increase the overall r^2, then transformation other than a $\log_{10}$ transformation might also be attempted.

The essential point to be derived from the analyses of Connor and Simberloff is that for a group of islands as well-known as the Galapagos, serious errors in measuring areas, elevations etc. have been made, and species numbers have been calculated erroneously. These mistakes have been sufficient to completely alter the conclusions of various studies. It seems likely that if such errors have been made for the Galapagos, then less well-known island groups may also have errors associated with them.

In this case, it is not only the dependent variable which must be regarded as having been estimated with error, but the independent variables as well. All multiple regressions in the literature have been Model I type regressions, but Model II is appropriate when independent variables may have measurement error. The use of Model I regressions on data for which Model II is appropriate will tend to overestimate regression coefficients (Sokal and Rohlf 1969).

Collecting bias was also shown to be important by Connor and Simberloff (1978). They included the variable "number of collecting visits" in the list of independent variables, and found that it entered the regression first. It was possible that this may have been the result of a strong correlation between area and collecting visits, i.e. large islands are visited more often. This was tested by using forced multiple regression, with area entering the equation first. When variables were untransformed, the number of collecting trips also entered the equation, indicating that it explained a significant amount of residual variance independently of its correlation with area. This was not true for the log-transformed data. Connor and Simberloff also showed that more collecting visits are made to islands with high elevation. This may be especially important when comparisons are made between early and recent surveys, since very early investigators on ships would be expected to miss small islands, but to notice larger islands with high elevations. The high elevation may be indicative of a higher probability of obtaining fresh water, so that longer and more frequent visits could have occurred.

1.4.2 Species-Area Curves

It has been implicitly assumed by many authors that the presence of a species-area (S-A) curve is indicative of equilibrium, and that islands which deviate from this curve are disturbed. These curves have been assumed also to be evidence in favour of the MacArthur-Wilson

model, and even as a test of the model (e.g. Grant, 1970). Simberloff (1974) has pointed out that there are a number of other ways in which a species-area curve could be obtained. While the MacArthur-Wilson model implies a species-area curve, the converse is certainly not true. Simberloff has frequently been ignored, however.

Connor and McCoy (1979) reviewed the published species-area curves with a number of questions in mind.

1. Is there a best form of the S-A curve?

2. Do the parameters c and z of the power function have any biological meaning?

1. There are a number of possible forms of the equation;

(a) $S = c + z\,A$ - linear (S/A)

(b) $\log S = c + z\,A$ - log species/area (logS/A)

(c) $S = c\,A^z$ or rather

$\log S = \log c + z \log A$ - power function (logS/logA)

(d) $S = \log c + z \log A$ - exponential function (S/logA)

It is the power function which has been predominantly used in the literature and, in most cases, the alternative models were not even examined. Connor and McCoy reexamined 100 data sets and fitted the above four curves to each of them. The best fitting curve was selected by eye, and if the r values for the regressions differed by less than 0.05 for two curves, they were deemed to fit the data equally well.

There is a problem if the value of Pearson's r is used to compare the fit of two curves. The amount of variation explained by the regression is r^2, and if we consider two regressions whose correlation coefficients differ by 0.05, i.e. $r_2 = r_1 + 0.05$, then the coefficients of determination (r^2) for the two curves will be r_1^2 and $r_2^2 = r_1^2 + 0.1\,r_1 + 0.0025$.

If we consider the coefficient of determination as a measure of goodness-of-fit, then Connor and McCoy's measure is not independent of

the value of r, since the difference between the fits of our two hypothetical curves is 0.1 r_1 + 0.0025. Consider two extreme cases, r_1 = 0.90 and r_1 = 0.01. If r_2 is r_1 + 0.05, then for r_1 = 0.01 the two curves would be regarded as different even though the r^2 values differed by only 0.0035, while for r_1 = 0.90, the difference between r^2s could reach 0.0925 without the curves being distinguished from each other.

The r values were never compared statistically. Sokal and Rohlf (1969) give the comparison between r_1 and r_2 as

$$t_s = \frac{r_1 - r_2}{\sqrt{\frac{1}{n_1-3} + \frac{1}{n_2-3}}}$$

, and the value of $t_{0.05,\infty} = 1.96$ is used as the critical value. Of the 100 data sets examined by Connor and McCoy, only three had sample sizes of greater than 50. If we conservatively take 50 as the sample size from which r_1 and r_2 were calculated, then we can calculate the minimally significant value for $r_1 - r_2$, as

$$|r_1 - r_2| \geq 1.96 . \left(\frac{2}{47}\right)^{\frac{1}{2}}$$

$$\geq 0.404$$

That is, for the sample sizes available from the literature, the two correlation coefficients need to differ by at least 0.404 to be regarded as significantly different. This suggests that it is almost impossible to distinguish statistically between curves, especially since in many cases the power curve will approximate the linear curve.

It is still possible to make a decision about which curve fits the data best, even though there may be not statistical significance, and given this, r^2 seems a more appropriate measure than r. I reexamined regression equations for the four curves for the 100 data sets (Connor and McCoy, 1979; Appendix 2). If the r^2s for two regressions differed by less than 0.05, they were designated equal. The resultant

conclusions (Table 1.1), did not differ qualitatively from those of Connor and McCoy (1979), viz. that all models fit at least some data sets well.

It is notable, however, that the two criteria give rather different results for a given data set. There was agreement for only 46 out of 100 data sets listed by Connor and McCoy. More models gave equally good fits when r values were low, and for high r, there were more cases of single models fitting best.

For 44 out of 100 cases, more than one model fitted the data well, and five were fitted by all four models. A particularly good example of the fit of various curves can be seen by examination of species numbers on patches of hard substratum in the marine epifaunal communities at Edithburgh. Two types of jarrah (*Eucalyptus marginata*) patch were used: cleared patches on pier pilings, i.e. patches surrounded by sessile organisms, and jarrah panels attached so as to be isolated. The other three examples are of animals epizootic on the bivalve mollusc *Pinna bicolor*. One data set is from a random sample of *Pinna* shells 5 metres south of Edithburgh pier. Two were from a random sample of *Pinna* shells beneath Edithburgh pier. The two valves of each shell were scored separately. The jarrah panels were censused visually, the *Pinna* shells beneath the pier were collected and surveyed visually in the laboratory, while those south of the pier were surveyed photographically. Further details appear in Chapter 2.

I plotted S/A curves using all four equations, and selected the best fit by (a) Connor and McCoy's (1979) criterion, i.e. the value of r for two equations,

(b) My criterion - Coefficients of determination for two equations,

(c) Testing of homogeneity amongst the significant coefficients, followed by pairwise tests to determine which pairs did

not differ significantly.

The results are shown on Table 1.2. The most conspicuous difference is between the Left and Right valves of *Pinna* beneath the pier. The S-A curve which best explains the Right valve sample is the exponential regardless of the criterion used. The Left valve is best described by a linear, power or log S/A by criterion (a), the power or log S/A curves are best by criterion (b), and all four fit the data equally well by criterion (c).

The three *Pinna* data sets also are not consistent in the equation which best describes them (Table 1.2). Similar inconsistency is shown by the jarrah patches. This lack of agreement occurs regardless of the criterion used.

There is thus no empirical justification for the use of the power curve, aside from its ability to linearize a great number of relationships. Its theoretical justification was derived from the log-normal distribution of species abundances by Preston (1962), but Preston stated that this distribution would be expected only if the islands are true isolates and if the number of species was high. These assumptions are never tested, and indeed the first is rather vague. The distribution of species abundances is never compared with a log-normal distribution, and so the theoretical basis for using this power curve is at best unsubstantiated.

2. The meanings of z and c.

Preston (1962), again assuming a log-normal distribution, predicted a value for z of 0.262. Arrhenius (1921), on the other hand, had suggested that both z and c are merely fitted constants. The slope (z) has been suggested to have some biological meaning and often to reflect differences in island type or isolation. MacArthur and Wilson (1967) noted that "most (values) cluster in the range 0.20 - 0.35", but suggested that for non-isolated sample areas, z values were usually

between 0.12 and 0.17. They further suggested that z values should rise with the degree of isolation of an archipelago.

MacArthur and Wilson (1967) also suggested that the value of c should vary among taxa, and depend upon species diversities, population densities, and isolation. Connor and McCoy (1979) found a mean slope of 0.310 for their 100 data sets detailed in the previous section. Standard deviation however was 0.277, and range -0.276 to 1.132. There is clearly no general value for z. Schoener (1976) and May (1975) suggested that frequently observed z values were merely coincidence, but Connor and McCoy were even stronger in their comments. They suggested that since $z = r(\frac{S_y}{S_x})$ for a log-log regression, and since r values are usually 0.5 to 1.0, while $\frac{S_y}{S_x}$ was 0.20 to 0.60 for their 100 data sets; random multiplication of these values gives most z values in the range 0.20 to 0.40, without any need to invoke biological meanings for z. As Connor and McCoy (1979) emphasise, values of z in this range should be treated as a null hypothesis, and only significant deviations from this range should be considered. Schoener (1976) proposed even more conservative criteria; he suggested that values in the range 0 - 0.50 should be a null hypothesis.

There is no general agreement on the null hypothesis values for z, and hence no testing is possible to determine whether it is necessary to invoke biological interpretations for "deviant" values.

There are fewer attempts to interpret the intercept, c. Johnson and Raven (1970) hypothesized that the intercept varies with latitude. Haas (1975) viewed it as little more than a fitted constant of little importance. Kilburn (1966) suggested that c measures in some way the average size of abundant species (!) and Wilson (1961) and Preston (1960) regarded c as a measure of the number of species and of individuals per unit area respectively. Gould (1979) collected families of S-A curves which had constant slopes, and compared intercepts.

He interpreted the differences in intercepts in terms of differing species richnesses and differing degrees of isolation and the presence of stepping-stone islands.

To ascribe a meaning to the value of c requires extrapolation back to A = 1, when the observed A-values are frequently well outside this range. Such extrapolation is dubious at best, since it assumes the shape of the curve to be constant outside the observed range of values. Similarly, the lumping together by Gould of S-A curves with the same or similar slopes presupposes some significance to the value of z. In view of the previous section, the searching for biological meaning for a series of c values from a series of curves which may have been collected together because of coincidence alone, seems pointless. It seems best to treat the c value as a fitted constant, with no biological meaning for the present.

1.5 More General Criticisms

Beyond a consideration of the validity of the "tests", there is a number of less specific doubts about the applicability of the MacArthur-Wilson model. They concern the use of species number, the importance of stochastic processes, disturbance, and unequal colonization rates.

1.5.1 Species Number

An implicit assumption is that species number reflects in some way the nature of the species assemblage in a given patch. It is similar to all other diversity measures in this respect, and various authors (e.g. Hurlbert 1971; May 1976) have suggested that such measures provide an inadequate description of community structure.

The use of nothing but species number to describe a community

implies that all species are regarded as equal, although many authors have made it clear that they regard this as a gross oversimplification. There are many examples in the literature of single species exerting an influence on other species which is disproportionate to their abundance. Such species are frequently predators, and examples may be found in many habitats (e.g. Paine 1966; Addicott 1976; Harper 1977). Menge and Sutherland (1976) proposed a qualitative model which predicted when such species might be expected to occur. Their model used trophic complexity and trophic level to predict whether predation or competition would be more important in organising a community (i.e. controlling species number). Such a predictive model is potentially important, since the MacArthur-Wilson model assumes that extinctions are brought about by competitive interactions and chance fluctuations in population size. No mention was made of the impact of predation. The model of Menge and Sutherland (1976) has been criticised by Keough and Butler (1979), who reported examples of communities where predation would have been expected to be important, but was not. They further noted that when predators had been shown to be important, the mechanism was the suppression of a potentially dominant competitor at a lower trophic level. The classic work of Paine (1966) is the best-known example. He showed that the seastar *Pisaster* preyed preferentially on the mussel, *Mytilus californianus*, preventing it from occupying all space on a rocky shore. The bare space created by the feeding of the seastars could then be occupied by species which would have been outcompeted by *Mytilus* in the absence of *Pisaster*. A number of marine epifaunal communities have been reported not to have potentially dominant competitors amongst the sessile organisms adhering to hard substrata (Keough and Butler 1979; Kay and Keough 1981; Sutherland and Karlson 1977; Osman 1977; Kay 1980; Jackson 1977; Buss and Jackson 1979; Sutherland 1974). Kay and Keough (1981) have suggested that competitive interactions in such communities

do not result in consistent superiority of one species over another, but that many interspecific competitive encounters are intrinsically variable. In this case, the question of competitive dominants becomes unimportant. Kay and Keough (1981) suggested also that the analysis of competitive relationships in the literature was often marred by poor replication; thus such variable situations may be more widespread in ecological communities than has been realized. Keough and Butler (1979) claimed that since a potential competitive dominant appears to be a prerequisite for predation to effect an increase in species number, the question of which kinds of community have competitive dominants is fundamental. As a consequence of this, models such as that of Menge and Sutherland (1976) have little value.

Accordingly, when we are completely unable to predict when and if predators or dominant competitors will be important, the assumption that all species are equally important is unjustified. It is thus of interest to know whether the equilibrium model is robust to violations of this assumption.

1.5.2 Colonisation Rates

Colonisation rates have also been assumed to be invariant in time, and although it has been acknowledged that probabilities of colonisation differ between species (e.g. MacArthur and Wilson 1967), there has been little consideration of the consequences of these differences. MacArthur and Wilson considered that differing colonising abilities between species would produce a concave immigration curve. They stressed that the shape of the curve was immaterial, as long as it was monotonic, thus implying that their general theory was to some degree robust to the effects of varying probabilities of colonisation.

MacArthur and Wilson (1967) also introduced the concept of "r-" and "K-" selected species. These terms have become somewhat confused, and are a gross oversimplification (e.g. Grime 1979; Stearns 1977), but nevertheless poor competitors frequently have high colonisation rates, and good competitors are often less prolific colonisers (Grime 1979; Kay and Keough 1981). In addition, predators tend to be less abundant than their prey. It is thus possible that species which might be expected to play an important role in influencing species number or some other aspect of community structure, may have low probabilities of colonisation. Therefore colonisation curves may not increase steadily with time, but may show points of inflexion which can be related to the arrival of biologically "important" species. To my knowledge, this question has not been investigated.

Many species show temporal variation in dispersive ability. There are frequently more dispersing individuals during warmer months. This has been noted by Osman (1978) for sessile marine invertebrates, Molles (1978)for coral reef fish, and Hunt and Hunt (1974) for birds. Many other examples exist. Osman (1978) suggested that seasonality in immigration rates should affect the shape of colonisation curves for bare patches, but that regardless of when colonisation commences, all curves should converge to an S value which cycles seasonally. He was able to observe only the first part of this convergence, and could not document fully any subsequent cycling in S. He was also not able to demonstrate any change in extinction rate, so that it is likely that the fluctuations in S represent changing immigration rates, and a steady number of chance extinctions. Osman suggested that the main value of his study was the demonstration of an effect of varying immigration rates, and that these fluctuations should be regarded as a base-line, against which fluctuations in S could be tested before invoking hypotheses such as competition to explain the changes.

1.5.3 Disturbances

Two types of disturbance are generally considered; biological and physical. The chief "biological disturbance" is predation, which has already been discussed. Physical disturbances have been demonstrated to be important in some communities by removing potentially dominant species and freeing a resource (e.g. space) for use by other species (e.g. Dayton 1971). Common disturbances may be elements such as wave-borne logs (Dayton 1971), wave action itself (Osman 1977), cyclones (Connell 1978), fire (Whittaker 1975), and volcanic eruptions (Dammerman 1948).

Disturbance has been used to account for observations where avifaunas contain fewer species than predicted by the S-A curve for a series of islands (Diamond 1974). Disturbance has thus been viewed as displacing island biotas from their equilibria with the implicit assumption tht the biota will return to the equilibrium number of species. If the frequency of disturbance is sufficiently high, relative to the time required for re-equilibration, then the biota in question will never reach equilibrium. Clearly then the concept of equilibrium will be of little use. Such systems have been demonstrated (Sousa 1979; Sale 1977, Richerson *et al.* 1970) or suggested (Connell 1978). Sousa (1979) suggests that such systems may be widespread, and that the small number of examples is due to lack of searching.

There is *a priori* no way to predict when disturbances will be important, and the only alternative is detailed investigation of individual patchy habitats to assess disturbance. Unless this is done the presence of disturbance and the application of an equilibrium model could produce misleading results. An example of this is the (erroneous) use of S-A curves to make inferences about turnover rates. If an S-A curve was plotted from a series of disturbed patches, the resulting inferences would be inaccurate, since the supposed

'equilibrium' S-A curve would have been plotted using non-equilibrium values of S. Therefore, islands which deviated from the curve could be those at equilibrium.

1.5.4 Chance

When islands are well-isolated from the source of their colonists, it is reasonable to expect that the probability of immigration per unit time is low for many species, i.e. there are many rare events. Indeed, Abbott (1979) suggests that this is the case for most birds on islands off the Australian coast. The probability of a given sequence of rare events is much lower than that of a single such event. We would thus expect two equidistant patches of equal size to differ greatly in the individual events which occur on them. This will be termed between-patch variation for the remainder of this thesis. Chance events are thus likely to be important, especially if there are important predators which colonise with low probability, or rare but important physical disturbances. Stochastic models are to be preferred in this situation.

MacArthur and Wilson (1967) envisaged that for a given island size and isolation, $\hat{S}$ would be a random variable, approximately normally distributed; the value displayed, for example, on Fig. 7 in MacArthur and Wilson (1967) would be the mean or expected value for this variate. They showed that for a series of identical islands with the same I and E curves, the turnover of species would produce changes in S, which would in turn alter the values of E and I, since they are functions of S. These changes would not be synchronous on all islands, and so at some time t, the set of islands would have a range of S values. From this, a mean and variance of S could be calculated. Although not stated, this presumably could also be applied to the distribution of S with time.

They suggested that it was possible to examine the distribution of species number on a series of similar islands and deduce immigration and extinction rates. In doing so, however, they assumed that all islands were at equilibrium. Again, if disturbances were frequent, some islands would not be equilibrium. Their deduction of immigration and extinction curves is based on the exact shape of the frequency distribution of $\hat{S}$ values, so that the estimation of E and I would be erroneous. Disturbances are themselves recognised as being patchy (e.g. Connell 1978; Dayton 1971), and the failure to consider these kinds of events must reflect on the usefulness of the above analysis.

Chance fluctuations in population sizes are responsible for an unstated proportion of the total extinctions on a given island. Chance is again assumed to play an important role, but it is strange that the equilibrium model takes little account of this. In other sections of their book, MacArthur and Wilson use Lotka-Volterra models of population growth, and so the emphasis is on deterministic processes. Nevertheless, parts of the book represent a real attempt to model a stochastic process.

Much of their section (Chapter 3) on variation in $\hat{S}$ values has become ignored in what appears an eagerness to use a model which seems to make simple unambiguous predictions. The value of $\hat{S}$ is generally regarded as a deterministic value, with no variance. If the crude estimates by MacArthur and Wilson are adopted as a guide to the variance of $\hat{S}$ for an island of a given size, there would at least be a simple null hypothesis. A S-A curve would then have an associated variance, or 95% "Confidence band" and points which lay outside the "confidence band" could be regarded as "non-equilibrium" or "disturbed" rather than simply any points which do not lie on the curve (cf Diamond 1974).

In most studies, the variance of $\hat{S}$ is difficult to calculate, since there are few islands of similar size. Abbott (1979) has

suggested that morphological and compositional changes in island avifaunas may be due as much or more to differences between islands in plant communities, and hence type and abundance of food for the birds, as to interspecific competition. Thus, if island floras are different, the islands in question cannot be regarded as replicates for estimating that part of the variance of $\hat{S}$ which is due to chance.

$\hat{S}$ is of course only one aspect of the equilibrium model. The immigration and extinction curves are subject to chance variation, and this is likely to affect the equilibrium, in view of Osman's (1978) result that cyclic, seasonal changes in immigration rate affect $\hat{S}$. Random changes in I or E are thus likely to produce unpredictable, short-term changes in $\hat{S}$. The magnitude of these is difficult to estimate.

1.5.5 Chance and Competition

Competition has frequently been postulated as an important determinant of community structure of island biotas (e.g. Diamond 1975; Lack 1969, and see especially the review by Abbott 1979). Many studies have used patterns of presence and absence of species across a series of islands to infer the existence of competition. Connor and Simberloff (1978) have criticised this view, because when the species pool is even moderately large and the number of islands small (both conditions are nearly always met), the number of possible combinations of species is so large that the majority of species combinations will necessarily be absent. Connor and Simberloff (1978) used the frequency of occurrence for each bird species to calculate a probability of its being on a given island. They then drew species randomly for a given island until the number of species was equal to the observed number for the island in question. They repeated this for all the Galapagos Islands, and repeated the procedure until there were 200 random species compositions for each island. They concluded that many of the

observed distributions could be explained by chance. Connor and Simberloff (1978) also criticized Abbott *et al.* (1977) for what they claimed was a deterministic view of the processes of community composition; they claimed that Abbott *et al.* (1977) ignored chance, and concluded that floristic diversity and interspecific competition were the main determinants of community structure. Grant and Abbott (1980) disputed this criticism, but part of their reply is illustrative of a common attitude to chance :

> "The logical primacy of randomness is debatable. Where different causal factors are implicated in the determination of complex phenomena like community structure, it is just as valid to test contrasting deterministic explanations against each other as it is to test each one against a random hypothesis."

It is unclear how other causal factors can be "implicated" without first generating a null hypothesis which is random and comparing the observations to this. A non-interactive hypothesis is more parsimonious, and should be the first to be tested on these grounds alone. This point is of course not specific to island theory; interactive models predominate in ecology, and while it is clear that biological interactions will frequently be important, it is nevertheless important that "neutral" models be used, even if only to provide "baseline" predictions for assessing the importance of such interactions.

1.6 Stochastic Models

It is likely that the persistence of deterministic approaches has occurred for two reasons. Firstly, the implicit aim of ecologists and scientists in general is to produce generalised explanations or models for natural phenomena. Simple models have obvious appeal, since they are unambiguous and can be used to generate clear predictions. They thus appear "tidier" and indeed, if their predictions are sufficiently accurate, this is a proper consideration. There is then a certain reluctance to invoke stochastic processes, since it constitutes an admission that there exists variation in the data which

can not be "explained", and hence the model cannot be used to make unequivocal predictions.

Secondly, it has been assumed that the mean outcome of a stochastic model is the same as the output from the equivalent deterministic model. Thus, it is sufficient to use a (usually) simpler deterministic model and regard the output as a normal variate, for example. This view has been challenged recently, for example by Chesson (1978). He showed that for a series of predator-prey models, the outcome of a properly constructed stochastic model may be qualitatively different from that of the equivalent deterministic one. In a subsequent paper (Chesson and Warner ms) he examined the coexistence of competing species. Sale (1977) proposed that coral reef fish communities were maintained by clearing of habitat and random colonisation by fish larvae. The species which first arrive are then able to persist, excluding all others. This is known as a lottery competitive system. May (1973, 1974) suggested that environmental variability, such as random clearing of space, tended to destabilize the interaction between competing species, making coexistence impossible. His models were derived from the Lotka-Volterra equations, i.e. were basically deterministic. Chesson and Warner produced a stochastic model which arrived at the opposite conclusion, i.e. that coexistence can be enhanced by environmental fluctuations.

These findings are not widespread, but stochastic models have received relatively little attention in ecology, although they have been in common usage in population genetics since the 1930's (e.g. Sewall Wright 1932). We may expect that further work will produce more results of this kind; clearly for the present we can no longer assume that a deterministic analogue is an adequate substitute for a stochastic model. The resemblance between the experimental findings of Sale (1977) and Talbot *et al.* (1979), and the stochastic model of Chesson and Warner (ms) suggests that the stochastic model may be more reasonable biologically

than the deterministic model used by May. There must thus be serious doubts about any model which does not have chance incorporated into it.

To sum up, the equilibrium model is basically stochastic, but it was assumed that the variances are not too large, and that other rather predictable interactions will occur, so that average rates (I and E) and "average" values of $\hat{S}$ provide an adequate description of events. The stochastic element has been ignored by workers who have been trying to maximize the amount of variation in species number which can be explained by factors such as area, isolation etc.

Again, it must be stressed that the use of "average" conditions depends on the magnitude of variances; it is not necessarily true that a stochastic process can be usefully described in this way. It is therefore crucial to decide on a useful level of fluctuation, and to measure and test observed fluctuations against this standard.

1.7 Alternative Approaches

There is a number of alternative models for patchy environments. None, however, have the simplicity of the MacArthur-Wilson model, nor do they make such apparently clear predictions. The approaches are generally more recent, and consequently less well-developed. I propose to outline these approaches, with emphasis on those features which are different from the MacArthur-Wilson model. It would be preferable if neat tests could be performed to distinguish between the variety of approaches, but this may not be possible.

The MacArthur-Wilson model is simple and uses a crude output variable, species number. The species-area curve and the uncertain nature of the equilibrium mean that the model perhaps presents a problem analagous to that with the log S/log A equation for the species-area curves discussed above. The log-log curve fits many data sets,

partly because it makes almost any curvilinear relationship linear. Other regression equations may also fit the observed data, and the problem was to distinguish between a number of plausible curves. The regression models often could not be distinguished. A similar problem may arise with the various approaches to patchy systems. They may all approximate the data moderately well and, rather than being able to reject one model, we may need to decide which approach gives the closest fit. As was also seen from the earlier section, selection of the criteria for goodness-of-fit can itself alter the decision.

Paine and Levin (1974) proposed that the events within an individual patch are highly variable, and that interest should be focussed on the assemblage of patches as a population. The individual patches then form the basic unit for study of such a system, and the community is regarded as a mosaic. This is obviously not suited to all habitat patches, since on large islands evolutionary changes in populations may occur, and to look across a series of such patches would be to ignore what could itself reasonably be termed a community.

Paineand Levin defined two important aspects of such systems; the "population dynamics" of the patches themselves, and the dynamics of the species living within a patch as a function of the age, size and "growth rate" of the patch. Their model specifically related to disturbance in space-limited communities, and only explored the first of the two above aspects. The paper exploring the second aspect has not yet appeared. The main advantage of their model was its recognition of stochastic factors as potentially important.

Sousa (1979) showed that the biota under boulders are frequently disturbed by wave action, so that few patches are at an equilibrium or climax. It is more appropriate to view the community as being composed of a series of patches at different successional stages, and to

investigate the factors which determine the frequency of disturbances. He also showed that for three species of red algae, very few populations remained constant, and frequent extinctions and colonisations were more typical. Osman (1977) proposed a similar explanation for the epifauna below boulders.

A similar model has been proposed by Connell (1978) to account for the diversity of reef-building corals and rain forest trees. The commonly proposed view is that niches are "coadjusted" so that the species are closely knit and resist invasions. The community is thus an equilibrium one. Connell proposed that if the time scale of these communities is taken into account, disturbances are not infrequent relative to this timescale, and so equilibrium is never reached. Patches of different sizes are cleared by disturbances of varying severities, and at any one time there will be a range of patches of different sizes and ages. Ideas like those of Connell and Sousa, although not a quantitative model, nevertheless represent a clear alternative to equilibrium ideas.

Hubbell (1979) also assumed occasional disturbances to be important, and proposed a simple stochastic model incorporating random extinction and immigration, together with localised, small scale disturbance. His model is essentially neutral, in that it uses Markov processes ("random walks"), which can generate the kinds of patterns of species abundances which could be construed as implying competitive dominance, without assuming competitive interactions. A species- area curve is also predicted by Hubbell, as is a lognormal distribution of species abundances. This model thus has several features in common with the MacArthur-Wilson model.

These approaches are all non-equilibrial, and rely on some form of disturbance. It remains to be seen how widespread moderate levels of disturbance are in natural communities. Certainly, their

proponents have not made sweeping claims of generality (e.g. Connell 1978).

1.8 Studies on Marine Hard Substrata

There have been few experimental studies of the equilibrium model for communities on marine hard substrata. This is perhaps surprising in view of the advantages of such communities.

The animals are frequently sessile, and thus provide unambiguous residency criteria, and may be surveyed readily. Such a system is essentially a guild of one trophic level, sessile filter feeders, and so provides a simplified experimental system.

The animals involved are small and invertebrate, and there are certainly no legal or ethical barriers to the introduction or removal of a species of, say, bryozoan, in a habitat island or patch. Manipulations are thus simple to perform, and the small scales mean that many replicates are possible. Similarly, life spans of many species are relatively short, and a single experimenter can observe a series of patches through a number of generations.

The question of whether area *per se* or habitat diversity is the cause of the observed species-area relationships becomes redundant also, since for many substrata there is very little habitat diversity. They are simply fairly uniform two-dimensional surfaces, to which the organisms attach. Exceptions to this occur, of course, notably the coral heads studied by Austin *et al.* (1980), Abele (1974, 1976), Abele and Patton (1976), and laminarian fronds (Boaden *et al.* 1976) where different species occur on different parts of the blade.

A final advantage is found when hypotheses about competition are to be tested. Sessile organisms on hard substrata compete for space (Jackson 1977; Connell 1975), and in such a simple community,

there is generally only one resource axis (two-dimensional space) which is important. It should be noted however, that one study has suggested that the organisms may also complete for food, or that the competition for space may be modified by competition for food (Buss 1979a). It is thus easy to measure the way in which the postulated important resource is being used.

Some aspects of the equilibrium model cannot be investigated in these systems. The epifaunal organisms are attached permanently to the substratum, but they produce dispersive larvae. It is highly unlikely that any of these larvae settle onto the same patch(es) as their parents, and so there is little or no chance of any genetic changes occurring within a given patch or habitat island. The many hypotheses about, for example, morphological changes in island populations (for a review see Abbott 1979) cannot be tested here.

The fact that dispersal is almost exclusively by reproductive propagules and almost never by adult organisms is a difference between marine systems and, say, birds on oceanic islands, where dispersal is almost exclusively by adults, or "post-larvae".

Similarly the existence of planktonic larvae which are readily dispersed means that there is no point source of colonists. Rather, the colonists must be regarded as having come from a source which completely surrounds the area in question, and hence all patches are equidistant from the source. Hypotheses about changes in biotas with degree of isolation are thus difficult to test.

Osman (1978) regarded the criticism that water can not be thought of as a physiological barrier to the dispersal of planktonic larvae as it can for birds on oceanic islands, as potentially serious. The analogy is not valid, however, since birds travel through air, not water, and the air is not a physiological barrier. It is the distance which must be travelled with little food which imposes the limits, and

this is true for both cases, since many planktonic larvae die if they are unable to find a suitable substratum.

More importantly, however, both cases are truly patchy habitats, and any model purporting to explain one should be applicable to other cases. It is the patchiness of the habitat which is important, rather than the nature of background to the patches.

Perhaps the best designed marine study is that by Osman (1978), who investigated the epifauna of subtidal rocks.

His work on seasonal changes in immigration and extinction rates has been discussed previously. Similarly, the work of Abele (1974, 1976), Abele and Patton (1976), and Austin *et al.* (1980) has been mentioned already.

Molles (1978) examined the colonisation by fish of artificial reefs, and concluded that equilibria were reached, and that turnover was high. He also showed a strong effect on S due to between-year variation in immigration and extinction rates. His experiments could only be continued for 415 days, however.

Schoener (1974a,b) reviewed the published studies on fouling panels and conducted her own experiments on the colonisation of artificial substrata. She concluded that most studies show little evidence of any equilibrium. This was interpreted as being due to very large species pools so that immigration rates did not fall off, and to seasonality, so that colonisation curves showed seasonal fluctuations. Sutherland and Karlson (1977), however, suggested that the short duration of many studies was the main reason. At Beaufort, North Carolina, species number for artificial substrata reached an equilibrium after 1 to 1½ years. Sutherland and Karlson (1977) based their conclusions on regressions of species number against time, and testing of the slope of regression for equality to zero. This is a rather crude test, since a graph where S fluctuated widely would still give a

zero slope. In this case, to speak of an equilibrium would seem not to be very useful, since the fluctuations would not be narrowly bounded. Examination of their analysis shows that the standard errors of the regression coefficients varied from forty to over four hundred percent of the regression slopes. It thus seems more likely that their zero slopes are due to highly variable species numbers, rather than fluctuations with a small amplitude. Moreover, six out of 21 panels for which they performed the calculations showed significant positive regression coefficients.

There is clearly no concensus about the existence of equilibria for marine communities in patchy habitats.

1.9 Equilibrium Theory - The Current State

The model of MacArthur and Wilson (1967) has been adopted and is widely used in both pure and applied ecological research. A large number of field studies has accumulated which have been regarded as support for the equilibrium model. Two major predictions have been generated by this model:

(a) Species number should increase with area of patch

(b) Species number should increase, then remain (relatively) constant with time, while species composition changes constantly.

The majority of field studies have produced evidence to support the first of these predictions. This has been regarded as a "test" of the model, but in fact a variety of other phenomena can produce identical curves of species against area, so that the observation of a monotonically increasing relation between species and area provides no evidence for or against the equilibrium model.

The second prediction has been tested less frequently but it is the prediction by which the equilibrium model can be rejected, providing

that "equilibrium" is defined *a priori*. Of the small number of studies which have been done, very few have survived critical scrutiny.

It therefore follows that the equilibrium model is far from fully tested. Despite this, it has been elevated far beyond the level of hypothesis. Indeed, Abbott (1979) considers it to have reached paradigmatic status (sensu Kuhn 1962). On the basis of the evidence presented this far, this elevation is certainly unwarranted. MacArthur and Wilson (1967) did not view the book as an end to speculation about communities, but rather as a beginning. The faulty elevation of the model is due to subsequent followers, rather than the original proponents.

There is thus adequate scope for good, replicated tests of the equilibrium model. In addition to this there are some serious general criticisms relating to aspects which are not included in the equilibrium model, or have not been incorporated into subsequent investigations despite being proposed in the original model. The importance of these is also amenable to testing. These criticisms include doubts about the usefulness of species number, the lack of definition of equilibrium, the failure to take account of disturbance and the assumption that chance fluctuations do not alter the predictions of the model.

A number of hypotheses were available to be tested, given a definition of equilibrium, for example that derived on pp. 5-6 . This study aimed to test some of these hypotheses.

1.10 Some Hypotheses to Test Equilibrium Theory

The existence of any "equilibrium" condition is the first area of investigation. MacArthur and Wilson (1967) postulated a variance of $\hat{S}$, but if the concept of equilibrium is to be of any use, most patches need to be at equilibrium, and preferably to have $\hat{S}$ as their species number. Hence :

Hypothesis 1. Most patches have fluctuations in S which are narrowly bounded, i.e. 95% of S values fall within the region $\bar{S} \pm w\bar{S}$, where w = 0.20.

Alternative: S fluctuates too widely on most patches (i.e. the bounds are too large) for the concept of an equilibrium to be useful. Patches are either frequently disturbed, or chance fluctuations are so great that the fluctuations never become damped.

If Hypothesis 1 were accepted, there would be little more to say. If however, the hypothesis were rejected, a number of alternative areas would be available for investigation. I had only three years to conduct this project, and the testing of Hypothesis 1 could take most of that time. I therefore was forced to assume that it would be rejected, and design other experiments under this assumption.

Hypothesis 2. The recruitment rates of individual species differ, but considering all species together smooths out this variation in recruitment, and colonisation events (i.e. numbers and abundances of species arriving per unit time) do not differ greatly between similar patches.

Alternative: Chance events are important and, together with the temporal variation, mean that colonisation rates for individual patches are highly dissimilar.

Hypothesis 3. This was to be tested assuming that hypothesis 2 would be rejected. Chance fluctuations in recruitment are large, but the S values are influenced more strongly by interactions between adult organisms, so that the variation in recruitment becomes unimportant.

Alternative: Subsequent patterns of abundance are determined primarily by the patterns of recruitment.

Two further hypotheses concern the implicit assumption that although individual species differ in their importance, regarding them as equivalent by simply counting species does not seriously affect the

model. Similarly, mobile species which visit for short periods are assumed not to have important effects on S. These require testing regardless of the results of hypotheses 2 and 3.

Hypothesis 4. The action of predators modifies the variation in S, and also the existence of a species equilibrium. Thus, events within patches change depending on whether particular predators visit a patch or not.

Alternative: Predators have little effect.

Hypothesis 5. Species have differing competitive abilities, and the variation between patches is modified by the presence or absence of particular species.

Alternative: Competitive interactions produce extinctions, but the effect is not confined to a few species.

1.10.1 This Study

The above hypotheses will be tested using a "community" of marine animals which live attached to naturally occurring hard substrata. These substrata are the shells of the bivalve *Pinna bicolor* Gmelin, which lives embedded in soft sediments with the posterior part of the shell protruding vertically above the sand. The sessile epifauna are unable to cross or to live on the stretches of sand between the *Pinna* shells. The habitat for these epifaunal species in their adult stages is thus truly "patchy", and the individual *Pinna* shells are the patches or "habitat islands".

The following chapters are not in the order of the above hypotheses, but rather are cast, for more logical development, in the form of an investigation into the organisation of the epifaunal assemblages on *Pinna*, i.e. recruitment processes, subsequent dynamics, including the importance of predators and competition, followed by an investigation of the epifaunal assemblages on hard substrata of sizes

different to that of *Pinna*.

Chapter 2 contains an introduction to *Pinna* and its epifauna, as well as the important characteristics of my two study sites.

Chapter 3 is an investigation of the degree of variability in recruitment events on similar patches. Attempts are made to determine the amount of variation in recruitment that can be explained. I then attempt to ascertain the causes of this variation. This chapter is thus a test of hypothesis 2 and provides part of the basic data for testing hypothesis 3.

Chapter 4 examines the dynamics of established epifaunal assemblages. It contains experiments designed to test the roles of predators and individual sessile species. Thus, hypotheses 1, 4 and 5 are tested, and the combination of Chapter 3 and this chapter allows testing of hypothesis 3.

The results in Chapters 2-4 lead to rejection of hypotheses 1, 2, 3, 4 and 5. Therefore in Chapter 5 I attempt to develop and test an alternative model to the equilibrium model. The model is stochastic, and makes only qualitative predictions about the abundances of certain "types of species".

The final chapter examines in detail the results of testing the five hypotheses postulated on page 44 and draws conclusions about the usefulness of the equilibrium model generally. It also contains an attempt to expand the model developed in Chapter 5.

1.11 Terminology

The MacArthur and Wilson model uses immigration rate as one parameter. The definition of what constitutes an immigrant varies in the literature, from temporary residency to the existence of breeding populations (Connor and Simberloff 1978). For sessile marine animals,

the decision is simpler. When a planktonic larva has settled, metamorphosed, survived and grown until it is detectable at the next census, it has immigrated. Immigration has various meanings, but the above process is described in marine environments by one specific term: *recruitment*. This will be used throughout.

Secondly, although the MacArthur-Wilson model is for "islands" it must nevertheless be applicable to patchy environments in general. Accordingly, rather than using island or the slightly vague "habitat island", I shall use *patch* to denote a section of favourable habitat surrounded by an area of more or less unfavourable habitat. When talking of recruitment studies, I use the term *panel* frequently. This refers simply to an artificial flat, two-dimensional patch of hard substratum to which the sessile organisms attach.

In many cases, the experimental patches are a series of identical replicates which are of a particular size, at a particular site and time of year. Panels may thus be classified according to a number of variables - time, space, size, etc. Frequently, the variation between panels of a particular category will be discussed. For clearness of expression, I use the term *between-.....*variation, omitting the state of the other variables. These are by implication held constant for the comparison to be described. For example, *between-panel* variation refers to variation between replicate panels of the same size, at the same site and at the same time. Similarly, *between-time* variation is the variation between two or more panels of the same size, at the same site but at different times. Finally, I shall use the name *Pinna* throughout. This refers to *Pinna bicolor* Gmelin, 1791 (see Rosewater 1961) unless stated otherwise.

TABLE 1.1 Comparisons between criteria for deciding goodness-of-fit among four species-area curves. Further details of the criteria appear in the text on pages 21-3. Entries on the table are the number of data sets in Connor and McCoy (1979) for which the model in question fits the data best.

	Best-fit criterion	
	Connor & McCoy	Mine
Regression model	r	r^2
Linear	50	48
Power curve	53	49
Exponential	52	42
Log species/area	24	20

Contingency $\chi^2_3 = 0.44$, $p > 0.9$

TABLE 1.2 Comparison of four regression models using five data sets from Edithburgh pier. For explanation of best-fit criteria, see pages 21-3. Entries in the table show coefficients of determination (r^2) for the given model and data set. All r values differed significantly from 0 at $\alpha = 0.05$ (t-test).

Regression model	Data sets				
	Jarrah isolates	Jarrah non-isolates	*Pinna* under pier L.valve	R.valve	*Pinna* S of pier
Linear	0.17	0.52	0.55	0.50	0.90
Power	0.36	0.43	0.58	0.50	0.87
Exponential	0.13	0.17	0.50	0.71	0.84
Log S/Area	0.43	0.25	0.63	0.32	0.90
Best-fit					
(a) Connor & McCoy	Log S/A	Linear	linear power Log S/A	exp.	all
(b) Mine	Log S/A	Linear	power Log S/A	exp.	linear power Log S/A
(c) Statistically	Power Log S/A	Linear power	all	exp.	all

Figure 1.1 Variation in Immigration (I) and Extinction (E) rates as a function of number of species present. $\hat{S}$ denotes the equilibrium number of species. (After MacArthur and Wilson 1967)

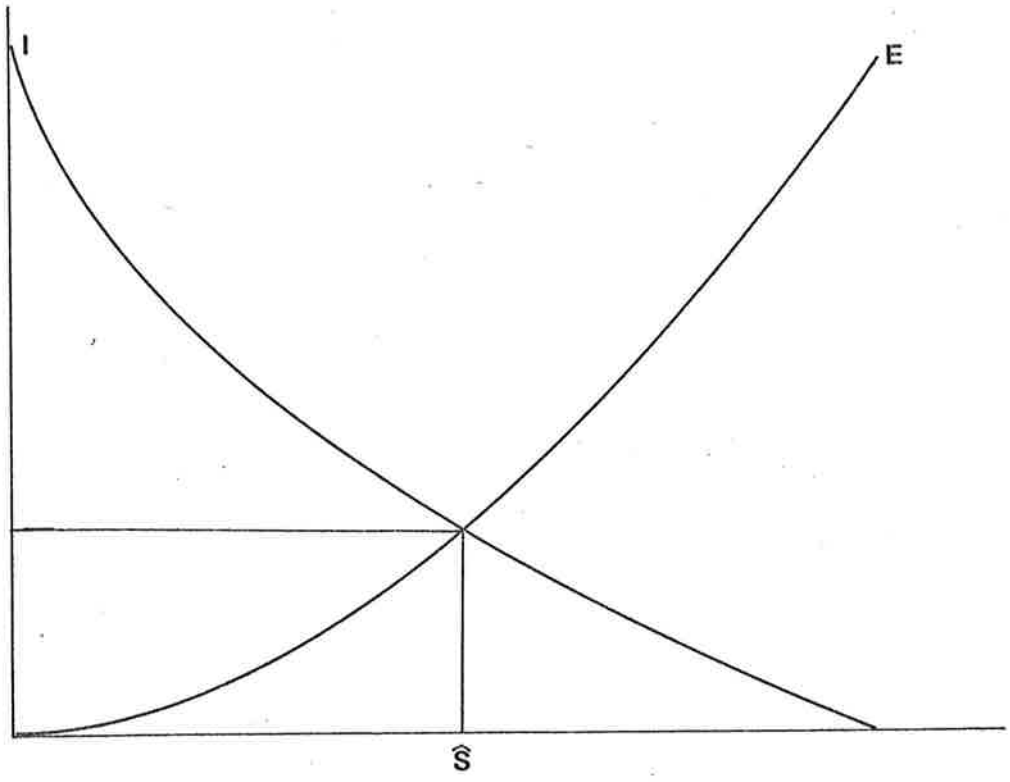
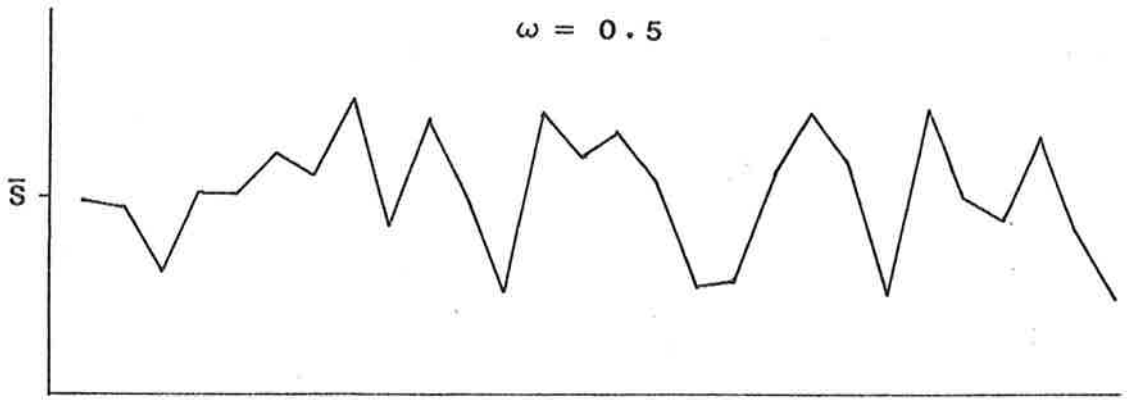
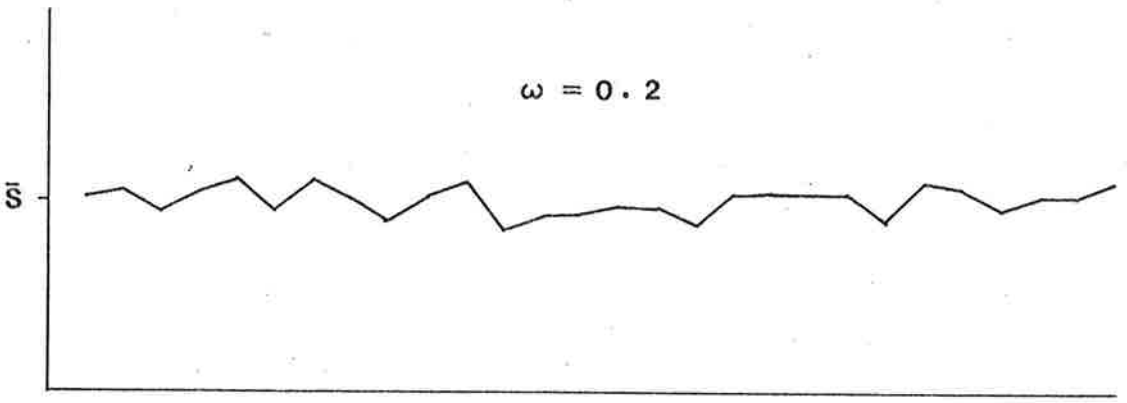
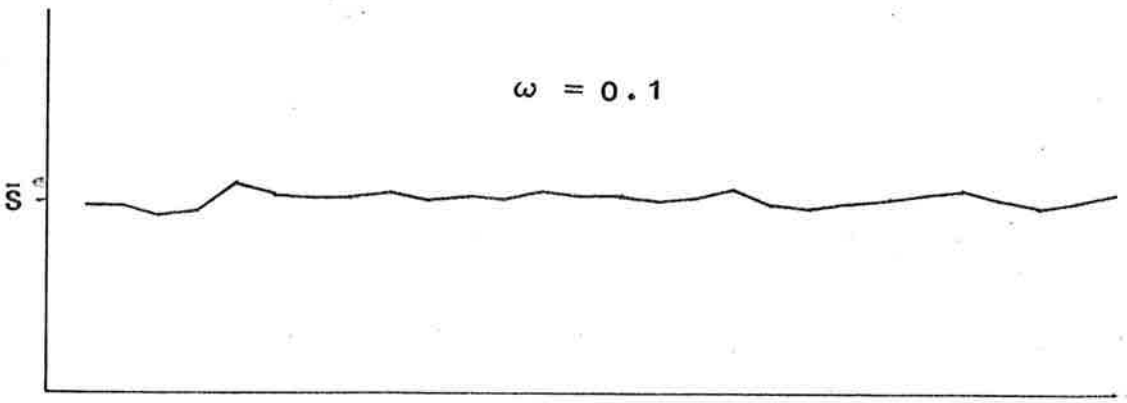

I
E
Ŝ
Number of species

Figure 1.2 Examples of random fluctuations in the number of species (S) that would fall with 95% certainty within a region $\bar{S} \pm w\bar{S}$, for three different values of w.


ω = 0.5
SI


ω = 0.2
SI


ω = 0.1
SI

2. STUDY SITES AND GENERAL BIOLOGY OF *PINNA* AND ITS EPIFAUNA

Two main study sites were chosen. Edithburgh pier was used because of its proximity to Coobowie Marine Research Station as a base, and because the fauna and the dynamics of the piling community were relatively well known (Butler 1979; Kay 1980; Kay and Keough 1981; Keough 1981a,b). All experiments concerning events after recruitment were conducted at this site. The second site, West Lakes, was used because of its accessibility and hydrodynamic properties. Water flow is unidirectional in large parts of the lake, so that recruitment experiments could be done easily.

A number of other sites were visited to examine variation in epifaunal assemblages, and the results of these comparisons will be detailed in this Chapter.

2.1 *PINNA*

Pinna bicolor Gmelin is a large bivalve of the family Pinnidae which reaches a length of approximately 45-50 cm (Butler and Brewster 1979; Butler and Keough 1981, see Appendix 4; Figure 2.1). The family was first recorded in the Paleozoic, and the genus *Pinna* dates from the Jurassic, 195-232 million years ago (Rosewater 1961). They live embedded in sand or mud, and adult molluscs have about 200 cm^2 of shell per valve exposed above the substratum. The genus is cosmopolitan, but it is regarded as tropical to warm-temperate (Rosewater 1961).

P. bicolor itself occurs from "East Africa to Melanesia, including southern Japan, the Philippines and Australia" (Rosewater 1961). Within South Australia, it is found west of Ceduna, but appears restricted in the east of the State. I have not seen specimens east of Fishery Beach, near Cape Jervis, although Cotton (1961) records the distribution as extending to Beachport, which is much further east. Shepherd and

Sprigg (1976) record that *Pinna* is a conspicuous part of the benthic fauna of most of Gulf St Vincent. Butler and Brewster (1979) suggested that longevities of 12 or 13 years are not unreasonable.

Large aggregations of *Pinna* occur from the intertidal down to 30 metres depth (Shepherd and Sprigg 1976), and densities may be as high as 40 m^{-2} (Butler and Keough 1981). Densities of 2 m^{-2} are not uncommon. Predators on large individuals appear few (Butler and Brewster 1979), and seem limited to rajid and heterodontid fish and the large asteroid *Coscinasterias calamaria* (Gray). The heaviest predation is probably on the juveniles up to 20 cm in length (Figure 2.1). Other asteroids such as *Uniophora granifera* (Lamarck) and *Luidia australiae* Doderlein, and gastropods such as *Polinices conicum* may be important.

Deposit feeders such as the holothurians *Stichopus mollis*, *S. ludwigi*, and *Holothuria hartmeyeri* are common on most *Pinna* beds. They may interfere with very small individuals.

Further details of the ecology of *Pinna* will be given in following sections of this Chapter.

2.2 SAMPLING METHODS

Connor and Simberloff (1978) and others have reported cases in which the conclusions of a study were influenced by differential sampling intensity. They found the number of collecting visits to an island to be the best predictor of species number when used in a stepwise multiple regression. They were able to show that this was not because the number of visits was highly correlated with area, for example, but because the variable "number of visits" accounted for extra variation in itself. It is of obvious importance to try and standardize sampling intensity for censussing all habitat patches.

Two-dimensional space is frequently postulated as the limiting resource for which marine hard-substratum organisms compete. If this is

accepted, then the appropriate measure of resource use is the percentage of two-dimensional space which is occupied. In these communities, most species are colonial, sheet-like forms, and so the percent cover is appropriate, in estimating both relative "population size" and the amount of the resource utilised. The most accurate and efficient method of measuring percent covers in the field is to photograph an area. The resultant colour slide can then be projected, and the two-dimensional projection of each occupant of the photographed area measured.

I thus designed a standard photographic frame (quadrupod) for sampling all epifauna (Figure 2.2). A Nikonos underwater camera was attached to a rectangular mount. Four 6.3mm steel arms protruded from the camera mount, and a rectangular quadrat 25 cm by 18 cm was screwed onto the four arms. The quadrat was placed parallel to the plane of the film, and quadrat to lens distance was 53 cm. An electronic flash was mounted approximately 20 cm from the camera, displaced to the side to reduce backscattering of light.(An Aqua-Sea flash housing was used with a National PE-200 flash unit, GN = 14 (metric) for ASA 64 film). The standard 35 mm Nikkor lens was supplemented by an "Aqua-Sea 12 inch"micro lens, which allowed focussing on objects from 37 cm to 70 cm distance. A diver swam up to a *Pinna* shell, placed the quadrat against the shell and released the shutter. All shells were thus photographed at the same magnification and hence resolution.

Photographs were taken on 64 ASA Ektachrome or 200 ASA Ektachrome professional slide film.

Most epifaunal organisms could be identified from these slides, with the reservations necessary due to the taxonomic state of many groups in southern Australia.

The slides were projected onto a mirror which was inclined at 45° to the vertical, and positioned so that the lens of the projector was directed at the centre of the mirror. A sheet of white paper was placed

beneath the mirror and the relevant portion of the slide traced. Areas were then measured by polar compensating planimeter.

2.2.1 Taxonomy and Identification of Animals

Many animal groups are poorly known in southern Australian waters. This is due to a restricted amount of collecting and also to the relative scarcity of specialists. Many species could not be identified further than generic level, and a few not further than family level. I will indicate the principal taxonomic sources and the means of identifications separately for each group.

Sponges proved the greatest problem. The keys of Bergquist and Skinner (1980) were used; these allowed identification to family level in most cases. Some were identified to generic level by Professor P.R. Bergquist.

Bryozoans were identified by reference to the collections at the National Museum of Victoria and the Geology Dept., University of Sydney. Further details are given by Kay (1980). A note is necessary about the systematics of the three species of *Celleporaria*. We have been given the names *C. valligera, C. fusca* and *C. pigmentaria* by Dr. R. Wass. The species "*C. fusca*" is orange and foliose, and it has been drawn to our attention that a form exists in North Queensland which is labelled *C. fusca*. This bryozoan is black, and its zooids differ considerably from the orange form. The same three species occur at both Edithburgh and Portsea, Victoria, but workers there have been given two specific names for their species by Dr. P.L. Cook. The third is *Celleporaria* sp. Only the name *C. fusca* is in common, and this does not refer to the same bryozoan at both sites! Specimens of "*C. valligera*" from Edithburgh have been examined by Scanning Electron Microscope, and this form bears a close resemblance to the published description of *C. fusca* (R Grove-Jones, pers. comm.). The dark grey species at Portsea pier appears identical to that at Edithburgh, and the form at Portsea has

been identified as *C. fusca*. It seems very likely that an error has been made with the specimens from Edithburgh, and so I propose to use the following names. The names in parentheses are those used by Kay (1980), Kay and Keough (1981), and Keough and Butler (1979). *Celleporaria fusca* (*C. valligera*) - dark grey, foliose; *C. pigmentaria* (*C. pigmentaria*) - dark brown, never foliose; *Celleporaria* sp. (*C. fusca*) - orange, foliose.

Cnidaria were not common, but were identified using Squires (1966) and Veron (1981). Taxonomy follows Veron. The most common Crustacea were barnacles, and the keys of Underwood (1977) and the synopsis of Newman and Ross (1976) were used. I followed the revisions of the latter.

The polychaetes of interest were all serpulids. They were identified by microdissection, using the accounts of Knight-Jones *et al.* (1974) and Dew (1959).

Gastropods were identified using Wilson and Gillet (1971), with reference to various issues of Indo-Pacific Mollusca. Chitons were not identified, and Dr. A.J. Butler identified the bivalves.

Echinoderms are summarized by Keough (1981b and see Appendix 1). They were always identified to generic and almost always to species level.

Tunicates were identified to generic level using the keys of Monniot and Monniot (1974) and to species using Kott (1972a,b; 1975).

Fish were identified using Scott *et al.* (1974) with modification due to the revisions of Hutchings (1976: Monacanthidae) and Allen and Heemstra (1976: Cheilodactylidae) and Scott (1976: Odacidae).

Where possible, specimens of each species were collected and *in situ* photographs of the living animal taken. The species was assigned a code number, and the specimens and photographs are held in the Zoology Department, University of Adelaide.

2.3 EDITHBURGH PIER AND GRID

Edithburgh is on the south-eastern section of Yorke Peninsula (Figure 2.3). It is about five kilometres from the Coobowie Marine Research Station of the University of Adelaide. The pier lies in 4.5 to 7.5 metres of water (depth below mean lower low water), and the seafloor is sandy, with abundant seagrasses *Posidonia australis* Hook and *Halophila ovalis* Hook.

The area has land to the west and southwest, and Troubridge shoals to the south and southeast (Figure 2.3) and so it is sheltered from all but north-easterly winds, which are relatively rare. Prevailing winds are west to south-west. Wave amplitudes rarely exceed 2 metres, and visibility is usually good for diving. On most occasions it was at least five metres, with a maximum of 13-15 metres and minimum of 0.3 metres. Tidal currents are generally slight (less than 0.5 m s^{-1}), and flow north-south but further south, between Troubridge Shoal and Sultana Point, currents reach 1.5-2 ms^{-1} (Butler and Brewster 1979). Sediments throughout the area are moderately coarse (particle size about 0.25 mm diameter (Shepherd and Sprigg, 1976)).

Water temperature varies from a minimum of 11-12^{o}C in late August to 20-22^{o}C in January-late February and is usually homogeneous with depth except on calm, hot summer days.

The pier is approximately 80 years old, and the pilings bear a diverse assemblage of sessile animals. The pilings have been adequately described by Butler (1979), Kay (1980) and Kay and Keough (1981 - see Appendix 2), and will not be discussed in greater detail here. Some experiments were conducted on the pilings of the pier (Chapter 5).

The main working area was centred forty five metres beyond the end of the pier, which itself extends for 173 metres from the shore in an easterly direction. A study grid 50 m by 50 m was constructed in May 1977 by myself and Dr. A.J. Butler. A central stake was driven

approximately 45 m east of the end of the pier. Twenty 1.8 m 3-rayed iron stakes ("star-droppers") were placed to form grid axes running North-South and East-West, with the original stake at the centre. Stakes were 5 metres apart, except for those at each end, which were 7.5 metres from their nearest neighbour. The star-droppers were then labelled with 5 cm x 5 cm engraved perspex tags. Those forming the East-West axis were designated E1 to E10, E10 being the most easterly. The others were correspondingly labelled S1 to S10. I used the 1250 m^2 northern half of the area, although some density measurements are from a wider area. Depth is about 7-8 metres below Mean Lower Low Water.

The area has scattered limestone outcrops, but the bottom is mainly coarse sand. The hammering in of the star-droppers showed that the sand is often 30 cm thick over a limestone base. The two seagrasses mentioned previously and the brown alga *Scaberia argardhii* are the most common large plants. The scallop *Chlamys bifrons* is the other conspicuous large bivalve, occurring at a density of about 0.50 m^{-2}, and the scallops *C. asperrimus* and *Notovola alba* are found. The three holothurians *Stichopus mollis, S. ludwigi* and *Holothuria hartmeyeri* are very common, and *Trochodota shepherdi* Rowe is common seasonally. The asteroid *Uniophora granifera* is abundant, although several other species are occasionally seen (Appendix 1). The ophiuroids *Ophiomyxa australis, Ophiopeza* spp. *Ophiocentrus pilosus* and *Ophionereis schayeri* are common.

The most abundant gastropods are the abalone *Haliotis cyclobates* and *Asteracmaea crebristriata*, both of which are usually seen attached to *Pinna* shells. Predatory gastropods are not uncommon. *Polinices conicum* is often seen at night, as is *Lyria mitraeformis*. The muricid *Pterynotis triformis* also occurs. Cephalopods are also very common. A number of species occur, many of which use dead *Pinna* shells for shelter. *Octupus australis, Hapalochlaena maculosa, Sepioloides lineolata, Sepia apama* and *Sepioteuthis australis* are all found.

The only abundant predatory crab is *Nectocarcinus integrifrons*, which is most abundant in spring-summer. Others such as *Naxia* spp., *Cryptodromia octodentata* and *Paguristes* spp. are also common.

Two solitary tunicates are found attached to rocks and pieces of debris; *Polycarpa pedunculata* and *Phallusia depressiuscula*.

Many fish species have been recorded from the study grid. A full list appears in Appendix 1. The most important in this study were the leatherjackets (Monacanthidae) *Eubalichthys mosaicus* (Ramsay and Ogilby) and *Brachaluteres jacksonianus* (Quoy and Gaimard), an unidentified odacid, and the silverbelly or low fin, *Parequula melbournensis* (Castelnau).

2.3.1 *Pinna*

Pinna density was measured by swimming over the seafloor with a 0.25 m^2 quadrat, which was turned end over end to give a line transect and the number within each quadrat recorded on a slate. The procedure was repeated at haphazardly chosen starting points until approximately 100 such quadrats had been sampled. This was done in a number of places; south of the pier, east of the pier, and in the study grid. Densities ranged from 2.52 m^{-2} to 8.68 m^{-2} at the end of the pier and 6.2 m^{-2} south of the pier.

A further survey on 18.ii.78 involved three line transects out from the end of the pier. 100 end to end quadrats were used in each of 3 directions; east, south-east and south. *Pinna* were most dense adjacent to the pier and generally decreased in density away from the pier (Figure 2.5) to densities of 1.6 to 4.8 m^{-2}.

Recruitment on the study grid appears low (A.J. Butler, personal communication), so the population of *Pinna* used in my experiments was predominantly 3+ years old (see Butler and Brewster 1979). The mean area of shell which was exposed above the sand was 180 cm^2 per valve.

Newly settled juveniles reach a valve area of about 25 cm^2 in their first year. In the grid itself, a survey on 18.viii.78 gave a mean density of 2.62 m^{-2} for an area of 185 m^2.

The epifauna of *Pinna* in the study grid consists mainly of a few bryozoan species, all of which are common, and serpulids, mostly *Spirorbis* spp. The latter were not distinguishable from photographs, but the most abundant species was *S.* (*Janua*) *pagenstecheri* Quatrefages, followed by *S.* (*Eualospira*) *convexis* Wisely, and two unidentified species, both of which were relatively rare. Tunicates and sponges were relatively uncommon. Table 2.1 lists the commoner species. Other attached species were rarely seen. The least rare of these were the stalked barnacle *Scalpellum peronii*, the sessile barnacle *Epopella simplex*, and an unidentified vermetid gastropod. The corals *Culicia* sp. and *Scolymia* (= *Homophyllia*) *australis* frequently live attached to the shells.

The epifauna is browsed upon or crawled over by a number of motile animals. The most conspicious of these are *Uniophora granifera*, *Haliotis cyclobates* and *Asteracmaea crebristriata*.

2.4 WEST LAKES STUDY SITE

West Lakes is an artificial marine lake which was built as the central point in a land development scheme in the western suburbs of Adelaide. The lake is approximately 3 km long and 175 m wide for much of its length (Figure 2.6). It is deepest in the centre, reaching a depth of about 4.9 m. Tidal amplitude is damped to about 0.6 m at most tides. Water enters through a 3.5 m diameter pipe which opens approximately 400 metres offshore from Grange beach. On a rising tide, flow gates are opened until the water level inside the lake has risen by 0.6 m, when the gates are closed. Similarly, when the tide ebbs, the outflow gates at the northern end of the lake are opened and water flows out into the Port River until the water level has dropped by 0.6 m.

Water flow is thus unidirectional within the lake, flowing south-north. Water turnover is about 16% per day. Temperature ranges from 10-11°C in August to 20-23°C in January-February.

The benthic fauna is totally different from that of Edithburgh. In most of the lake, current flow is negligible. The size of the lake prevents waves of amplitude greater than 0.6 m from building up, so that fine particles settle out and most of the lake floor is fine mud. Occasional *Pinna* are seen, but the most abundant bivalve is the oyster *Ostrea angasi* Sowerby. Polychaete tubes, solitary ascidians and Congollis, *Pseudaphritis bursinus* (Cuv. and Val.) are the most conspicuous large benthic organisms. Predatory and scavenging gastropods are the most common, notably *Polinices conicum, Nassarius pyrrhus* Lamarck and *Bedeva hanleyi* Angas. The sides of the lake are lined with rocks and concrete surfaces which are covered by mussels, serpulid and spionid polychaetes, tunicates and barnacles. The introduced European shore crab, *Carcinus maenas* Linnaeus is also common. A detailed list of the fauna of the lake is given in Appendix 1.

Because the lake bottom is vastly different from the benthic fauna and substratum at Edithburgh, I decided to use only the lake to test hypotheses about the recruitment of hard substratum organisms. My subjective impression was that the development of epifaunal communities in turbid low water movement areas such as wharf pilings in harbours is fundamentally different from that in cleaner more open water. I did not have time to investigate this proposition, and so simply decided not to investigate events subsequent to recruitment at this site.

2.5 *PINNA* ELSEWHERE

The main thrust of this work is to investigate the generality of models of communities in patchy environments. Some of the data will probably be used for studies which are possibly more biogeographic or

parochial. It is useful therefore to indicate how the epifauna of *Pinna* at Edithburgh is related to epifauna in other parts of the range of *Pinna bicolor*. This section describes qualitatively the epifauna of *Pinna* over a wide geographic range.

2.5.1 Methods

The research project on *Pinna* by Dr. A.J. Butler involves periodic sampling at a number of sites in Gulf St Vincent (Figure 2.4). I have participated in some of these samplings and recorded the epifauna both photographically and by visual inspection from the deck of the boat. From March 1977 to July 1980 I have visited a number of other sites to make the same observations.

The major survey, however, was done in January 1980. I conducted a survey of *Pinna* assemblages and *Pinna* epifauna from Port Broughton in upper Spencer Gulf, down the east coast of Eyre Peninsula to Port Lincoln, and up the west coast to Davenport Creek, west of Ceduna. Approximately fifty dives were done in a three week period. These consisted of a number of separate sites, and at some sites, a number of short dives separated by distances of 100 to 1000 metres.

Further sites were visted in December 1979 and February 1980. The purpose of the surveys throughout this summer was to enable some broad comparisons to be made between a number of localities. Many of these surveys were single point-in-time censuses and so bias could be introduced because of non-synchronisation of reproductive periods of different epifaunal species. The comparisons to be made here will be qualitative, and the short interval between most surveys should minimize this bias. The sites are shown on Figure 2.4.

At each site, one of a number of types of survey was done.

Type 1. Underwater survey only. The diver (usually myself) swam over the bottom and used a one-metre rod divided into 10 cm sections to estimate *Pinna* density. The abundance of several *Pinna*-associated species, such as various seagrasses, scallops, potential predators, etc., was estimated subjectively. Casual notes were made of the epifauna.

Type 2. The diver swam over the bottom and collected all *Pinna* shells visible in a one metre wide strip until 100 to 150 animals had been collected. These were measured either in the boat or on shore. Length and height were measured. Notes were made on the epifauna, which was scored into one of a number of qualitative categories - see results below.

Type 3. The same as type 2, except that each shell was opened up and the gonads examined and adductor muscle scars counted. Scars left by the posterior adductor muscle in the nacreous layer of the shell have been suggested to be an index of the age of the mollusc (ETSA 1976). Butler and Brewster (1979) gave qualified support for this idea within a single locality. They reported that the variance of muscle scar counts within a size class was quite high, however. Further, although the scars obviously represent growth checks, they may occur as a result of various influences other than the low temperatures during winter. The frequency distribution of muscle scar counts nevertheless may allow some qualitative statements about the age structure of a particular population.

Frequencies and types of survey done at each site are shown on Table 2.2. The data on *Pinna* themselves will be presented elsewhere (Butler and Keough 1981; Appendix 4).

2.5.2 Results

I had originally intended to calculate the distribution and abundances of bryozoans, serpulids, tunicates etc. at each site and compare these between sites. However, when I began sampling turbid, fine-sediment localities, it was found that the occupancy of *Pinna* shells differed greatly from Edithburgh. In many areas, each shell bore a canopy of red algae and beneath the canopy were bryozoans, barnacles, serpulids, spionids, sabellids, terebellids, etc. The presence of this algal canopy means that it is not sufficient to measure the occupation of two-dimensional space, since there is a three-dimensional aspect to the epifauna. The fauna was more similar to that of wharf pilings, in that many solitary animals exist, and there are few species in common with areas such as Edithburgh.

I therefore made subjective assessments of the epifauna. A number of types were distinguished; with/without algal canopy, dominated by tunicates/bryozoans/solitary forms, etc. The categories are detailed below. They are obviously arbitrary, and intermediate types exist. Most sites could nevertheless be allocated into one of these categories. I will discuss some of the characteristics of sites falling into each category.

Colonial forms, no canopy

This type is best illustrated by Edithburgh itself. Percent cover is low, often 50% or less, and most *Pinna* bear mainly bryozoans. Occasional shells bear sponges or tunicates. Spirorbid polychaetes are the only common solitary form, but their occupation of space is low. Only four sites of this type are known; Edithburgh, Stansbury, and the *Pinna* beds between Sultana Point and Troubridge Island. These are areas of relatively clear water and coarse sediment (see Shepherd and Sprigg 1976). Queen scallops, *Chlamys bifrons* are frequently common in these localities.

Algal canopy, solitary forms

This was the most common type of epibiota. The subtidal sites in this category were those in upper Spencer Gulf, Ardrossan, and turbid, fine-sediment areas elsewhere (Port Lincoln, Streaky Bay, Ceduna, Semaphore). All were dominated by this assemblage.

Massive colonial forms, canopy variable

The St Kilda-Port Gawler area has many *Pinna* shells which are covered by massive sponges of a number of species. Some sponges were as much as 30 cm in diameter, so that the *Pinna* shell was almost totally obscured. Some *Pinna* at Sultana Point were covered similarly, but they were rare.

A number of *a posteriori* hypotheses can be erected to explain differences in these epifaunas, but since I have no tests of these, there is little point in discussing them.

Intertidal *Pinna*

At many localities there are dense beds of *Pinna* in the intertidal zone. At Streaky Bay, for example, densities may be as high as 30-40 cm^{-2}. All of these *Pinna* have depauperate epibiotas, composed mainly of limpets, *Galeolaria caespitosa*, the oyster *Ostrea angasi*, and the anomiid *Monia ione* and a number of chitons and spirorbids. Small sponges are found in some localities. Solitary animals predominate, however, and percent cover is usually no more than 10%. Algae are rare.

The epifauna of intertidal *Pinna* is clearly very different from the situation at Edithburgh, and no generalisation to cover other events on intertidal *Pinna* is possible. Similarly, subtidal *Pinna* in other areas bear epifaunas which are not even amenable to the same methods of estimating abundance. Comparisons between such assemblages and Edithburgh would clearly be of little value. The statements that will be made about the epifauna of *Pinna* at Edithburgh must be regarded as applying only to a restricted area, from Stansbury to Sultana Point.

TABLE 2.1. Main epifaunal organisms on *Pinna* at Edithburgh study site.

A = abundant; C = common; R = rare

Species	Abundance
Cnidaria	
Scolymia australis	RC
Culicia sp.	R
Annelida	
Spirorbis pagenstecheri	A
Spirorbis convexis	A
Spirorbis sp C	R
Spirorbis sp D	R
Galeolaria hystrix	C
Porifera	
SP 35	RC
SP 36	RC
Aplysilla sulphurea	RC
Ectoprocta	
Schizoporella schizostoma	A
Membranipora perfragilis	A
Parasmittina raigii	A
Celleporaria sp.	C
C. fusca	A
B7	C
Crustacea	
Epopella simplex	C
Scalpellum peronii	R
Tunicata	
Didemnum patulum	RC
Didemnum sp. A	R
Podoclavella cylindrica	R
Botrylloides leachii	R
Polycarpa pendunculata	C

TABLE 2.2 Details of geographic areas surveyed. A dash in the number of dives column indicates an intertidal sample; a "p" in the photos column indicates that a set of random photos were taken as described in the methods section.

Locality	Date	No. of Dives	Survey Type	Photos
Troubridge Island	12/79	-	2	-
Edithburgh	12/79	5	3	p
Sultana Point	12/79	2	3	p
Ardrossan	12/79	3	3,1,1	p
Fishery Beach	12/79	1	1	-
Franklin Harbour	1/80	4	3,3x1	-
Franklin Harbour	1/80	1	3	-
Tumby Bay	1/80	4	3,3x1	p
Tumby Bay	1/80	-	3	p
Port Lincoln	1/80	4	3,3x1	-
Coffin Bay	1/80	10	1	-
Coffin Bay	1/80	-	1	-
Streaky Bay	1/80	1	3	-
Streaky Bay	1/80	2	3,1	-
Ceduna	1/80	1	3	p
Venus Bay	1/80	10	1	-
Elliston	1/80	1	1	-
Playford Power Station	1/80	2	3,1	p
Redcliff	1/80	5	3,4x1	-
Rapid Bay	2/80	1	1	-
St. Kilda-Port Gawler	2/80	2	3,1	-
Wallaroo	3/80	1	1	-
Semaphore	4/80	1	1	-
Stansbury	12/79	-	3	-
Other				
Outer Harbour	1977	4	1	-
Semaphore	1977/8	3	1	p
Stansbury	5/80	1	1	p
Port Gawler	1977/8	6	1	p
St Kilda	1977/8	2	1	-
Stenhouse Bay	5/80	1	1	-

Figure 2.1 Diagram of Pinna bicolor (left valve).
L - length, H - height.

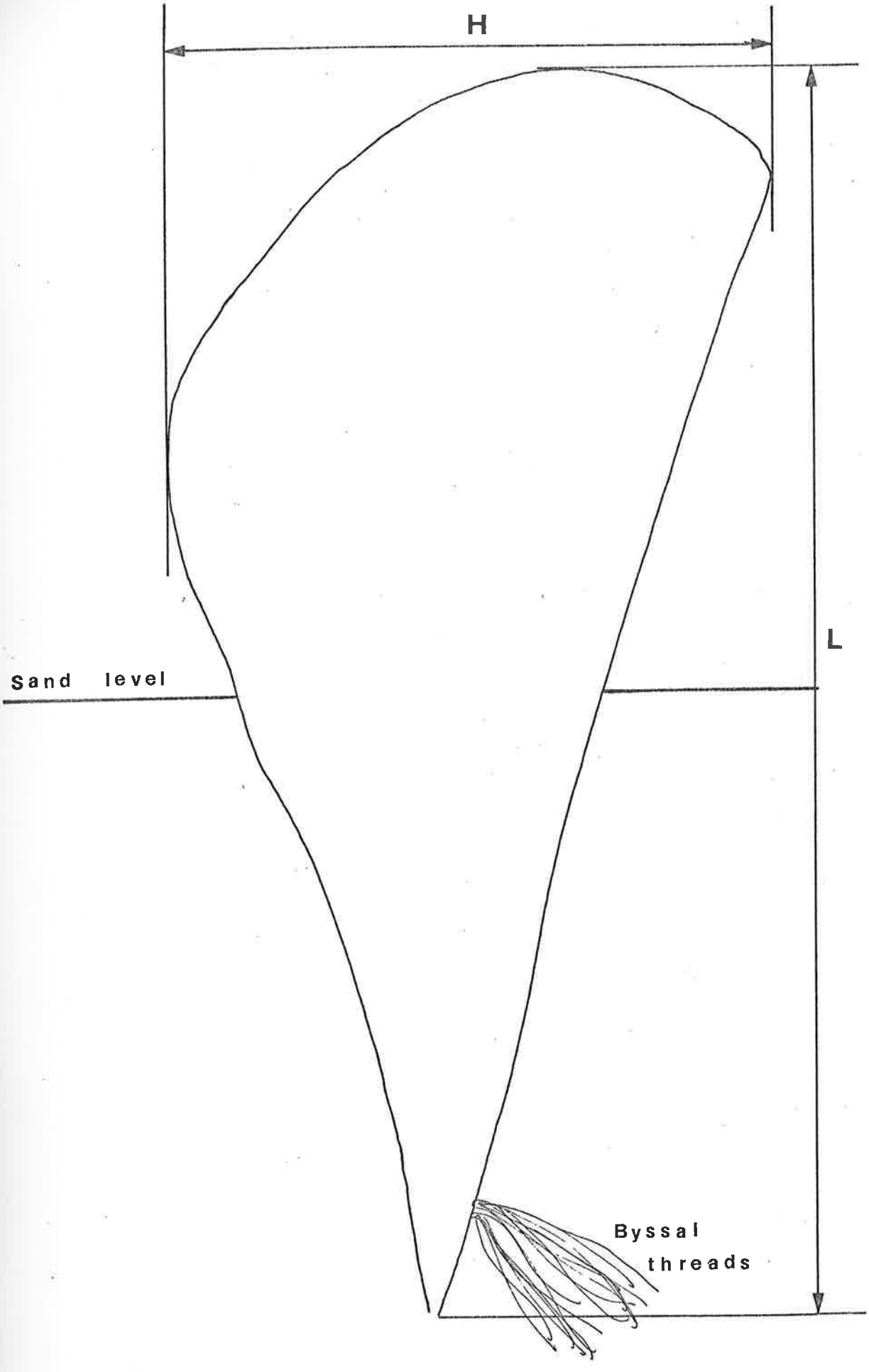

H
L
Sand level
Byssal
threads

Figure 2.2 Photographic quadrupod.

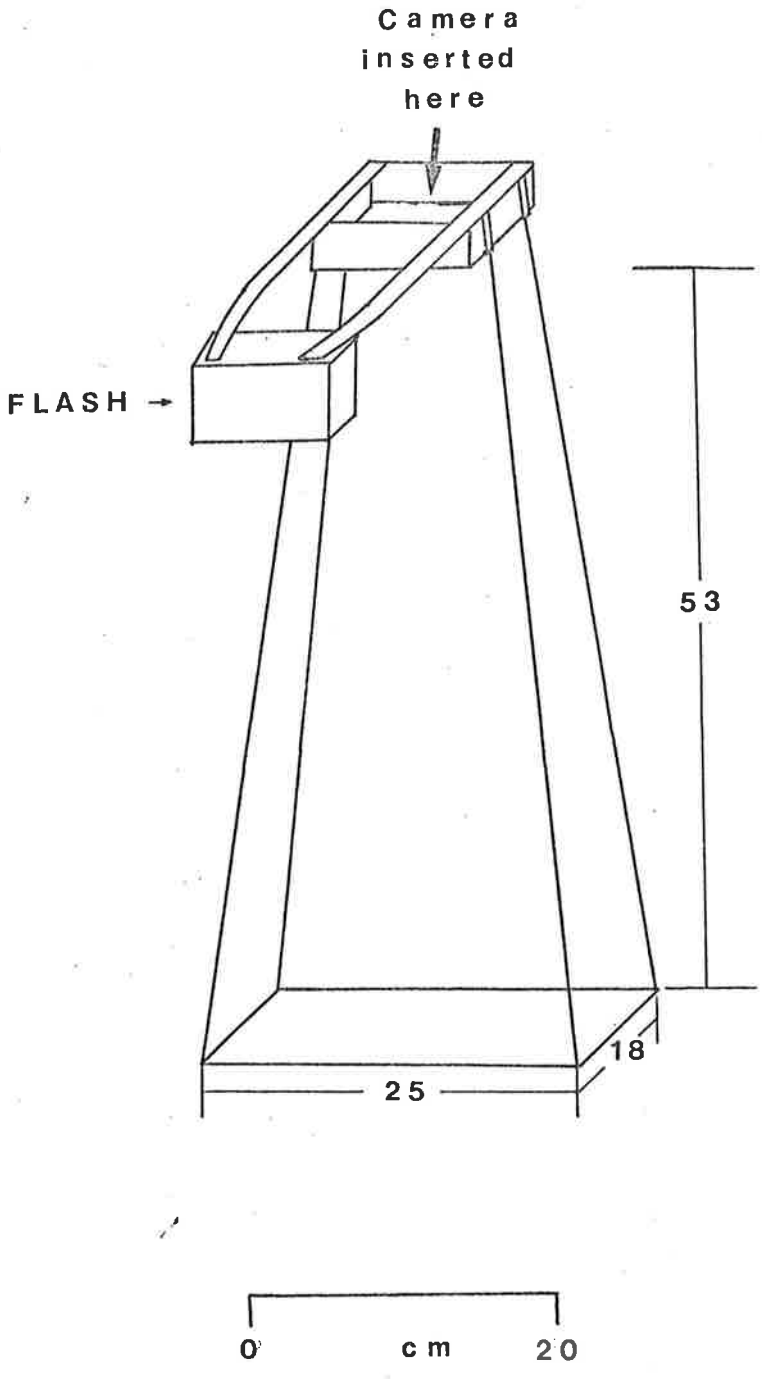
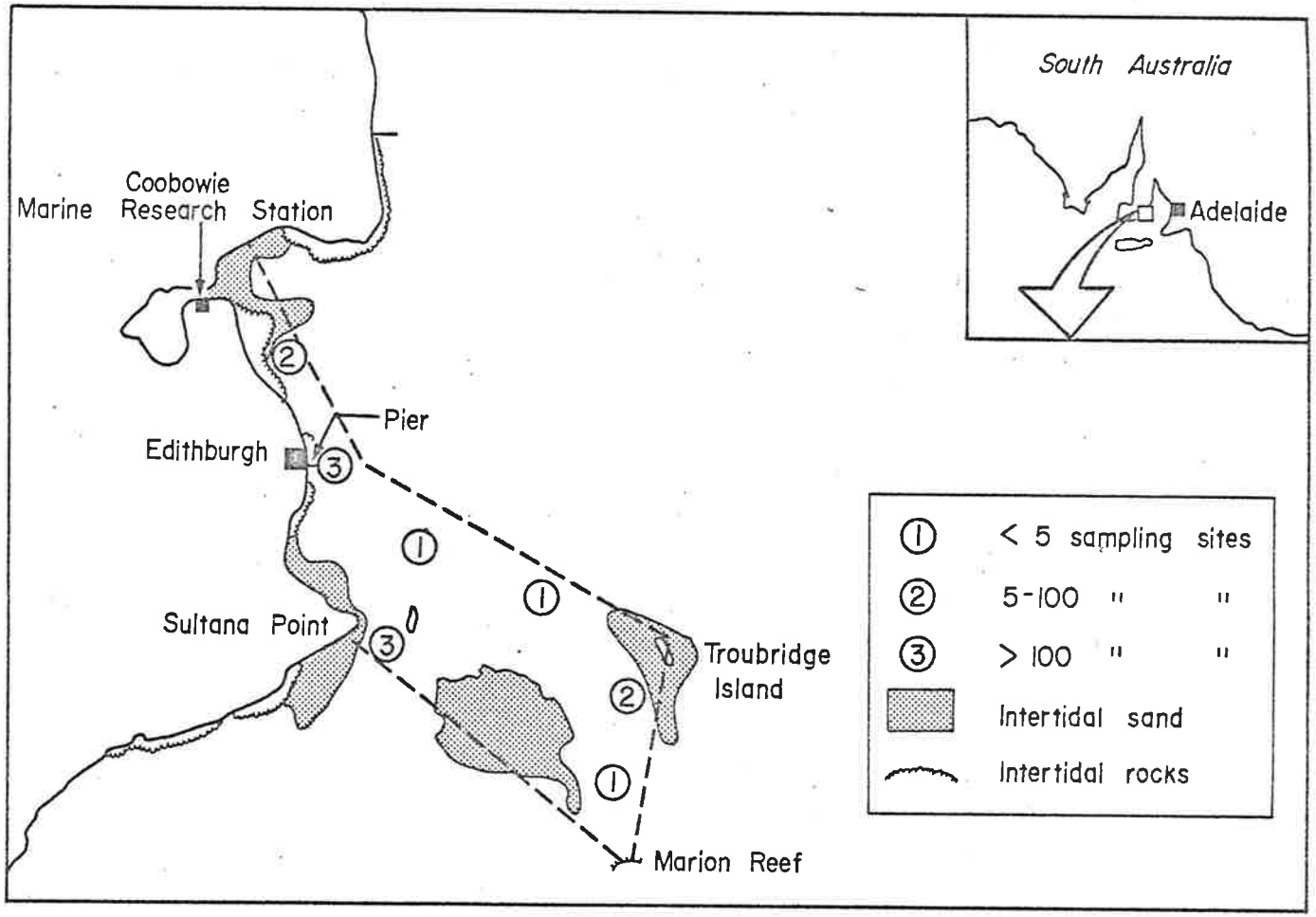

Camera
inserted
here
FLASH
53
18
25
0
cm
20

Figure 2.3 General map of Edithburgh area.



Return to Page width

Figure 2.4 Sites at which Pinna were surveyed during 1979-80. Code for sites: 1. Ceduna 2. Streaky Bay 3. Venus Bay 4. Elliston 5. Coffin Bay 6. Port Lincoln 7. Tumby Bay 8. Franklin Harbour 9. Port Augusta 10. Redcliff 11. Wallarroo 12.Stenhouse Bay 13. Edithburgh 14. Troubridge Island 15. Stansbury 16. Ardrossan 17. Port Gawler 18. Outer Harbour 19. Semaphore 20. Rapid Bay 21. Fishery Beach

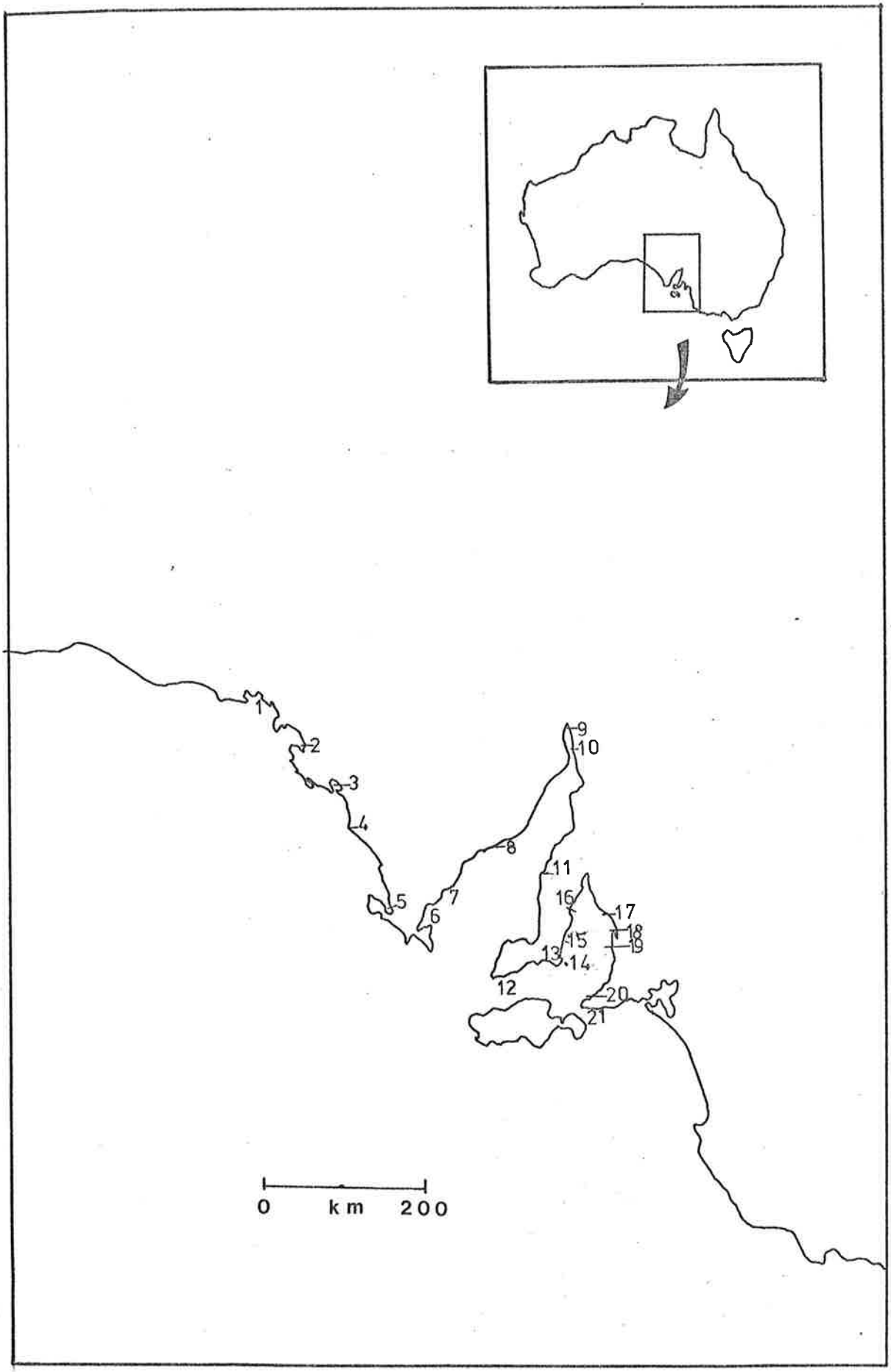

1
2
3
4
5
6
7
8
9
10
11
16
17
18
19
15
13
14
12
20
21
0 km 200

Figure 2.5 Density of *Pinna* near the end of the pier. The figures are the number of shells.m^{-2} for five-metre intervals along three line transects from the end of the pier.

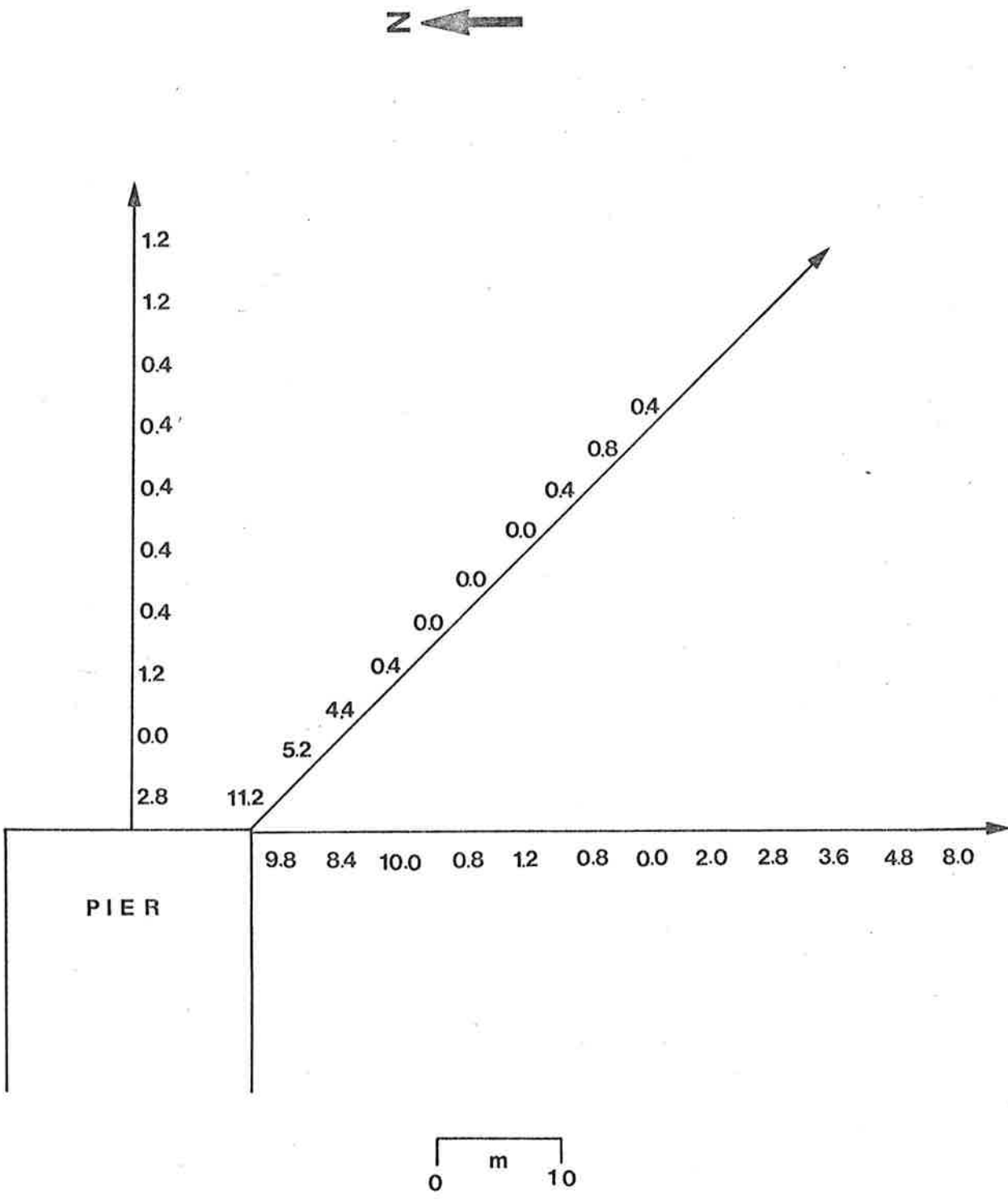
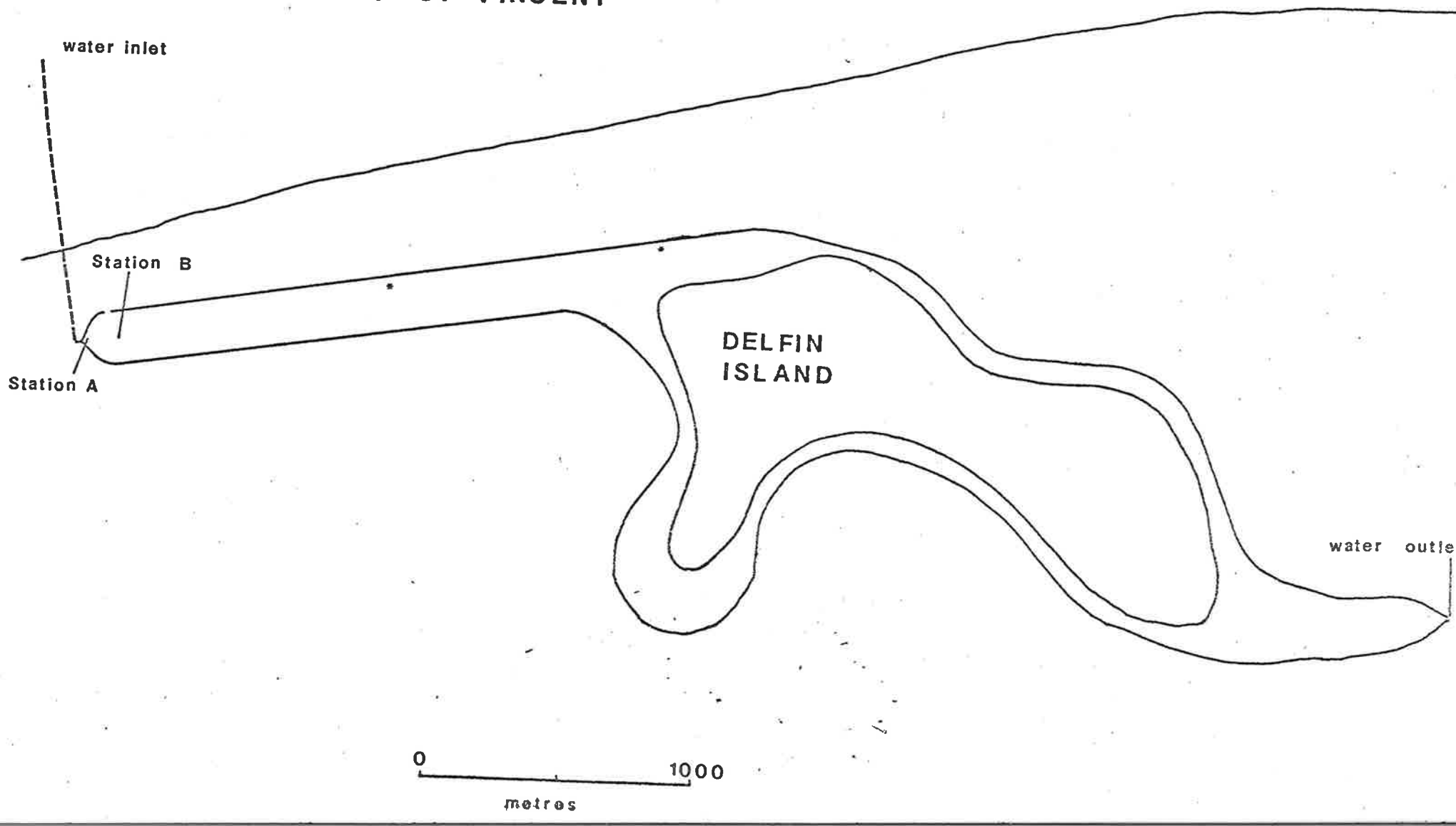

N
1.2
1.2
0.4
0.4
0.4
0.4
0.4
1.2
0.0
2.8
11.2
5.2
4.4
0.4
0.0
0.0
0.0
0.4
0.8
0.4
9.8
8.4
10.0
0.8
1.2
0.8
0.0
2.0
2.8
3.6
4.8
8.0
PIER
m
0
10

Figure 2.6 Plan of West Lakes. Asterisks denote locations of recruitment panels.


GULF ST VINCENT
water inlet
Station B
Station A
DELFIN
ISLAND
water outle
0
1000
metres

3. RECRUITMENT

In Chapter 1 I discussed the problem for equilibrium theory in describing a stochastic process with an essentially deterministic model. This is particularly true for colonisation events, which for many patchy environments have a low probability of occurrence in an individual patch. Many patchy environments have patches which are difficult to replicate for various reasons (see Connor and Simberloff 1978). Differences in the nature of patches in such systems have allowed an essentially deterministic view of colonisation events (see Abbott 1979). Variation between patches has commonly been attributed to subtle physical differences, and token mention has been made of "noise". Diamond and Gilpin (1980) provide an example of this, coining a new term, "turnover noise", to describe stochastic variation in species turnover rates.

It is only relatively recently that island biogeographers have focussed on the importance of chance (Connor and Simberloff 1978; Connor and McCoy 1979). Simberloff (1978) has stressed the need to produce testable null hypotheses about colonisation events. He suggested that the appropriate null hypotheses were those in which colonisation was assumed to be random, and explanations involving interactions between species invoked only when the null hypothesis could be confidently rejected. Workers in marine environments have long been aware of the variability of colonisation events for individual patches. Coe and Allen (1935) state, for example, for panels immersed in 1929-30, "The blocks for this year show many inconsistencies". Despite this, few studies up until the late 1960's were well replicated. A number of factors were varied in some studies. Coe and Allen, for example, used three different types of substrata, of varying sizes, and placed them at different positions on the Scripps Institution of Oceanography pier in different years. They nevertheless preceded to make between-year

comparisons. Similar examples may be found in the literature.

The mid-1960's saw an increased emphasis on replicated experimental methods in marine environments. Nevertheless, examples of unreplicated studies have appeared in the literature as recently as 1980 (Marshall *et al.* 1980). The seriousness of this fault is evident when work such as that by Jackson (1977b) is considered. He reported coefficients of dispersion for recruitment of individual species greater than 100%. This is larger than the magnitude of differences reported by Marshall *et al.* (1980) between caged and uncaged panels and ascribed to predation. Schoener *et al.* (1978) were similarly unable to comment on between-panel variation because they were only able to census a single panel at each of a number of widely separated sites. They were able to give some estimates of between-panel variation for one site, and gave standard deviations for species number as being low, usually two or three (species). It must be noted, however, that means were often only seven to eight species, in which case the variance becomes relatively large (C.D. = 0.50-1.00). They in fact give details of 35 sets of replicate panels spread over three sites in Hawaii and three depths, 9, 15 and 30 metres. The panels varied in time of immersion, but I simply calculated a coefficient of dispersion for each data set. The mean C.D. for these 35 data sets is 0.656 (S.D. = 0.651), and the range is 0 to 2.88. There is clearly a great amount of between-panel variation, despite the crude nature of this analysis.

Many other studies are replicated and controlled, and they show that recruitment processes vary on a number of scales. Bowman and Lewis (1977) report a large amount of between-year and between-site variation in the recruitment of *Patella vulgaris*. A large volume of literature exists for bivalves of the family Ostreidae, and variations in recruitment are known on almost all scales. The literature on this subject has been comprehensively reviewed by Andrews (1979). *Pinna*

itself shows large between-locality variation in recruitment (Butler and Keough 1981; Appendix 4).

Loosanoff (1964, 1966) demonstrated considerable variation in the recruitment of *Asterias forbesi* L. and *Crassostrea virginica* Gmelin over a period of 25 years. Again, there was little investigation of variation within sites within time periods. He noted that for the two years that replicate collectors were used, counts between pairs of collectors showed correlations of 0.65 to 0.98. This was presumably a Pearson product-moment correlation coefficient, although Loosanoff gave no details. The two years, 1944 and 1955, for which this was done were years of high settlement for both species; when years were ranked according to the level of recruitment, these two years were ranked 5 and 6 respectively. The number of larvae recruiting onto 100 oyster shells was as high as 24,700 in some stations. Under these circumstances, we might expect that this correlation might be higher than when fewer recruits are available, when chance variation may become more important.

One of the few studies to have produced reliable data on between-patch variation is that by Denley and Underwood (1979). They investigated the settlement of two barnacle species, *Tesseropera rosea* and *Tetraclitella purpurascens*, on a rocky shore in New South Wales. Coefficients of dispersion ranged from 57.9 to 655.5% for series of replicated patches cleared on rock surfaces.

Day (1977) has suggested that changes in physical conditions occur on such small scales as to make identical panels separated by small distances not true replicates. This would seem to be a rather extreme view, but does emphasize the great variability in settlement or recruitment between similar patches. In practice, it means that recruitment must be modelled as a random process with high variance. We have no way of measuring such small changes in physical conditions.

A number of other reasons may be postulated for this variation. Many planktonic larvae settle gregariously. The behaviour of these larvae has been well reviewed by Meadows and Campbell (1972) and Scheltema (1974). The ranges of behaviour include gregariousness for species such as *Balanus balanoides* (Knight-Jones 1953), while some spirorbid polychaetes are known to settle very evenly (Wisely 1960; Crisp 1961). Day (1977) also reported many bryozoans at Heron Island to be gregarious. Alternatively, patchiness may exist in the plankton, and the distribution of planktonic patch sizes will influence the between-patch variation on recruitment panels. Little is known of small scale patchiness in the plankton. Steele (1976), for example, reports on planktonic patchiness on scales of kilometres, but there are few data for scales smaller than this. A variety of types of patchiness can be envisaged, and these will produce different patterns of similarity between panels. (Similarity will for the moment be used in its intuitive sense, and during analysis a precise measure of similarity will be used; this will be defined in section 3.2.3).

Firstly, consider a variety of types of patchiness in the distribution of planktonic larvae, and examine their consequences.

1. No patchiness at all. A completely mixed larval soup is transported along by currents and encounters panels at random. We expect no relation between similarity of panels and distance between them.

2. Small patches on scales of centimetres. These may possibly be represented as "larval swarms". If they hit a panel which is far from any others, the swarm is unlikely to hit any other panel in the series. If the swarm hits one panel of a cluster, there is a good chance that all panels of that cluster will be colonized. We expect in this case a negative correlation between the similarity between two panels and their distance apart.

3. Larger scale patches. Metres to tens of metres. If a clustered panel is encountered, then it is likely that all panels in the cluster will be, since the patch is large relative to the size of the cluster. Reasoning is as follows.

Assume that the patches are circular in cross-section, and of diameter D. Let the cluster of panels be in a circle of radius a/2, so that the diameter of the cluster is a. Assume that the northern panel is encountered by the patch (P1 on Figure 3.11). Assume also that the patch is travelling East-West. Panel P1 will thus intersect the patch at some point α along its diameter. The rest of the cluster of panels will also be encountered by the plankton patch if $\beta > a$. The position of the patch will be random with respect to the cluster of panels, and so $P(\beta > a) = \frac{D-a}{D} = 1 - \frac{a}{D}$.

This clearly increases as D increases, since $\frac{dP}{dD} = 1+aD^{-2}$ which is greater than 0 for all D,a. Thus, the larger the patch, the more likely that recruitment on the clustered panels will be very similar. Distant panels will remain dissimilar, since the patch size necessary so that all panels will be encountered by most patches is very large. Again, a negative correlation between similarity and distance is expected.

4. There is also one model which produces a positive correlation between similarity and distance without the existence of patchiness in the plankton. Consider larvae which settle near previously settled conspecifics, and assume that the density of larvae in the water column is low. For distant panels, the larvae which encounter the panels settle, and subsequent larvae are attracted to the established postlarvae or adults. All distant panels would receive a number of recruits, and the between-panel variation would simply reflect chance variation in the events on individual panels. Consider now panels clustered within a distance over which larvae can detect conspecifics. One panel will

receive a larva, and subsequent larvae are attracted to this juvenile and settle near it. The nearby panels receive few recruits, since most settle on the panel which was first colonized. In contrast, the distant panels all receive moderate numbers, since they are sufficiently far apart so as not to interfere with each others' recruitment.

As a consequence, clustered panels are very dissimilar and distant panels similar. With higher recruitment rates, all clustered panels would be expected to receive moderate recruitment, and no correlation should occur. This will depend, *inter alia*, on the distances over which larvae respond to conspecifics.

Next the behaviour of individual species could affect the patterns of similarity. Species which settle near adult conspecifics may produce patchy distributions whereby panels which are close together show great similarity. An examination of recruitment patterns for individual species would allow this possibility and the previous one to be assessed.

The main hypotheses to be tested were thus:

1. Distribution of larvae in the water is random, and the between-patch variation is simply due to chance. The occasions when panels become more similar as they are closer together can be explained as consequences of the gregarious behaviour of individual species at settlement.

2. No species recruits preferentially onto substrata of a particular size.

3. Recruitment patterns of individual species do not differ. This could be tested by examining the frequency distribution of recruits of a particular species for all panels and testing it against a Poisson distribution. Within-panel distributions of recruits and inspection of size distributions between panels should provide the supplementary evidence to classify species as recruiting near adult conspecifics,

occurring as larval swarms, recruiting randomly, or recruiting in an overdispersed manner.

4. Are the main sources of between-panel variation spatial or temporal, and on what scales do they operate?

1. Temporal. Between seasons, between years.

2. Spatial. Between localities, i.e. tens of kilometres, or on smaller scales of metres.

As a part of the investigation of these questions, a description of the variation in recruitment rates would be produced which is replicated, and seasonal trends could thus be viewed against the background of between-patch variations.

A note on Terminology

Some confusion or imprecision exists in the literature concerning the terms settlement, colonization and recruitment. Settlement is the attachment and subsequent metamorphosis of a planktonic larva. Recruitment refers to the settlement and survival of a planktonic larva so that it is counted at some later stage. The two terms are frequently used interchangeably, or more often settlement is used in reference to the juvenile marine forms which are counted often on a piece of substratum after some period of time. This should be termed recruitment, since mortality may, and frequently does, operate before the census of the substratum. There is an implicit assumption that mortality processes for newly settled larvae of a given species do not vary between patches. In all probability mortality will have a large stochastic component, since for example patches will not all be visited by predators, nor receive identical food-bearing currents. The relation between settlement and recruitment has not, to my knowledge, been investigated thoroughly. It is extremely difficult, since the time scale of mortality processes is generally unknown. The laboratory

facilities necessary to do this certainly did not exist in Adelaide. In all cases, I will be speaking of recruitment, but many arguments must assume that it is related to settlement. Specifically, I must often assume that the density of recruitment is proportional to that of settlement; this assumption must be borne in mind at all times.

The use of the term colonization varies. In terms of the MacArthur-Wilson model, it is the net gain of species, while in other ecological work the term means the acquisition of new species, regardless of the simultaneous rate of loss of species. It is thus equal to Immigration in the MacArthur-Wilson model. Where this term is used, its meaning will be made clear at the time of usage.

3.2 METHODS

3.2.1 West Lakes

Uni-directional water flow through the single inlet pipe results in a decreasing rate of current flow with increasing distance North from the inlet. Increased current flow means that more larvae should encounter a particular piece of substratum. I thus used two stations approximately 100 metres apart at the Southern end of the lake (Figure 2.6).

Station A was 15 metres North of the central concrete vane which directs water out from the pipe. This station had very sluggish current flow (< 0.05 m s^{-1}). Station B was 100 metres further North, and there was never any detectable current. My activities while working always reduced visibility at this station to 0.3 m or less, and the clouds of sediment had not dispersed 30 minutes later. The two stations thus should have provided two sites of differing total colonization rate. I assumed the species pool of colonists to be the same for each site. Station B was marked by a line of 2 cm x 2 cm jarrah stakes, which were hammered into the bottom at 0.6 to 1 m intervals from the western shore of the lake. Station A could be reliably

relocated despite poor visibility. Two other stations (C and D) were established 1000 and 2000 metres further down the lake. After an initial series of panels was set up, I was never able to relocate these stations.

Settlement panels were constructed of asbestos cement ("Hardieflex") which was cut into rectangular panels. Three sizes were used; 15 x 12 cm (180 cm^2), 10.5 x 8.5 cm ($\sim$90 cm^2) and 7.5 cm x 6 cm (45 cm^2). These sizes were chosen to correspond to the mean above-sand area of a *Pinna* valve (180 cm^2), and 0.5 and 0.25 times that area. Shape of each panel was the same. A small hole was drilled at the top of each panel. One panel of each size was attached to a single jarrah stake (Figure 3.1) which was hammered into the bottom so that the panels were almost touching the mud surface.

The panels were arranged in concentric circles so that each panel at a given radius was equidistant from its nearest neighbour on each side. Circles of four arbitrarily chosen radii were used; 0.1 m, 0.3 m, 1 m and 5 m. Six replicates of each panel size at each radius were used, so that the design was a 4 x 3 array with 6 replicates, arranged as shown on Figure 3.2.

The panels were immersed for two months, removed and brought back to the laboratory. They were examined under a dissecting microscope at 10x magnification and all recruits counted. If the number of recruits of a particular species was greater than 100 on a panel, 20 1 cm^2 quadrats were randomly counted to give a mean number per cm^2, and this number multiplied by the panel area. Panels were then scraped clean, scrubbed, washed in fresh water and finally air dried before being re-immersed at a later date. The interval of two months was chosen because work by Kay (1980) had shown that in this time the recruits were unable to occupy sufficient space to restrict greatly

subsequent recruitment. Similarly, there were few overgrowth interactions so that no recruits were eliminated in this way. This time period was adequate with the exception of the period from October 1977 to December 1977 when *Balanus amphitrite* settled at very high densities, and occupied greater than 95% of space on most panels. Such high levels of settlement were not repeated.

The bimonthly program was commenced at both stations in May 1977, and continued until 19/3/79. At this time, all but three panel trios at Station A were destroyed during the West Lakes annual fishing contest. This station was discontinued at this stage. Station B was continued until March, 1980.

3.2.2 Edithburgh

An identical experimental design was used at Edithburgh in the study grid (see Figure 4.1). Sampling was again bimonthly, and sample dates corresponded as closely as possible to those at West Lakes.

Two subsequent experiments were conducted at this site. It was noticed that when panels were separated by 0.1 m, recruitment rates appeared lower than for panels at lower densities. It is possible that one panel may "shade" another when spacings between panels are small. To test this, I ran a concurrent series of panels which were suspended in trios, but were arranged linearly rather than in a circle. Between-panel distance was 0.1 m. Thirty replicates of each panel size were used.

The second experiment was designed to test the effect of browsing by fish on recruitment, and will be detailed in Chapter 4.

3.2.3 Analysis

A general measure of between-patch variation was needed. The alternatives available were limited by the fact that some colonists could only be counted as : 0, some, many, very many (i.e. qualitative

multistate characters, in the sense of Sneath and Sokal 1973). Other species were counted (i.e. quantative characters). This restriction prevented the use of standard measures of variance. I therefore reversed the concept to one of between-patch similarity, and the hypotheses to be tested could be viewed in terms of increased similarity. (Equivalent to decreased variance, where this is appropriate). A wide range of similarity measures are given by Sneath and Sokal (1973). Of these, only one uses characters[1] (= counts of recruits) which may be quantitative, qualitative multistate, or presence/absence. This is Gower's similarity index, defined by

$$S_{jk} = \frac{\left(\sum_{i=1}^{n} W_{ijk} \cdot s_{ijk} \right)}{\sum_{i=1}^{n} W_{ijk}}$$

which defines the similarity between two panels, j and k, colonised from a pool of n species.

The weight, W_{ijk} is set to 1 when the comparison is valid, in this case if species i did actually settle on at least one panel during the time period in question. The expression ΣW_{ijk} then is the number of species which settled during that time period.

s_{ijk} is the difference between the scores for recruitment of species i on panels j and k.

For presence/absence characters, it is 1 for (+,+); 0 otherwise.

For qualitative multistate characters, the interval 0,1 was divided into a number of intervals corresponding to the number of states,

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1 In the terminology of Sneath and Sokal (1973) panels are OTU's and counts of recruits are the characters.

and agreement in states assigned a value of 1 for s_{ijk}. For the four-state character above, a difference of 1 in the states was given $s_{ijk} = 0.67$, a difference of 2 $s_{ijk} = 0.33$, and 3, $s_{ijk} = 0$.

For quantitative characters, $s_{ijk} = 1 - (|x_{ij} - x_{ik}|/R_i)$, where: x_{ij} is the number of recruits of species i on panel j

R_i is the range of recruitment scores for species i over all panels for a time period

s_{ijk} then has a range (0,1)

The situation where two panels both lacked a particular species caused some problems. Numerical taxonomists by convention exclude any character from the calculation of S if 0's are recorded for both organisms (OTU's : Sneath and Sokal 1973), i.e. set $W_{ijk} = 0$ if $|x_{ij} - x_{jk}| = 0$ and $x_{ij} = 0$. This is because the absence of characters is not evidence of similarity. An overstated example is that of wings. Neither annelids nor primates possess them, but this is not evidence of similarity between the two groups. In this case the character: number of wings would be excluded from the calculation of $S_{annelid\text{-}primate}$.

The situation for recruitment is rather different. We are interested in questions about how the subsequent events in a patch are influenced by recruitment, and if two panels both fail to receive a species which is recruiting at the time, then they must be regarded as being more similar than two panels, one of which received the species in question, and the other did not. I thus calculated the R_i's for each time period, and set $W_{ijk} = 1$ for all i for which $R_i > 0$. Otherwise $W_{ijk} = 0$. Thus, zero-zero matches were only considered if the species in question was settling at the time. The term $\sum_{i=1}^{n} W_{ijk}$ was then reduced to the number of species recruiting for the time period (s) under consideration.

There was a methodological reason for this decision. The quantity S_{jk} is the mean of $m = \Sigma W_{ijk}$ numbers, all of which are in the

interval (0,1). Then, by the Central Limit Theorem, as m becomes moderately large, the S_{jk}'s should become normally distributed, and hence amenable to parametric analysis. If zero-zero matches had been excluded, m would have varied between pairs of panels, and the deductions about the distribution of the S_{jk}'s would be suspect.

A variety of similarities were calculated. For each time period, at least 25, and usually 45 pairs of panels of a given size were selected. The similarity was calculated for each pair of panels. The procedure was repeated for each panel size. At the same time, the distance between each pair of panels was calculated. These similarity values will be designated between-panel similarities, and the distance between-panel distances. These two measures were then correlated using Pearson's r (Sokal and Rohlf 1969), which was then tested for significance using a t-test.

Small panels would be expected to have lower similarities than large since with fewer recruits, chance variation should be more important. Accordingly, one-way analysis of variance was performed to test for differences in between-panel similarity between panels of different sizes. There were thus three treatments: Large, medium and small panels, and equal replication, since the replicates were sets of 45 random pairs. Homogeneity of variances was tested using the F-max test (Sokal and Rohlf 1969), and when the F-statistic from the ANOVA proved to be significant, the Student Newman-Keuls procedure (SNK) was used to identify homogeneous subsets of means.

Throughout this chapter Asterisks are used to denote significance: * $p<0.05$, ** $p<0.01$, *** $p<0.001$. If no asterisk appears, the statistic in question did not warrant rejection of the null hypothesis in question. The SNK test is displayed by listing the treatment means in decreasing order, and underlining all homogeneous subsets. For this procedure, a significance level of 0.05 was used at

all times.

3.2.4 Choice of substratum

The initial series of panels (until January 1978) used only one panel size, 180 cm^2, and the panels were made from large *Pinna* shells. These were scraped clean, and then ground and sanded down until they were a standard size and shape. This procedure became too time-consuming, and a number of alternative substrata were investigated. In December, 1977, a series of different substrata, each replicated five times, was immersed. Five types of substratum were used: *Pinna* shells, asbestos cement, smooth perspex, sand-blasted perspex, and wood. After two months, they were removed and recruitment compared.

The coefficient of similarity was calculated between panels of *Pinna* shells and between *Pinna* shells and panels of other types. Analysis of variance was then used to test whether some panels were more similar to *Pinna* shells than others in their recruitment (Table 3.1). There were significant differences between treatments, and I was interested in the substratum which most resembled *Pinna* shells in recruitment events. This was the asbestos cement, which subjectively appeared to have a texture and colour which resembled *Pinna* shells most closely. A t-test was then used to compare *Pinna-pinna* and *Pinna*-asbestos cement similarities. Mean similarities did not differ significantly (92% and 90% respectively, $t = 0.93$, $df = 33$, $p = 0.2\text{-}0.4$).

The experiment was only done for one time period, when the number of larvae was very high, especially for *Balanus amphitrite*. It is thus possible that the levels of similarity were somewhat higher than unusual. The important point is that the differences were not great, and the asbestos cement is a reasonable substitute for *Pinna* shells. I will not be extrapolating from asbestos cement panels to *Pinna* directly, but I believe that patterns of recruitment on the two types of substrata are similar.

3.3 Individual species

This tested for clumped patterns of recruitment. The recruitment pattern of individual species was examined by calculating the mean and variance of the number of recruits per panel, and testing this ratio for equivalence to unity. This was done for each species for each panel size and time period, and corollary evidence was gained by the examination of within-panel patterns of recruitment.

There were many such tests to be done, and so a quick method was used to investigate within-panel patterns. For a given number of quadrats, the maximum non-significant value of the coefficient of dispersion could be calculated as follows:

$$C.D. = t_{.05,u}\sqrt{2/u+1} + 1$$

For various quadrat numbers, the value is shown on Table 3.2. Each panel was divided into 1 cm by 1 cm squares, and the number of recruits of the species in question was recorded for each square. Groups of four adjacent quadrats were then pooled, and the number of recruits for 4 cm^2 squares recorded. The coefficient of dispersion was calculated and compared with the least significant value from Table 3.2.

3.4 RESULTS

Recruitment patterns - individual species

All species showed considerable between-year and between-season variation in recruitment patterns (Figures 3.12-3.17). Some had only one substantial recruitment during the entire study, such as *Scrupocellaria* or *Electroma* in West Lakes, while others, such as some serpulids, showed peaks in recruitment at approximately the same time each year, although the sizes of the peaks varied between years.

The recruitment patterns of individual species will be considered in detail in the following section.

Elminius modestus

Only settled in large numbers once during the study (Figure 3.15). The coefficient of dispersion (C.D.) was 33.95 for large panels, which were the only ones in use at the time. This gave $t = 90.2384$, $p << 0.001$, for a comparison of the C.D. with unity, i.e. the distribution over patches showed strong clumping. Some information on the causes of this was gained by examining within-panel patterns. Four large panels were divided into 1 cm^2 squares, and the barnacles counted. A few of the 90 cm^2 panels at a later time also received recruits, and the same procedure was adopted for these panels. In all cases, the C.D. was much greater than unity (Table 3.3). When the 1 cm^2 squares were pooled, the pattern was even more strongly contagious, with probability levels of less than 10^{-9}, as calculated by an HP-67 program. A "typical" within-panel pattern can be seen on Figure 3.18. The aggregated barnacles varied greatly in size, suggesting that recruitment is stimulated by adults. Gregarious behaviour is well known for larvae of this species (Knight-Jones 1953; Knight-Jones and Stephenson 1950).

Spirorbis (Eualospira) convexis

For each panel size at West Lakes Station B, the coefficient of dispersion differed from unity at the 0.01 probability level for all time periods.

The same was true for recruitment of this species at Edithburgh. Unfortunately, only one analysis of within-patch variation could be conducted, for logistic reasons. This was for Station A for August-October 1978. Results are shown on Table 3.4. The C.D. did not differ significantly from unity in any of the eleven cases. Detailed testing of the observed distribution for goodness-of-fit to a Poisson distribution was not possible, since in many cases the expected number of quadrats with more than one serpulid was much less than one,

and so the resultant Chi-squared or G-test (Sokal and Rohlf 1969) would have no degrees of freedom remaining. In most cases, the deviation from Poisson expectations was very small. It appears that within-panel distributions are close to random.

Monia ione

Again, this species only settled in large numbers once during the study period (January-March 1979). Coefficients of dispersion were high for all panel sizes, for example at West Lakes Station B, they were all over 40, indicating very strong between-panel clumping. Smaller numbers settled during the previous two months. Coefficients of dispersion ranged from 2.45 (45 cm^2 panels) to 36.4 for 180 cm^2 panels. All differed significantly from 1 at $\alpha = 0.001$.

At Edithburgh, recruitment was more regular, and a small number of recruits was recorded for a number of time periods. The total number of recruits was never more than ten individuals, and coefficients of dispersion did not differ significantly from one, except for one occasion when the ratio was less than one for the 90 cm^2 panels.

Within-panel patterns were assessed for West Lakes on the January-March panels. Three 180 cm^2 panels were scored as described earlier. Coefficients of dispersion are shown on Table 3.5. The species shows moderate to strong clumping (Figure 3.18). Again, the size of the bivalves varied widely within panels, suggesting that the aggregations occur because larvae recognize adults of their own species. No information exists for *Monia ione*, but larvae of *Ostrea edulis* are known to be induced to settle by extracts from adult tissue (Bayne 1969). This is also known for *Crassostrea virginica* (Crisp 1967). Both of the latter species belong to the Ostreidea, but *Monia* belongs to the Anomiacea.

Hydroides norvegica

Did not settle at Edithburgh, but showed strong summer peaks in recruitment in West Lakes (Figures 3.12-3.17). The coefficient of dispersion was significantly greater than one at the 0.01 level on all occasions for all panels sizes except on one occasion when it was only significant at the 0.05 level. Within-panel analysis showed strong clumping on the 1 cm^2 scale (Table 3. 5 and Figure 3.18). The clumps in this species appeared to be composed of animals of more uniform size. Wisely (1958) also reported that *H. norvegica* larvae appear to settle at random, and do not search over the substratum after encountering it. When combined, these observations suggest that the between- and within-panel patchiness may be due to gregarious behaviour of larvae in the plankton, or patches of larvae in the plankton, so that swarms of larvae encounter a panel. If so, the swarms are small, in the order of a few cm in diameter.

Spirorbis (Janua) pagenstecheri

This cosmopolitan species was the third most abundant recruiter of all serpulids at Edithburgh (Figures 3.12-3.14). It settled throughout the year, but reached peaks in spring-early summer. The between-panel distribution was variable (Table 3.6). Numbers settling were generally too low to analyse within-patch variation, but Knight-Jones (1951, 1953) reported that the species settles preferentially near adults of its own species.

The inconsistency in recruitment patterns may be a result of variations in recruitment density. For example, if the overall density is low, then the probability of a larva encountering a conspecific adult is low, and many larvae become less selective with increasing time spent in the plankton (e.g. Knight-Jones 1953; Sastry 1979). The larvae may then settle at random. Conversely, when the chance of a larva

encountering a conspecific adult is higher, aggregated distributions may result.

I defined the density of recruitment in Table 3.6 as the mean number of recruits per panel, scaled by 180/panel size, to bring all densities to a standard of the number per 180 cm^2. I used the coefficient of dispersion as an index of the degree of "clumpedness" of the between-panel distribution, and calculated Kendall's rank correlation coefficient (Siegel 1956) between the two. There was no significant correlation between density and clumpedness of distribution. (Tau = 0.27, N = 12, $p > 0.05$).

The recruitment pattern for this species must remain confusing!

Galeolaria hystrix

Recruited consistently at Edithburgh, but only sporadically at West Lakes. Data were analysed for Edithburgh only. Between-panel patterns were variable (Table 3.7), and so the Kendall's correlation coefficient was calculated between density of recruitment and the coefficient of dispersion. There was a significant positive correlation (Tau = 0.35, N = 30, $p < 0.01$). There is thus some tendency for recruitment, and, by implication, settlement, to be gregarious. Little appears to be known of the behaviour of larvae of *Galeolaria hystrix*, and there were generally too few recruits to analyse within-panel patterns. Casual inspection showed a variable size distribution for tubes within individual panels, and so the tentative suggestion is one of recruitment near adult conspecifics.

Celleporaria fusca

Only one major recruitment was observed for this species, during March-May 1980. Coefficients of dispersion were 3.00 for 180 cm^2 panels and 4.01 for 90 cm^2 panels. Both of these represent

significant deviations from unity at $\alpha = 0.001$. No recruitment was observed on the 45 cm^2 panels. All colonies were of similar size, suggesting that the clumped distribution resulted from patchy distribution of larvae in the plankton.

Didemnum sp.A (T9)

Was observed to recruit during September-November of each year at Edithburgh, although more recruits were observed in 1978 than in 1979. Coefficients of dispersion are shown on Table 3.9. They are generally variable, but increase generally with density of recruitment. I will be presenting evidence elsewhere that the newly metamorphosed larvae of this species are heavily preyed upon by fish, and so the recruitment pattern will not be analysed in detail.

Observations over shorter time periods on the pilings suggest that recruitment is spatially patchy (Kay and Keough 1981), and with shorter time periods, the impact of predators is likely to be less. Clusters of newly settled colonies (<3 mm in diameter) are often seen on piling surfaces, and so I tentatively suggest that clumps of larvae occur in the plankton and settle together. Further, long term experiments are in progress to examine the recruitment patterns and their causes in four species of colonial tunicates at Edithburgh and Stenhouse Bay (Keough and Butler, unpubl.obs.).

Balanus amphitrite

There were two major peaks of recruitment in West Lakes, both during spring-summer of 1977. At the second peak, the panels were all at least 75% covered with *B. amphitrite*. Coefficients of dispersion were 27.1 for August-October and 0.6 for December-February. The latter occurred because the mean number of recruits per panel was over 2000, and it became physically difficult for more barnacles to settle.

For August-October, within-panel patterns showed strong clumping (C.D. = 3.50 for 1 cm^2 quadrats, C.D. = 25.17 for 4 cm^2 quadrats, both different from unity at $\alpha = 0.001$). Moreover, there was a wide range of sizes, with diameters of 2 mm to 10 mm. Gregarious settlement has been reported previously for this species (Daniel 1955), and other species of the genus are known to settle on detection of chemicals in the shell of adult conspecifics (Meadows and Campbell 1972).

Schizoporella shizostoma

Settled for much of the year, with few definite peaks. Only one coefficient of dispersion differed significantly from unity, but since over 20 tests were done, about one would have been expected by chance. It appears that there is no between-panel patchiness, and that colonies are distributed approximately at random. The number of recruits was generally too small to test the within-panel patterns.

Parasmittina raigii

Consistent recruitment was observed for this species at Edithburgh. Coefficients of dispersion varied from 0.64 to 4.0 (Table 3.9), but there was no correlation between the degree of clumpedness and the density of recruitment (Kendall's Tau = 0.14, N = 10, p = 0.3). Nothing is known of the larval behaviour of this species.

Cryptosula pallasiana

Settled consistently throughout the study in West Lakes. The number of recruits per panel had a coefficient of dispersion which only differed significantly from one in one case (Table 3.10). The number of recruits per panel was usually too low to test within-panel patterns.

Bryozoan BX1

Again, settled fairly consistently throughout the study. Coefficients of dispersion sometimes differed from unity (Table 3.10), and the degree of aggregation was positively correlated with the density of recruitment (Kendall's Tau = 0.76, N = 7, $p < 0.05$). The colonies were not sufficiently abundant to investigate within-panel patterns.

Ciona intestinalis

Recruitment varied greatly between and within years (Figures 3.15-3.17). There was no recruitment at all in 1978, and I observed that the large population of *Ciona* inside the water intake tunnel at West Lakes had died off, and for much of 1978 and early 1979, few *Ciona* were seen in the lake. In 1977 and June 1980, many concrete faces at the southern end of the lake had densities of the order of 50-100 m^{-2}. Such fluctuationsin the density of *Ciona* have been recorded anecdotally for some time, but are little documented.

Coefficients of dispersion varied widely (Table 3.11), but differed from unity in most cases. I do not propose to analyse the recruitment patterns for these panels any further, since there are reasons to believe that juvenile tunicates may be eaten by a variety of fish (Russ 1980; Kay 1980; Chapter 4 of this thesis). Since this involves foraging by fish, it is likely that not all patches will be visited by fish, and this will produce between-panel heterogeneity, which is independent of any behaviour of the tunicate. The assumption that recruitment is representative of settlement is thus likely to be violated.

Some support for this decision comes from an examination of recruitment to both sides of panels. One side is closer to the stake (Figure 3.1), and produces an area to which predators may not be able to gain access readily. For the time period January-March 1980, when

recruitment was greatest, I compared the recruitment of *Ciona* to the two sides of the panels. It was higher on the "reverse" side of the panels (Wilcoxon matched-pairs signed-ranks test, $T = 12.5$, $N = 12$, $p < 0.05$). There is still the problem of distinguishing between differential settlement and differential survival. The area which offers shelter is also shaded by the stake, and *Ciona intestinalis* larvae have been reported to be photonegative (Millar 1953).

Accordingly, a second experiment was done in West Lakes from March to May of 1980. Twenty panels were hung in a cage made from 1 cm galvanised mesh ("Waratah Welded Fabric") at the same time as the regular recruitment panels. The panels were hung so that pairs of panels shaded each other, giving one shady side and one well-lit side. Unfortunately the experiment was a cooperative venture, and my collaborator allowed some of the tunicates to die before the panels had been scored. My subjective impression was that recruitment was (a) much higher on caged than uncaged panels, and (b) higher on shady than bright sides.

I suggest that predation on these tunicates is sufficient to make inferences about the causes of recruitment patterns unreliable.

Ascidia aspersa

Settled at the same time as *Ciona intestinalis*, and patterns of recruitment were variable (Table 3.11). No inferences can be made about the causes of this, for the same reasons as for *Ciona*.

Other species - Edithburgh

Many species only settled once during the study, and will not be considered in any detail, since they are rare on *Pinna* . They include a number of bryozoans, *Scrupocellaria* sp., two *Bugula* species, the wing-shell *Electroma georgiana*, and the scallop *Chlamys asperrimus*. The latter two were easily dislodged from panels, and so data on their

recruitment are unreliable.

Sponges recruited very rarely (Figures 3.12-3.14). The graphs on figures 3.12-3.14 show the total number of sponge recruits rather than data for individual species.

Table 3.12 gives a summary of the inferred recruitment patterns of all of the common species.

3.4.2 Shadow Effect

Recruitment was compared between all linearly arranged panels and those of the concentrically arranged series which were 0.1 m apart. This was only done at Edithburgh. Panels were treated as replicates, and within the two arrangements, replicate numbers were kept constant for all panel sizes of a given arrangement by randomly removing replicates to compensate for the accidental loss of panels. Two-way ANOVA with unequal but proportional subclass sizes was performed after an F-max test for homogeneity of variances.

I only analysed the total number of recruits, since the shadowing is postulated to be a physical constraint, and thus likely to affect all species equally.

Each time period was analysed separately. This was done because panels were lost at various times, and to have produced a balanced design would have necessitated the removal of too many panels. Further, with unequal sample sizes, the design ceases to be orthogonal, so comparison of treatment means and partitioning of sums of squares in a 3-way analysis becomes tedious and difficult (Sokal and Rohlf 1969). Indeed, the only reason for the two-way analysis was to minimize the number of individual analyses, and decrease the likelihood of Type I errors. The important part of each ANOVA is the F-statistic for the effect of the arrangement of the panels.

Results of the analysis are shown on Tables 3.13 to 3.18. Of

the six time periods, three show significant variation due to the arrangement of panels. Inspection of treatment means (Tables 3.13, 3.17, 3.18) shows that on one occasion the clustered panels received more recruits, on another the linearly arranged panels received more, and on the third occasion, there was a significant interaction between panel size and panel arrangement, so that neither panel arrangement received consistently more recruits for all panel sizes.

Clearly, there is no strong or consistent shadow effect due to patches or substrata being clustered together.

3.4.3 Between-site comparisons

3.4.3.1 Total recruits

Panels immersed in West Lakes received considerably more recruits than those at Edithburgh (Figures 3.3-3.8). It should be noted that data from West Lakes are plotted on a scale one tenth that for Edithburgh. The two years of recruitment at Edithburgh produced summer peaks of approximately the same magnitude. In contrast, the size of the summer peaks in West Lakes varied considerably between years (Figures 3.6-3.8). Although the same seasonal trends are present at both sites, the relative sizes of maxima and minima differed between sites. Winter of 1978 was notable for the low levels of recruitment at Edithburgh, while in West Lakes the lowest year was 1979, and winter recruitment rates were highest in 1978. Similarly, the summer of 1978-9 had higher recruitment rates at Edithburgh, while that year showed the smallest summer peak of the three in West Lakes.

The duration of the summer peaks varied between years and between sites as well.

There is clearly no synchrony of events between the two sites. There is thus no support for the idea of "good" or "bad" years for the Gulf St Vincent as a whole. This picture is similar to that for *Pinna*

itself, where recruitment rates in 1978-9 and gonad states in 1979-80 varied greatly between localities (Butler and Keough 1981; Appendix 4).

3.4.3.2 Number of colonising species

In West Lakes, species number rose steadily to summer peaks and fell to minima in May (Figure 3.9). At Edithburgh, summer peaks were identified only with some imagination (Figure 3.10). This is probably a reflection of the differing recruitment rates at the two sites. With large numbers of recruits, more species are likely to colonise reliably. Correspondingly, with recruitment rates generally less than 10 recruits (all species pooled) per 180 cm^2 per 60 days, fewer species are likely to occur on each panel, and species number is more likely to vary by chance alone.

3.4.4 Density of recruitment and habitat selection

It is possible that some species may not settle equally frequently on substrata of different sizes (Jackson 1977b), and so recruitment density was compared between the three panel sizes. Counts of recruits for a given panel were multiplied by 180/panel size to give a number of recruits per 180 cm^2. One-way ANOVA was performed for each species which recruited sufficiently abundantly, for each time period. This was also done for total recruits, total serpulids, bryozoans, tunicates and molluscs. Bryozoans and molluscs could not be analysed for Edithburgh, since they did not recruit sufficiently frequently. Tunicates were only analysed for one time period, September-November 1978.

A large number of analyses of variance were performed, and a moderate number had F-max values which were significant at $\alpha = 0.01$. Snedecor and Cochran (1967) state that heterogeneity of variances biases the ANOVA towards significance. Very few of the ANOVA's were significant, and those had variances which were not heterogeneous, and

so the analyses of variance were not recalculated with transformed data.

3.4.4.1 Edithburgh

A total of 45 one-way ANOVA's were done. Of these, eight were significant (Table 3.19, 3.22). The significant values were for *Spirorbis convexis*, *Galeolaria hystrix*, and total serpulids, all for the period January to March 1980. The values for total serpulids was almost certainly a consequence of heterogeneous recruitment for *Spirorbis* and *Galeolaria*, which were summed to give serpulid recruitment.

With a significance level of 0.05, eight significant results is more than would have been expected by chance alone (Binomial test for large samples (Siegel 1956), $z = 3.97$, $p < 0.001$). The significant F-values for total recruits and total serpulids at both times were almost certainly due to the heterogeneous recruitment for *Spirorbis convexis*, *S. pagenstecheri*, and *Galeolaria hystrix* (Table 3.19), and so a more sensitive test for the presence of Type I errors is to consider only those F-values for individual species. Of the 25 such values, four were significant (Tables 3.19, 3.22). The probability of obtaining four or more significant results by chance alone, is 0.034, calculated by expansion of a binomial, with $p = 0.05$, $n = 25$.

There were thus more significant values than could be ascribed to chance, but the probability of three or more significant results is 0.12, and so we could only claim confidently that one of the significant results is not a Type I error. There is, of course, no way of selecting which of these four values is the "true" significant result.

Therefore, I concluded that there is no strong evidence to reject the null hypothesis of no differential recruitment between small panels of different sizes.

3.4.4.2 West Lakes

Forty-six one-way ANOVA's were performed using individual species, total serpulids, and total recruits of all species as the dependent variable, and only two significant results were obtained (Tables 3.21, 3.22). If we again assume that there is no difference between treatments, with a significance level of 0.05, and 46 tests, the probability of obtaining at least two significant results by chance alone, is 0.677, as calculated by an expansion of a binomial with $p = 0.05$ and $n = 46$.

Again, there is no reason to reject the null hypothesis that no species or higher taxonomic grouping recruits preferentially to small substrata of a particular size.

3.5 RESULTS - SIMILARITY ANALYSES

3.5.1 Distance - similarity relations

3.5.1.1 Edithburgh

Four time periods produced correlations which were significantly less than 0 for large panels, while for medium-sized panels, none of the correlations differed from 0 at the 0.05 level. There were four significant correlations between similarity of recruitment and distance between panels for the 45 cm^2 panels. Two of these were positive correlations and two negative (Table 3.23). The large number of correlations makes significant correlations likely by chance, but the observed number of significant results (8) is more than would be expected by chance alone (Binomial test for large samples (Siegel 1956), $z = 5.445$, $p < 0.001$).

There are two causes for the observed relation, planktonic patchiness and gregarious settlement. If the recruitment data are examined, it can be seen that the only two species which were recruiting heavily onto large panels at the time of the negative correlation were

Spirorbis convexis and *Galeolaria* (Figure 3.12). Neither of these two appears to settle near adult conspecifics, although there was a hint of such behaviour with *G. hystrix*. *S. convexis* never showed strongly heterogeneous recruitment patterns, and so for large panels, the observed correlations can not be explained by the settlement behaviour of individual species.

We might expect that if patchiness in the plankton were present, it would be manifest to varying degrees, depending, for example, on the density of recruitment. We might hypothesize that at low recruitment densities, chance is more important, and trends become obscured by random variation. However, there was no relation between the level of similarity or the distance-similarity correlation, and the total density of recruits (Tables 3.23-3.26).

In order to infer causes for the correlations between distance and similarity for small panels, we must again examine the recruitment of individual species. Firstly, examine the negative correlations. During September-November 1978, four species were recruiting (Figure 3.14), and none of these showed strong clumping between panels (Tables 3.7, 3.8, 3.5). The other negative correlation occurred for the time period January-March 1979, and three species were recruiting. Of these, only *Galeolaria hystrix* (Table 3.7) shows any hint of aggregative settlement. It appears that both negative correlations may be explained best by patchiness in the plankton.

Now consider the positive correlations. The earlier hypothesis to explain such correlations requires a gregarious species at reasonably low densities. This is the case for March-May 1979, where *Galeolaria* was recruiting at low densities, and showed a clumped between-panel distribution. The other occasion involved species which showed no clumping. In thirty tests, the expected number of positive correlations is 0.75 if all correlations arise by chance. There is no

reason to select either of these positive correlations as being a Type I error, however. There is no simple model of larval distributions which gives a positive correlation between similarity and distance, but which does not assume gregariousness by one or more species, and so the positive correlation of November-January 1979 cannot be explained readily.

3.5.1.2 West Lakes

Again, there were nine significant correlations out of thirty two comparisons (Table 3.27). These cannot be explained by chance alone (Binomial test for large samples (Siegel 1956), $z = 6.00$, $p < 0.001$). Four were for large panels (Table 3.28), and the species involved, *Hydroides* and *Spirorbis convexis*, showed no between-panel clumping, and nothing could be said of the recruitment of *Ciona* and *Ascidia aspersa*. Only *Bugula* sp.A showed a clumped distribution during November 1978-January 1979. The negative correlations cannot be explained by the behaviour of individual species.

On the 90 cm^2 panels, the first negative correlation (August-October 1978) (Table 3.29) was for a time period when *Hydroides*, *Balanus*, and *Spirorbis convexis* were settling. *Balanus* larvae are known to settle near conspecifics, and this may be sufficient to produce the observed result. The other time period, July-September 1979, had only *Hydroides*, *Galeolaria*, and *S. convexis* recruiting, none of which show strong between-panel clumping.

The negative correlation for small panels (Table 3.30) was during August-October 1978, when *Balanus* larvae were settling, and this is sufficient to explain the correlation. Again, two positive correlations were observed. *Monia* was settling for one of these times, and this may produce a positive correlation, since *Monia* settles near previously settled conspecifics. The other positive correlation

occurred when *Ciona* and *Ascidia aspersa* were settling, and nothing can be said of the reason for the correlation.

In most cases, the coefficient of determination (r^2) was low, even when the correlation was significant. Of the 62 correlations, only three produced a value of r^2 which exceeded 20%.

The evidence from the similarity analyses can thus be summarised as sufficient to reject a null hypothesis of no small-scale patchiness in the distribution of larvae in the plankton. This is true for some time periods only. Therefore, there is good evidence for the existence of small patches of larvae in the plankton. The degree of patchiness is not constant throughout the year, and its effect is more pronounced on patches of larger sizes.

The presence of a negative correlation between similarity and distance requires the cluster of panels to be struck by at least one plankton patch. If the total density of larvae is low then this becomes less likely, and we would expect at least some periods not to reflect any patchiness, as was observed.

3.5.2 Comparison of similarities for panels of different sizes

The random sets of similarities were compared for each time period by one-way ANOVA. The results of these comparisons are summarized on Tables 3.31,3.2. Complete ANOVA tables may be found in Appendix 3. Results of the SNK procedure for those occasions when similarities differed significantly between panel sizes appear on Table 3.31,3.2. Small panels almost always had lower similarity than larger panels, although the two larger sizes frequently did not differ from each other. Standard deviations of similarity coefficients for each panel size were generally larger for small panels than for large (Appendix 3), again reflecting greater between-panel variation.

These differences are as predicted, since small panels

sample a smaller amount of plankton and sampling variation should be correspondingly larger.

3.5.3 Between-time within-site similarities

The graphs of recruitment (Figures 3.12-3.17) show that most species only recruited for short periods each year. Comparisons between time periods would then involve many species which were present at time period a, but not at b and *vice versa*. The similarity values would thus be low for these types of comparisons. There would seem to be little point in calculating similarities when there are so few species in common.

3.5.4 Between-site within-time similarities

Similar arguments apply in this case, since there are many species which are common at one site, but absent at the other, and again, similarities would be much lower than for comparisons made within-times within-sites.

3.6 DISCUSSION

Figures 3.12-3.17 and 3.4-3.10 show that the mean number of recruits per panel for individual species and for all recruits summed, all have large standard deviations. The recruitment behaviour of individual species varies from gregariousness to randomness and for some species, planktonic patchiness is superimposed on this variation. The combination of these factors means that the actual nature of the recruitment events on individual patches varies highly between patches. Indeed, for most species, the number of recruits on individual patches had a minimum of zero, with a standard deviation frequently equal to the mean; the range was frequently over 50 for common species, and as high as 2900 in some cases (*Balanus, Hydroides*).

If we consider predictability as the accuracy with which we can predict the events which will occur on an individual patch, we see that this is therefore low, despite the often high value for the similarity coefficients. These were inflated, as follows. Rare species were only present on one or a few panels, and so most pairs of panels lacked such species. Such pairs were obviously more similar in the composition of their recruits than a pair in which one panel received a rare species, but the other did not, and so zero-zero matches were considered valid (see Methods), and the s_{ijk} and W_{ijk} given a value of 1. Thus, a pair of panels had their similarity increased by $1/\Sigma W_{ijk}$ for each species both panels lacked. For this reason, similarity between panels is not a direct measure of predictability. A more realistic measure would be the similarity between panels where zero-zero matches were assigned a W_{ijk} of zero, even if species i occurred elsewhere in the set of panels. The comparison would then be for the numbers of recruits for species which were present on both panels. This would result in lower values of similarity. For example, the West Lakes between-panel similarities for January-March 1980 were recalculated setting W_{ijk} to zero for zero-zero matches. The resulting similarities are shown on Table 3.33. Similarities were reduced by 29, 36 and 39% for the three panel sizes respectively. These similarities relate specifically to the numbers of recruits, while those in the rest of the text compared both numbers and composition of recruits.

The former is conceptually more similar to predictability, and serves to demonstrate the low predictability of recruitment between-panels within sites and times.

Superimposed on this variation is that between-times and between-sites. Both sites showed considerable variation between years and between seasons, although there were consistent differences between

sites in the density of recruitment. Edithburgh showed consistently lower recruitment rates than West Lakes. This is in agreement with data for *Pinna* (Butler and Keough 1981; Appendix 4) which suggested that some sites had consistently good recruitment while others had highly variable recruitment.

Both sites showed strong seasonal fluctuations, but the peaks frequently failed to coincide, and their relative sizes also differed. There is thus little support for the concept of "good" or "bad" years for recruitment of sessile organisms.

The settlement of most species occurs at a predictable time of year, but the level of recruitment fluctuates so widely between years that the chronological sequence of recruitment cannot be predicted even qualitatively. Between-patch variation is enhanced by planktonic patchiness and the larval behaviour of individual species. These make accurate quantitative predictions about recruitment onto individual patches almost impossible. Predictability increases with patch size, but even for larger sizes of panel, between-panel variation is high.

Most of the factors which explain part of the between-panel variation operate on very small spatial scales and are themselves influenced by chance. For those species which settle near adult conspecifics, the position of the first few adults is likely to be random, and subsequent settlement becomes predictable when this is known. Similarly, we can assume that the position of plankton patches is effectively random with respect to the position of individual panels. In addition, the lack of correlation between similarity and between-panel distance for many time periods indicates that plankton patches occur unpredictably in space and time.

We thus have no *a priori* way of predicting the exact way in which either of these factors affect a given set of panels. Events on panels must be regarded as processes with means, but high variances,

and can only be understood by stochastic approaches, since the number of patches in which "mean" events occur will be very small, and the majority of patches will follow trajectories which deviate markedly from this "mean".

Aside from all else, this emphasizes the deficiencies in previous studies, many of which used too few replicates to estimate accurately the means, let alone the variances of the processes involved in recruitment.

TABLE 3.1 Analysis of variance of similarities between *Pinna* shells and a variety of other substrata.

ANOVA TABLE

Source	SS	df	MS	F	
Between substratum types	203	4	50.75	6.61	***
Within	806.2	105	7.68		
Total	1009.2	109			

$F_{.001(4,60)} = 5.31$, $F_{.001(4,105)} = 4.95$

Fmax = 3.40, $P > 0.05$

TABLE 3.2 Maximum non-significant value (for retention of null hypothesis of C.D. = 1) for coefficient of dispersion when sampling within panels. P values are for the next lowest number of degrees of freedom.

No. quadrats (n)	P		
	.05	.01	.001
180	1.21	1.28	1.36
90	1.30	1.40	1.52
45	1.43	1.58	1.76
22	1.64	1.88	2.19
12	1.95	2.35	2.96

TABLE 3.3 Analysis of within-panel settlement patterns for *Elminius modestus*. Data are the number of barnacles per quadrat for 1 cm^2 and 4 cm^2 quadrats. P is the probability that the C.D. does not differ from unity.

		$1cm^2$		$4cm^{-2}$	
Panel size	$\bar{x}$	C.D.	P	C.D.	P
180	.0333	2.98	$<10^{-3}$	5.86	$<<10^{-3}$
180	.05	2.29	"	3.65	$<10^{-3}$
180	.0611	4.05	"	6.16	"
180	.283	3.09	"	8.00	"
180	.089	4.94	"	7.95	"
180	.039	1.83	"	2.375	$<10^{-3}$
180	.239	7.08	"	21.12	"
180	.061	1.675	"	3.19	"
90	.6125	5.13	"	12.55	"
90	.225	2.33	"	3.73	"
90	.122	3.83	"	7.38	"
90	.089	6.230	"	8.00	"
90	.122	1.623	"	2.81	"

Table 3.4 Within-panel patterns of recruitment for *Spirorbis convexis* in West Lakes 8/78-10/78. Data are the number of recruits per 1 cm^2 and per 4 cm^2 quadrat. P is the probability that the C.D. does not differ from unity.

	1 cm^2			4 cm^2	
Panel size	$\bar{x}$	C.D.	P	C.D.	P
180	.0722	1.1654	>0.05	1.36	>0.05
180	.0222	0.9832	"	.9318	"
180	.0555	1.152	"	1.409	"
180	.1055	1.0053	"	1.209	"
180	.1389	.9464	"	1.11	"
90	.0375	.9775	"	3.80	"
90	.2125	.976	"	1.2105	"
90	.2125	.7975	"	.77708	"
90	.10	.9101	"	.62	"
90	.1333	.8764	"	.8254	"
45	.238	1.1907	"	1.42	"

TABLE 3.5 Analysis of within-panel recruitment for *Monia ione* and *Hydroides norvegica* at West Lakes. Data are the number of recruits per 1 cm^2 and per 4 cm^2 quadrat. P is the probability that the C.D. does not differ from unity.

(a) *Monia ione*

		1 cm^2		4 cm^2	
Panel size	$\bar{x}$	C.D.	P	C.D.	P
180 cm^2	0.911	3.063	$<10^{-3}$	21.722	$<10^{-5}$
180	0.656	3.210	$<10^{-3}$	4.612	$<10^{-3}$
180	0.533	2.564	$<10^{-3}$	3.486	$<10^{-3}$

(b) *Hydroides norvegica*

180 cm^2	0.33	1.94	$<10^{-3}$	2.33	$<10^{-3}$
180	0.66	2.61	$<10^{-3}$	4.43	$<10^{-3}$

TABLE 3.6 Between-panel variation in recruitment of *Spirorbis pagenstecheri*. Data are the number of recruits per panel, and density is the mean number of recruits per panel multiplied by 180/panel size (i.e. recruits per 180 cm^2).

Time	Panel size	$\bar{x}$	C.D.	P	Density
9/78-11/78	180 cm^2	1.6	3.31	$<10^{-3}$	1.6
	90	0.6	1.07	>0.05	1.2
	45	0.3	1.20	>0.05	1.2
1/79-3/79	180	0.5	1.62	<0.05	0.5
	90	0.5	5.12	$<10^{-3}$	1.0
	45	0.1	1.28	>0.05	0.5
3/79-5/79	180	0.6	8.8	$<10^{-3}$	0.6
	90	1.0	1.96	$<10^{-3}$	2.0
	45	0.1	0.600	>0.05	0.3
11/79-1/80	180	0.1	1.6	>0.05	0.1
	90	0.1	0.60	>0.05	0.3
	45	0.05	1.01	>0.05	0.2

TABLE 3.7 Between-panel patterns of recruitment for *Galeolaria hystrix*. Data are the number of recruits per panel. P is the probability that the C.D. does not differ from unity. Density is the number of recruits per 180 cm^2.

Time period	Panel size	$\bar{x}$	C.D.	P	Density
7-9/78	180	0.1	0.9	>0.05	0.1
	90	0.17	1.06	>0.05	0.34
	45	0.08	1.88	<0.05	0.3
9-11/78	180	0.8	2.11	$<10^{-3}$	0.8
	90	0.5	1.13	>0.05	1.0
	45	0.15	1.23	>0.05	0.6
11/78-1/79	180	0.9	8.71	$<10^{-3}$	0.9
	90	0.2	1.1	>0.05	0.8
	45	0.125	0.98	>0.05	0.5
1-3/79	180	1.5	3.23	$<10^{-3}$	1.5
	90	0.4	3.91	$<10^{-3}$	0.8
	45	0.115	3.29	$<10^{-3}$	0.46
3-5/79	180	1.0	2.89	$<10^{-3}$	1.0
	90	1.05	2.14	$<10^{-3}$	2.1
	45	0.42	2.88	$<10^{-3}$	1.7
5-7/79	180	0.3	1.20	>0.05	0.3
	90	0.4	1.41	>0.05	0.8
	45	0.20	1.35	>0.05	0.4
7-9/79	180	0.4	1.23	>0.05	0.4
	90	0.5	1.81	<0.05	1.0
	45	0.2	1.15	>0.05	0.8
9-11/79	180	1.8	3.2	$<10^{-3}$	1.8
	90	3.1	3.3	$<10^{-3}$	6.2
	45	0.5	1.62	>0.05	2.0
11/79-1/80	180	4.5	3.74	$<10^{-3}$	4.5
	90	3.0	2.00	$<10^{-3}$	6.0
	45	1.15	2.66	$<10^{-3}$	4.6
1-3/80	180	1.7	3.68	$<10^{-3}$	1.7
	90	1.75	1.96	<0.05	3.5
	45	0.48	1.27	>0.05	1.9

TABLE 3.8 *Didemnum* sp. T9. Between-panel recruitment patterns. Data are the number of recruits per panel. P is the probability that the C.D. does not differ from unity.

Time	Panel size	$\bar{x}$	C.D.	P
9-11/78	180	1.0	3.61	$<10^{-3}$
	90	1.3	3.08	$<10^{-3}$
	45	0.33	0.85	>0.05
9-11/79	180	0.4	1.23	>0.05
	90	6.25	1.44	>0.05

TABLE 3.9 *Parasmittina raigii*. Analysis of between-panel recruitment patterns. Data are the number of recruits per panel. P is the probability that the C.D. does not differ from unity. Density is the number of recruits per 180 cm^2.

Time	Panel size	$\bar{x}$	C.D.	P	Density
9/78	180	0.2	2.45	$<10^{-3}$	0.2
	90	0.1	1.6	>0.05	0.2
	45	0	-		
11/78	180	0.1	2.5	$<10^{-3}$	0.1
	90	0	-		
	45	0	-		
1/79	180	0.05	0.8	>0.05	0.05
	90	0.16	4.0	$<10^{-3}$	0.32
	45	0	-		
9/79	180	0	-		
	90	0.05	0.8	>0.05	0.1
	45	0	-		
7/78	90	0.1	1.3	>0.05	0.2
	45	0.05	0.64	>0.05	0.2
3/80	180	0.24	1.19	>0.05	0.24
	90	0.14	0.90	>0.05	0.28

TABLE 3.10 Between-panel recruitment patterns for *Cryptosula pallasiana* and Bryozoan BX1 at West Lakes. Data are the numbers of recruits per panel. P is the probability that the C.D. does not differ from unity. Density is the number of recruits per 180 cm^2.

(a) Bryozoan BX1

Time	Panel size	$\bar{x}$	C.D.	P	Density
10/77	180 cm^2	1.2	1.88	$<10^{-3}$	1.2
6/78	180	0.05	0.8	>0.05	0.05
	90	0.05	0.8	>0.05	0.1
	45	0.05	1.5	>0.05	0.2
8/78	180	0.2	0.8	>0.05	0.2
	90	0.05	0.8	>0.05	0.1
	45	0.05	0.96	>0.05	0.2
11/78	180	0.1	0.9	>0.05	0.1
	90	0.1	0.45	>0.05	0.2
	45	0	-		0
1/79	180	0.05	0.8	>0.05	0.05
	90	0	-		0

(b) *Cryptosula pallasiana*

Time	Panel size	$\bar{x}$	C.D.	P	Density
10/77	180	0.3	1.2	>0.05	0.3
8/78	180	2.3	2.3	$<10^{-3}$	2.3
	90	0.9	2.6	$<10^{-3}$	1.8
	45	0.5	1.62	>0.05	2.0
1/79	180	0.3	1.2	>0.05	0.3
	90	0.24	1.01	>0.05	0.5
	45	0.07	0.83	>0.05	0.3
11/78	45	0.05	1.01	>0.05	0.2

TABLE 3.11 Between-panel recruitment patterns for *Ciona intestinalis* and *Ascidia aspersa*. Data are the numbers of recruits per panel.

		CIONA		*ASCIDIA*	
Time	Panel size	$\bar{x}$	C.D.	$\bar{x}$	C.D.
1/80	180	3.69	2.25	2.62	2.97
	90	2.83	1.80	3.28	1.71
	45	1.86	1.80	2.21	4.66
11/79	180	0.5	3.54	0.1	1.6
	45	0.27	2.20	0.14	1.58
	90	0.9	3.84	0.5	3.38
9/79	180	0.09	1	0.53	5.65
	90	0.1	5.33	1.03	3.5
	45			0.7	2.80
3/80	180	0.19	1.68	0.04	1
	90	0.04	1	0.04	1
	45			0.05	1
8/77	180	1.2	4.41		
1/79	180			0.5	1.28
7/79	180	0.05	1	0.45	1.4
	90			0.1	0.89
11/78	180			0.06	2.01
	90			0.05	1.01

Table 3.12 Summary of recruitment patterns of common species

SPECIES	INFERRED PATTERNS OF RECRUITMENT
Spirorbis convexis	Consistent between years; random within-panel recruitment, between-panel clumping.
S. pagenstecheri	Consistent between years. No consistent small-scale pattern.
Hydroides norvegica	Consistent summer peaks. Between- and within-panel clumping. Probably larval swarms.
Galeolaria hystrix	Consistent at Edithburgh, sporadic at West Lakes. Settlement probably near adult conspecifics.
Elminius modestus	Between-year variation. Settlement near adult conspecifics.
Balanus amphitrite	Between-year variation. Settlement near adult conspecifics.
Monia ione	Between-year variation. Possibly settles near adult conspecifics.
Celleporaria fusca	Between-year variation. Possibly larval swarms.
Schizoporella schizostoma	Consistent recruitment. Approximately random settlement.
Parasmittina raigii	Consistent between years.
Cryptosula pallasiana	Consistent between years. Approximately random settlement.
BX 1	Consistent between years. Possibly settles near adult conspecifics.
Ciona intestinalis	Between-year variation.
Ascidia aspersa	Between-year variation.
Didemnum sp. A	Consistent between years. Tentatively larval swarms.

TABLE 3.13 Analysis of recruitment (all species pooled) for high density panels with different arrangements. Data were number of recruits per 180 cm^2 per 60 days. Time period 1/79-3/79.

ANOVA

Source	df	SS	MS	F
Subgroups	5	1004.6	200.92	2.41*
Panel size	2	448.17	224.08	2.68ns
Arrangement	1	672.8	672.8	8.02**
Interaction	2	183.63	81.82	0.98ns
Error	138	11521.15	83.49	
Total	143	13830.35		

F_{max} = 4.12 ns

Treatment means

Panel size

Arrangement	L	M	S
Linear	9.18	14.45	12.90
Clustered	7.63	7.00	4.50

Linear > clustered

TABLE 3.14 Analysis of recruitment (all species pooled) for high density panels with different arrangements. Data were number of recruits per 180 cm^2 per 60 days. Many small panels were lost so analysis is a one-way ANOVA using 180 cm^2 panels only. Time period 3/79-5/79.

ANOVA

Source	df	SS	MS	F
Arrangement	1	124.9	124.9	3.43 ns
Within	50	1820.16	36.40	
	51	1945.06		

F_{max} = 3.82 ns

TABLE 3.15 Analysis of recruitment (all species pooled) for high density panels with different arrangements. Data were number of recruits per 180 cm^2 per 60 days. Time period 5/79 - 7/79.

ANOVA

Source	df	SS	MS	F
Subgroups	5	28.65	5.73	4.56**
Panel size	2	11.37	5.69	4.52*
Panel arrangement	1	0.07	0.07	0.06 ns
Interaction	2	17.21	8.61	6.84**
Error	42	52.8	1.26	
Total	47	81.45		

F_{max} = 13.56 ns

Treatment Means

Panel Size

	L	M	S
Linear	2.00	0.9	0.20
Clustered	0.33	2.33	0.66

TABLE 3.16 Analysis of recruitment (all species pooled) for high density panels with different arrangements. Data were number of recruits per 180 cm^2 per 60 days. Time period 7/79 - 9/79.

ANOVA

Source	df	SS	MS	F
Subgroups	5	18.42	3.68	2.12 ns
Panel size	2	8.88	4.44	2.55 ns
Panel arrangement	1	5.03	5.03	2.89 ns
Interaction	2	4.51	2.26	1.30 ns
Error	78	135.82	1.74	
Total	83	154.24		

F_{max} = 9.34 ns

TABLE 3.17 Analysis of recruitment (all species pooled) for high density panels with different arrangements. Data were number of recruits per 180 cm^2 per 60 days. Time period 9/79 - 11/79.

ANOVA

Source	df	SS	MS	F
Subgroups	5	2041.79	408.36	4.99***
Panel size	2	1039.39	519.7	6.35***
Panel arrangement	1	377.12	377.12	4.61**
Interaction	2	625.28	312.63	3.82**
Error	60	4907.33	81.79	
Total	65	6949.12		

Treatment means

	Panel size		
	Large	Medium	Small
Linear arrangement	6.17	10.88	4.88
Clustered arrangement	13.00	26.5	1.00

TABLE 3.18 Analysis of recruitment (all species pooled) for high density panels with different arrangements. Data were number of recruits per 180 cm^2 per 60 days. Time period 11/79 - 1/80.

ANOVA

Source	df	SS	MS	F
Subgroups	5	1125.26	225.05	3.44**
Panel size	2	130.77	65.39	1.00 ns
Panel arrangement	1	759.28	759.28	11.62***
Interaction	2	235.21	117.61	1.80 ns
Error	84	5490.84	65.37	
Total	89	6616.1		

Treatment means

	Panel size		
	L	M	S
Linear	6.55	6.09	5.41
Clustered	13.85	12.63	7.88

TABLE 3.19 Results of one-way ANOVAS to test for differences in density of recruitment between three panel sizes at Edithburgh. Data were numbers of recruits per 180 cm^2 per 60 days. The table entries show the significance of the F-statistic for MS (between panel sizes)/ MS error. Full ANOVA tables appear in Appendix 3.

(a) total number of recruits (all species pooled)
(b) number of serpulids
(c) number of *Galeolaria* recruits
(d) number of *Spirorbis convexis* recruits
(e) number of *S. pagenstecheri* recruits

Time	(a)	(b)	(c)	(d)	(e)
9/78-11/78	ns	ns	ns	ns	ns
11/78-1/79	ns	ns	ns	ns	ns
1/79-3/79	ns	ns	ns	ns	-
3/79-5/79	ns	ns	ns	ns	-
5/79-7/79	ns	ns	ns	-	-
7/79-9/79	ns	ns	-	ns	-
9/79-11/79	**	**	**	**	*
11/79-1/80	ns	ns	ns	ns	-
1/80-3/80	*	*	ns	*	-
3/80-5/80	ns	ns	ns	ns	ns

A negative sign denotes an occasion when there were too few recruits for analysis.

TABLE 3.20. Results of SNK procedure on these time periods in Table 3.19 which showed significant heterogeneity between treatments. Panel sizes are shown in order of the mean number of recruits per 180 cm^2 per 60 days for the independent variable in question, and homogeneous subsets of means are underlined..

Time	Independent variable	SNK
9/79-11/79	total recruits	180 90 45
9/79-11/79	serpulids	
9/79-11/79	*Spirorbis convexis*	45 180 90
9/79-11/79	*S. pagenstecheri*	90 45 180
9/79-11/79	*Galeolaria*	45 90 180
1/80-3/80	total recruits	90 180 45
1/80-3/80	serpulids	90 45 180
1/80-3/80	*Spirorbis convexis*	90 45 180

TABLE 3.21 Results of one-way ANOVA's to test for differences in density of recruitment between three panel sizes at West Lakes. Data were number of recruits per 180 cm^2 per 60 days. Table entries show the significance of the F-statistic for MS (between panels)/MS error. Full ANOVA tables appear in Appendix 3. '-' denotes too few recruits for analysis.

(a) total number of recruits (all species pooled)
(b) number of serpulids
(c) *Hydroides norvegica* recruits
(d) *Spirorbis convexis* recruits

Time	(a)	(b)	(c)	(d)
6/78-8/78	ns	ns	ns	ns
8/78-10/78	ns	ns	ns	ns
11/78-1/79	ns	ns	-	ns
1/79-3/79	ns	ns	ns	ns
3/79-5/79	ns	ns	ns	-
5/79-7/79	ns	ns	-	ns
7/79-9/79	too few recruits			
9/79-11/79	ns	ns	ns	ns
11/79-1/80	ns	ns	ns	ns
1/80-3/80	*+	ns	ns	-
3/80-5/80	*+	ns	ns	ns

+ Only two significant F's were obtained. These could be Type I errors, since they form less than five percent of the ANOVAs. No SNK results will be presented.

TABLE 3.22 Results of one-way ANOVAs to test for differences in density of recruitment of individual species between three panel sizes at West Lakes and Edithburgh. The data are for species which recruited too rarely for inclusion in Tables 3.19 and 3.21. The entries in the table show the significance of the F-statistic comparing MS between panel sizes/MS error. Complete ANOVA tables are in Appendix 3.

Species	Time	F
WEST LAKES		
Ciona	1/80-3/80	ns
Ascidia aspersa	1/80-3/80	ns
Bugula sp. A	11/78-1/79	ns
	11/79-1/80	ns
	3/80-5/80	ns
Galeolaria	6/78-8/78	ns
Electroma	11/78-1/79	ns
Scrupocellaria	11/78-1/79	ns
Elminius modestus	8/78-10/78	ns
Bryozoan BX1	8/78-10/78	ns
EDITHBURGH		
Didemnum sp. A	9/78-11/78	ns
	9/79-11/79	ns
Total bryozoans	3/80-5/80	ns

TABLE 3.23 Edithburgh. Results of correlation (Pearson r) of between-panel similarity with distance between panels. 0 : correlation did not differ from 0; + significant positive correlation, - significant negative correlation*

	180 cm^2	90 cm^2	45 cm^2
Time period	sig. r		
9/78-11/78	0	0	-
11/78-1/79	0	0	+
1/79-3/79	-	0	-
3/79-5/79	0	0	+
5/79-7/79	-	0	0
7/79-9/79	0	0	0
9/79-11/79	0	0	0
11/79-1/80	-	0	0
1/80-3/80	-	0	0
3/80-5/80	0	0	0

* correlation coefficients were tested by two-tailed t-test, $\alpha = 0.05$

TABLE 3.24 Relation between total recruitment rate, between-panel similarity and the similarity-distance correlation. Edithburgh 180 cm^2 panels.

Time period	Mean total colonists	Mean similarity	r
9/78-11/78	12.73	0.75±0.15	.173
11/78-1/79	15.25	0.80±0.13	+.048
1/79-3/79	9.5	0.69±0.21	-.699***
3/79-5/79	2.29	0.66±0.25	.085
5/79-7/79	2.53	0.73±0.24	-.354**
7/79-9/79	2.88	0.76±0.20	.192
9/79-11/79	11.61	0.74±0.16	-0.153
11/79-1/80	12.95	0.81±0.13	-.399**
1/80-3/80	3.68	0.475±0.23	-.264*
3/80-5/80	6.33	0.66±0.12	-.029

TABLE 3.25 Total colonists, between panel similarities and correlation between similarity and distance for Edithburgh 90 cm^2 panels at different time periods.

Time period	Mean total colonists	Mean similarity	r
9/78-11/78	10.5	0.75±0.13	-.161
11/78-1/79	10.0	0.82±0.11	.075
1/79-3/79	5.0	0.54±0.13	.130
3/79-5/79	1.95	0.73±0.22	.087
5/79-7/79	1.95	0.75±0.20	.033
7/79-9/79	2.61	0.77±0.13	.054
9/79-11/79	14.15	0.73±0.15	.046
11/79-1/80	8.45	0.77±0.11	-.049
1/80-3/80	3.65	0.75±0.13	.189
3/80-5/80	3.50	0.68±0.24	-.073

TABLE 3.26 Total colonists, between panel similarities and correlation coefficients between similarity and distance for Edithburgh 45 cm^2 panels at different time periods.

Time period	Mean total colonists	Mean similarity	r
9/78-11/78	4.77	0.80±0.12	-0.27*
11/78-1/79	3.50	0.78±0.16	0.399**
1/79-3/79	1.57	0.44±0.39	-0.394*
3/79-5/79	0.69	0.86±0.21	0.286*
5/79-7/79	0.69	0.79±0.30	-.009
7/79-9/79	0.63	0.55±0.38	-.205
9/79-11/79	3.15	0.064±0.29	0.194
11/79-1/80	3.45	0.77±0.25	-.015
1/80-3/80	1.05	0.72±0.18	-.208
3/80-5/80	1.25	0.49±0.17	.150

TABLE 3.27 Results of correlations of between-panel similarity and distance for panels in West Lakes at different times.

0: no sign. correlation,- $r < 0$ at $p = 0.05$, + $r > 0$ at $p = 0.05$

Coefficients are Pearson's r and were tested by t-test.

	PANEL SIZE		
Time period	180 cm^2	90 cm^2	45 cm^2
8/77-10/77	0	/	/
10/77-12/77	0	/	/
1/78-3/78	Balanus	/	/
6/78-8/78	0	0	0
8/78-10/78	0	-	-
11/78-1/79	-	0	0
1/79-3/79	-	0	+
3/79-5/79	0	0	0
7/79-9/79	0	-	0
9/79-11/79	0	0	0
11/79-1/80	0	0	+
1/80-3/80	-	0	0
3/80-5/80	-	0	0

TABLE 3.28 Relations between total recruitment rate, between panel similarity and the correlation coefficient r for between-panel similarities and distance. West Lakes 180 cm^2 panels.

Time period	Mean total recruits	Mean similarity	r
8/77-10/77	>2000.0	0.77±0.13	.225
10/77-12/77	2675.9	0.59±0.11	-.119
1/78-3/78	Balanus amphitrite at ≃ 98% cover on all panels		
6/78-8/78	29.67	0.76±0.13	.062
8/78-10/78	19.11	0.73±0.16	.033
11/78-1/79	23.6	0.79±0.12	-.489***
1/79-3/79	222.9	0.76±0.16	-.414**
3/79-5/79	11.25	0.75±0.21	.210
5/79-7/79	too few recruits for analysis		
7/79-9/79	14.07	0.76±0.22	.095
9/79-11/79	261.71	0.80±0.11	.049
11/79-1/80	97.58	0.69±0.12	.018
1/80-3/80	10.00	0.76±0.14	-.395*
3/80-5/80	327.57	0.72±0.11	-.202*

TABLE 3.29 Relations between total recruitment rate, between-panel similarity and the correlation coefficient r for between-panel similarities and distance. West Lakes 90 cm^2 panels.

Time period	Mean total recruits	Mean similarity	R
6/78-8/78	15.80	0.85±0.13	0.062
8/78-10/78	14.23	0.82±0.15	-.601****
11/78-1/79	20.3	0.83±0.14	-.058
1/79-3/79	106.6	0.77±0.16	-.005
3/79-5/79	7.34	0.80±0.27	.179
5/79-7/79	Too few recruits		
7/79-9/79	12.58	0.67±0.27	-.443**
9/79-11/79	141.47	0.74±0.17	.224
11/79-1/80	42.5	0.74±0.15	.072
1/80-3/80	12.45	0.63±0.13	.126
3/80-5/80	35.92	0.77±0.12	-.067ns

TABLE 3.30 Relations between total recruitment rate, between-panel similarity and the correlation coefficient r for between-panel similarities and distance. West Lakes 45 cm^2 panels.

Time period	Total recruits	Similarity	r
6/78-8/78	6.16	0.76±0.24	-.012
8/78-10/78	6.06	0.81±0.25	-.799****
11/78-1/79	7.1	0.77±0.14	-.168
1/79-3/79	27.81	0.77±0.18	.282*
3/79-5/79	3.13	0.68±0.26	.108
5/79-7/79	Too few recruits		
7/79-9/79	7.33	0.67±0.30	-.087
9/79-11/79	62.46	0.65±0.16	-.126
11/79-1/80	25.22	0.68±0.18	.325*
1/80-3/80	3.22	0.62±0.21	-.165
3/80-5/80	89.31	0.71±0.16	-.002

TABLE 3.31 Results of ANOVAs on between-panel similarities at Edithburgh. The dependent variable was the similarity between pairs of panels of a given size, and there were three panel sizes (treatments). One-way ANOVA's were performed, and the significance of the F-statistic is shown. Where this was significant, the result of the SNK procedure is shown. Treatments are displaced in decreasing order of means. Homogeneous subsets of means are underlined. Complete ANOVA tables appear in Appendix 3.

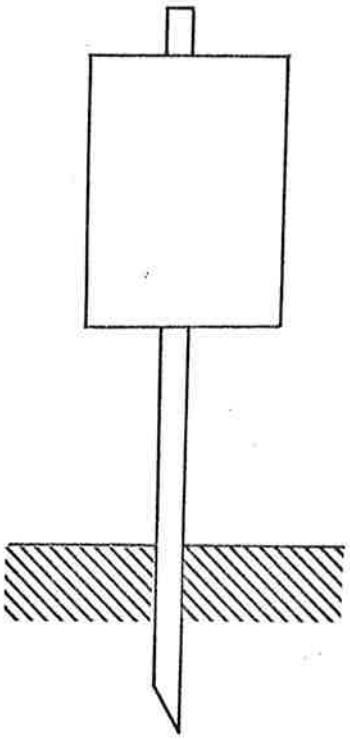
Time	F	SNK
9/78-11/78	ns	
11/78-1/79	ns	
1/79-3/79	*	180 90 45
3/79-5/79	***	180 90 45
5/79-7/79	ns	
7/79-9/79	***	180 90 45
9/79-11/79	*	180 90 45
11/79-1/80	ns	
1/80-3/80	ns	
3/80-5/80	**	180 90 45

TABLE 3.32 Results of ANOVA's on between-panel similarities at West Lakes. The dependent variable was the similarity between two panels of a given size. All analyses were one way ANOVA's with three panel sizes (treatments). Complete ANOVA tables may be found in Appendix 3. (The F-value is for MS between panel sizes/MS error. ns; not significant; * $p < 0.05$; ** $0.01 > p > 0.001$; *** $p < 0.001$.

Where the F-value was significant, the results of the SNK procedure are also shown. Panel sizes are arranged in decreasing order of mean between-panel similarity. Homogeneous subsets of means are underlined.

Time	F	SNK
6/78-8/78	*	45 180 90
8/78-10/78	ns	
11/78-1/79	*	90 180 45
1/79-3/79	ns	
3/79-5/79	*	90 180 45
5/79-7/79	insufficient recruits	
7/79-9/79	ns	
9/79-11/79	***	180 90 45
11/79-1/80	ns	
1/80-3/80	*	180 90 45
3/80-5/80	ns	

Figure 3.1 Recruitment panels and their method of suspension.



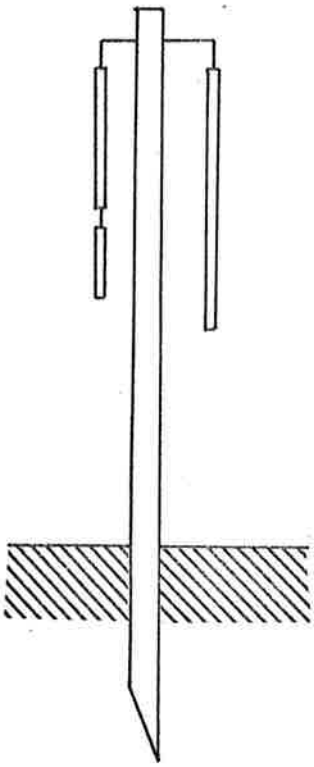


Figure 3.2 Arrangement of settlement panels at a given station.

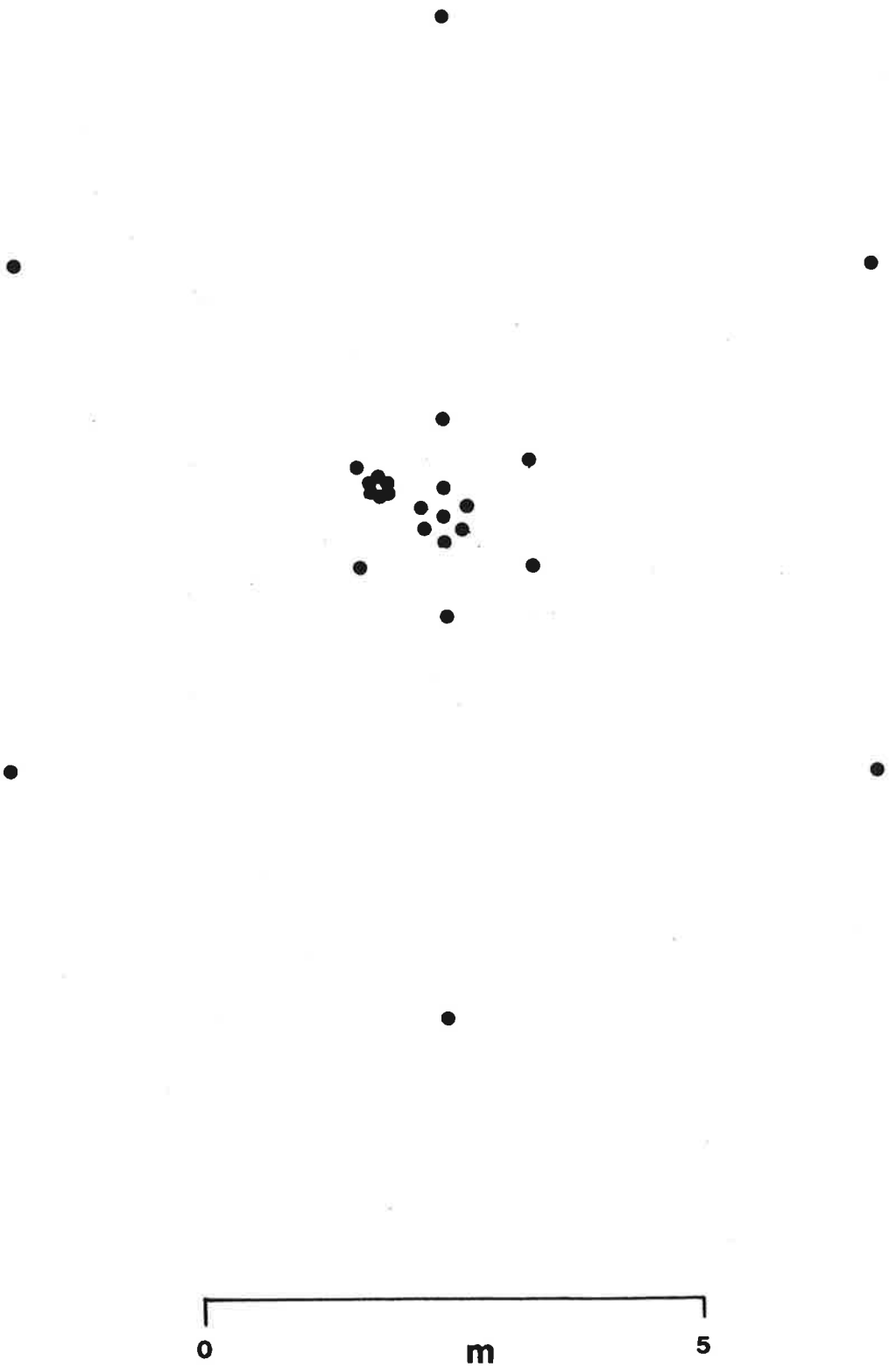

0
m
5

Figure 3.3 Variation in total recruits with time on 180 cm^2 panels at Edithburgh. Numbers are number of recruits per panel per 60 days. Means and S.D. bars are shown.

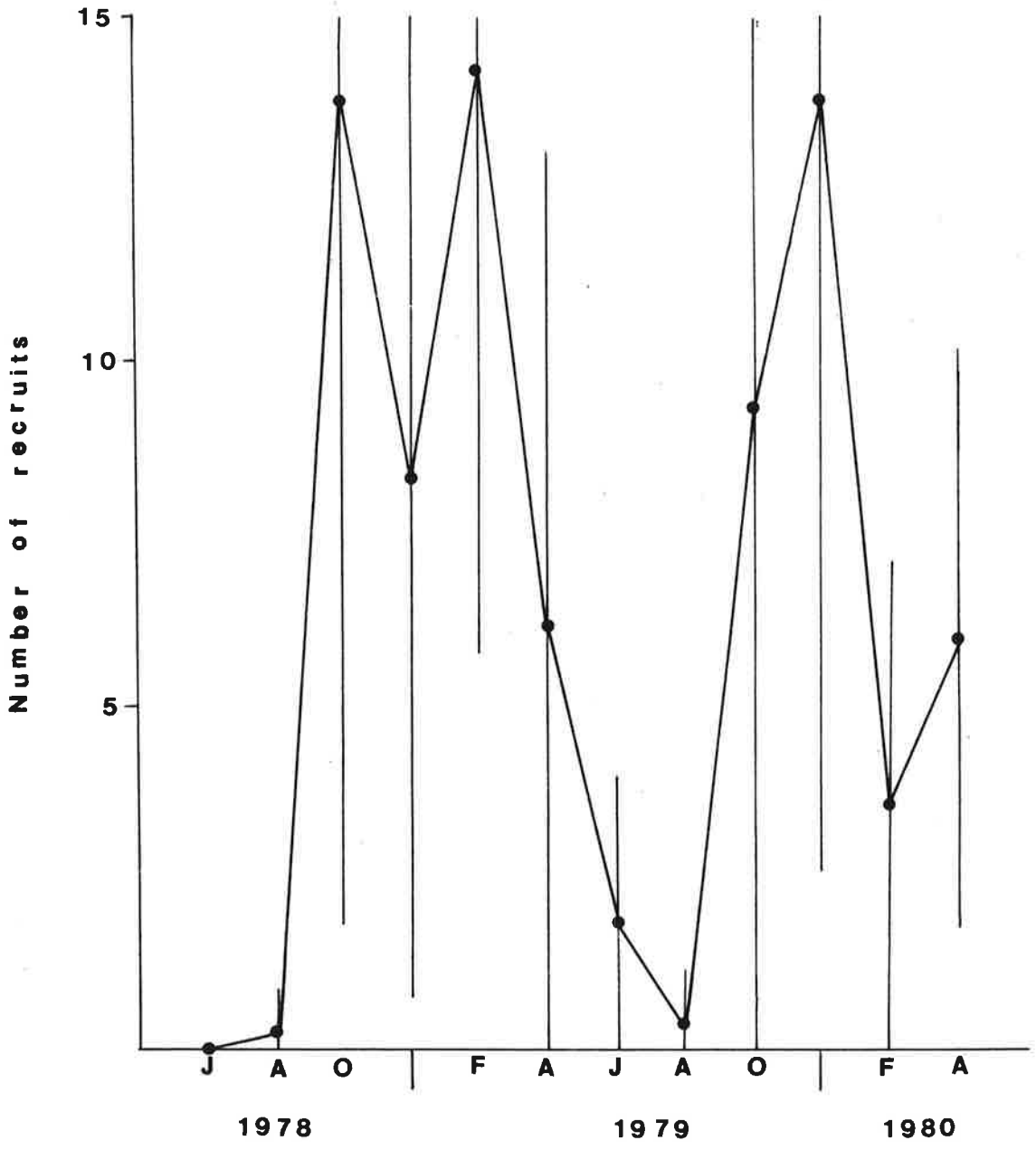

15
10
5
Number of recruits
J
A
O
F
A
J
A
O
F
A
1978
1979
1980

Figure 3.4 Variation in total recruits with time on 90 cm^2 panels at Edithburgh. Numbers are number of recruits per panel per 60 days. Means and S.D. bars are shown.

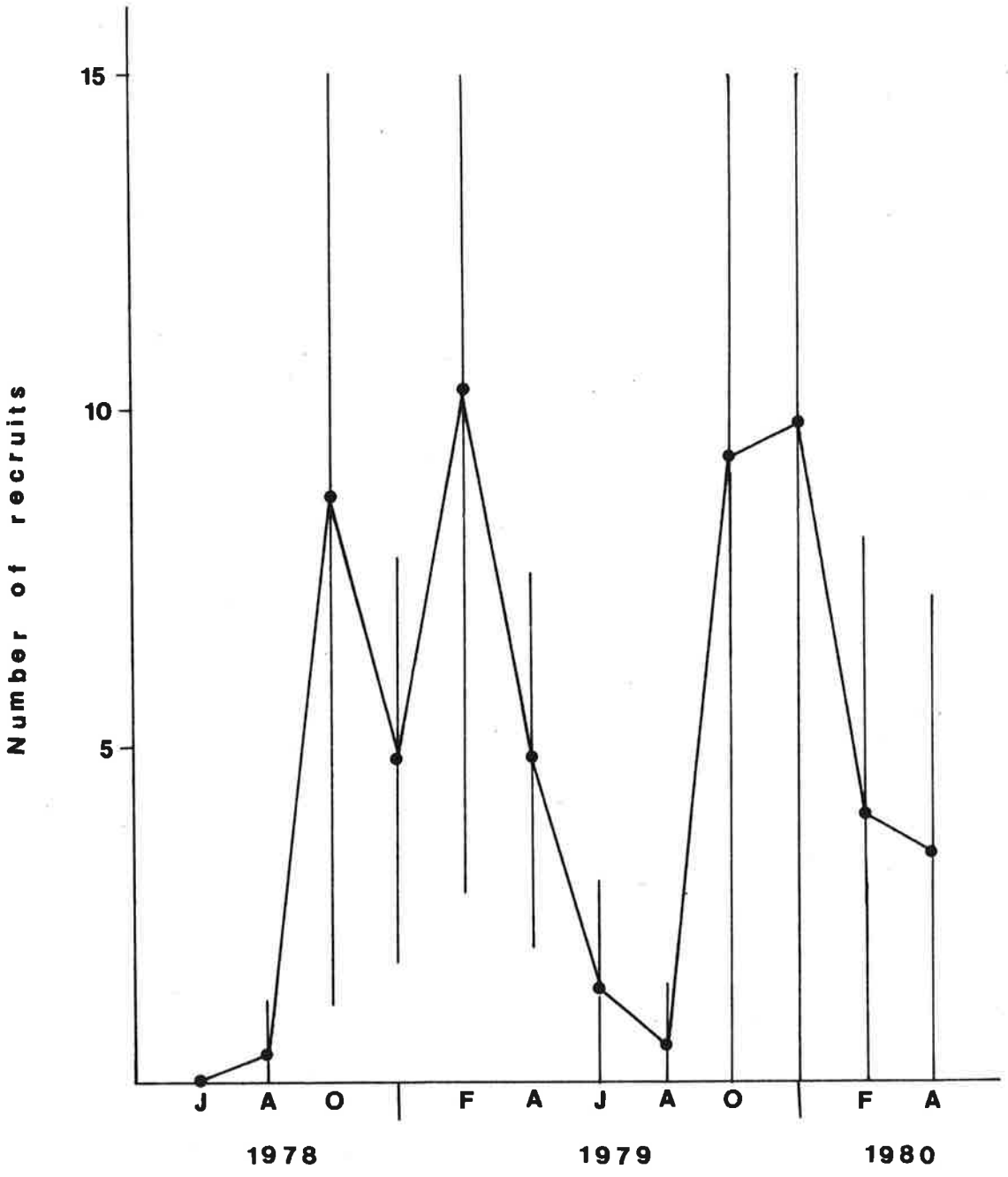

Number of recruits
15
10
5
J
A
O
F
A
J
A
O
F
A
1978
1979
1980

Figure 3.5 Variation in total recruits with time on 45 cm^2 panels at Edithburgh. Numbers are numbers of recruits per panel per 60 days. Means and S.D. bars are shown.

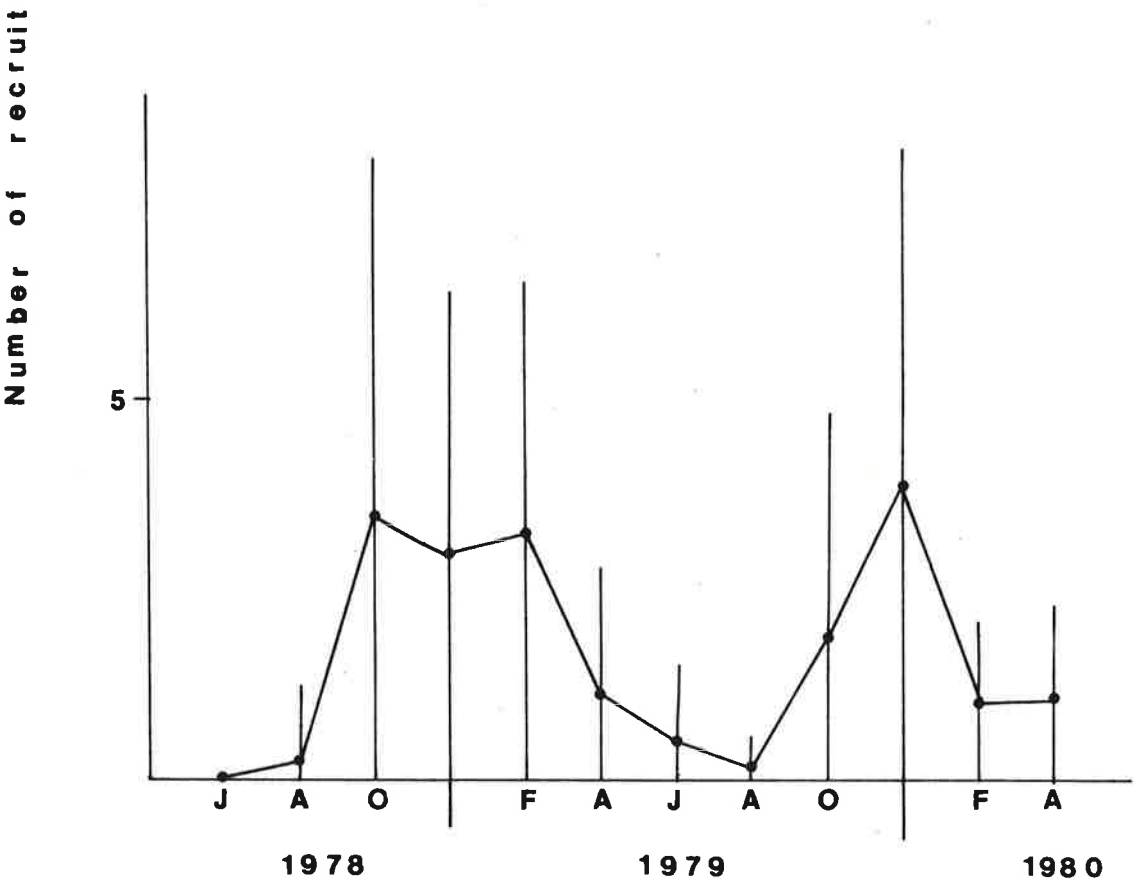

Number of recruit
5
J
A
O
F
A
J
A
O
F
A
1978
1979
1980

Figure 3.6 Variation in total recruits with time on 180 cm^2 panels at West Lakes. Numbers are number of recruits per panel per 60 days. Means and S.D. bars are shown.

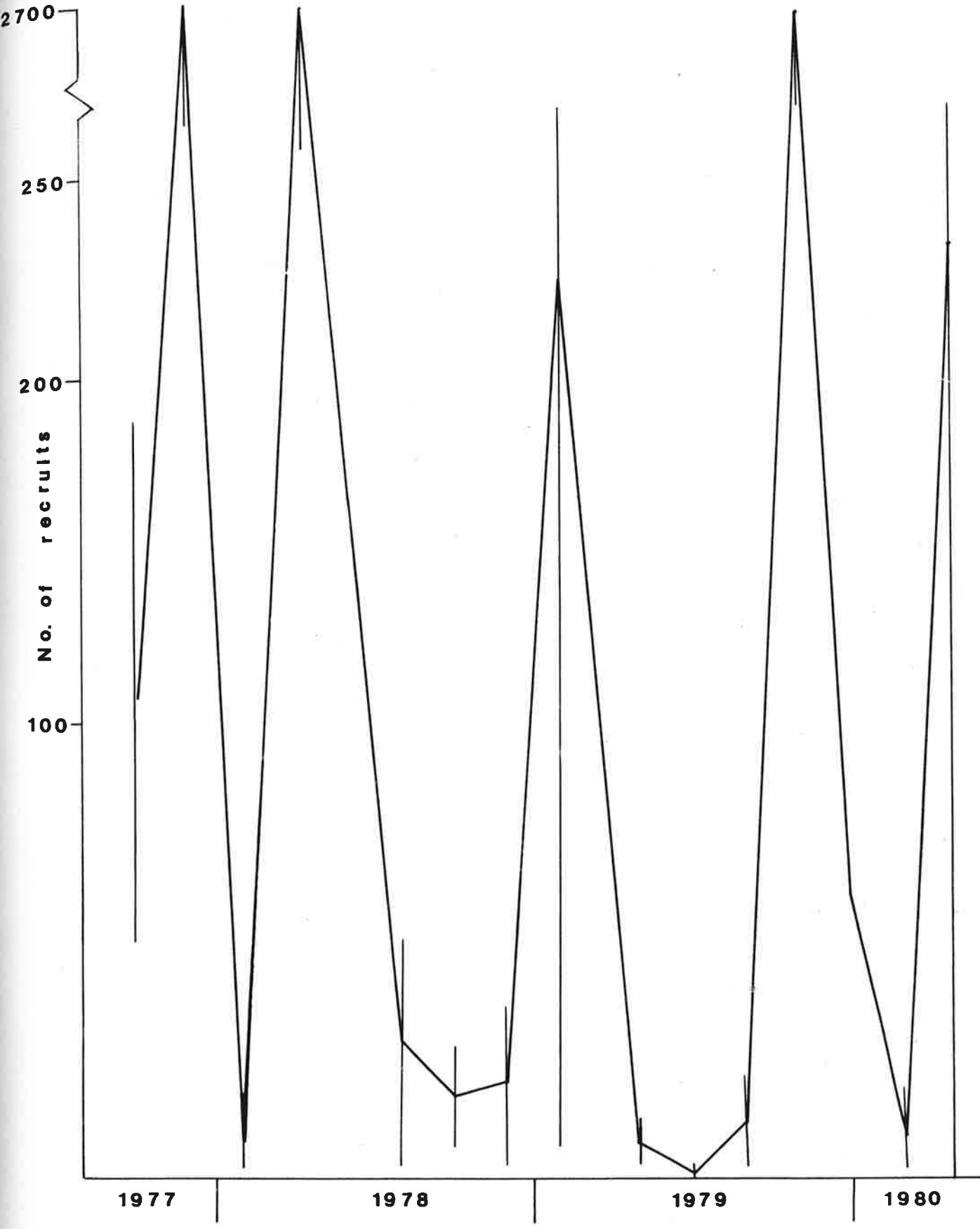

2700
250
200
100
No. of recruits
1977
1978
1979
1980

Figure 3.7 Variation in total recruits with time on 90 cm^2 panels at West Lakes. Numbers are number of recruits per panel per 60 days. Means and S.D. bars are shown.

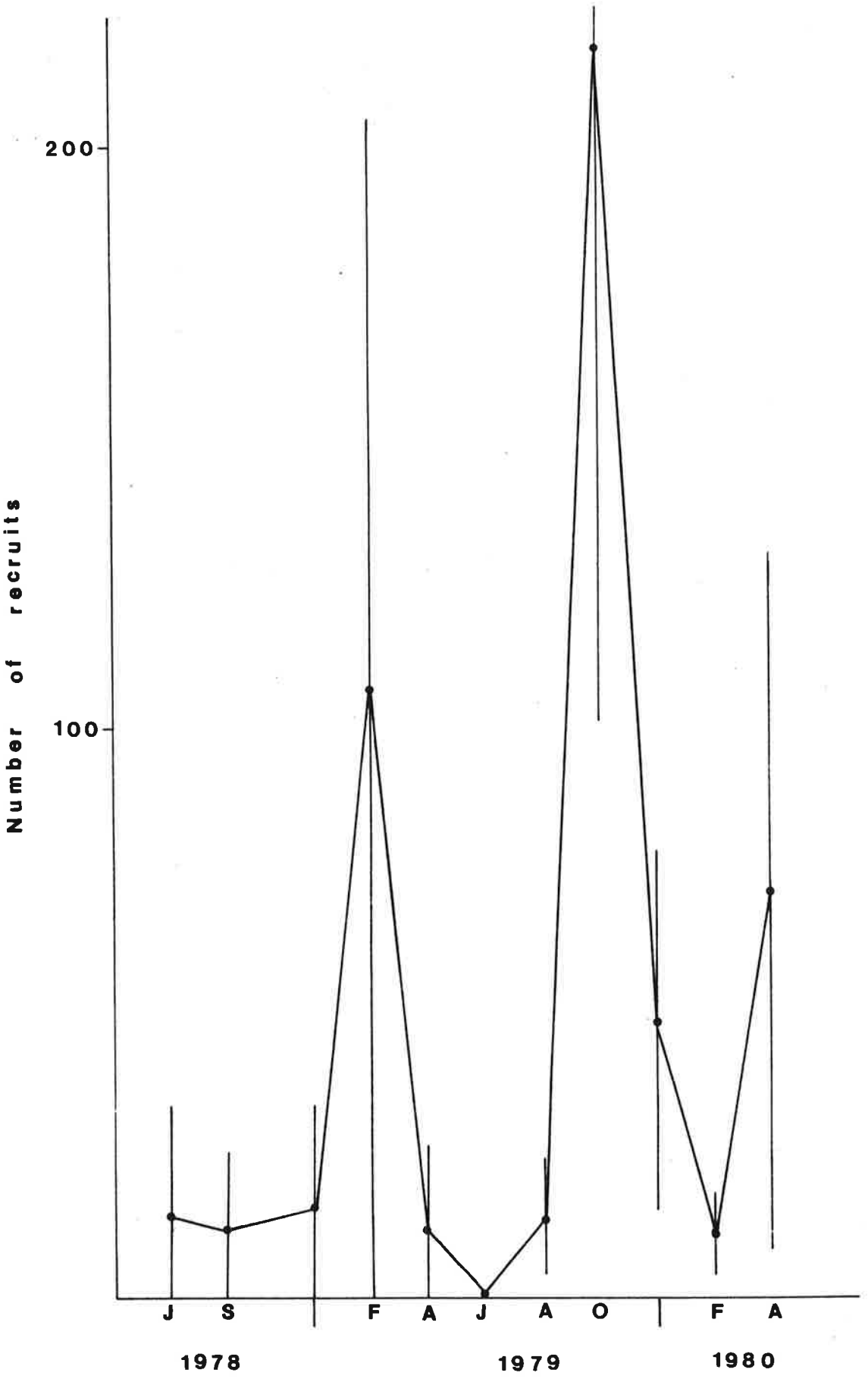

200
100
Number of recruits
J
S
F
A
J
A
O
F
A
1978
1979
1980

Figure 3.8 Variation in total recruits with time on 45 cm^2 panels at West Lakes. Numbers are number of recruits per panel per 60 days. Means and S.D. bars are shown.

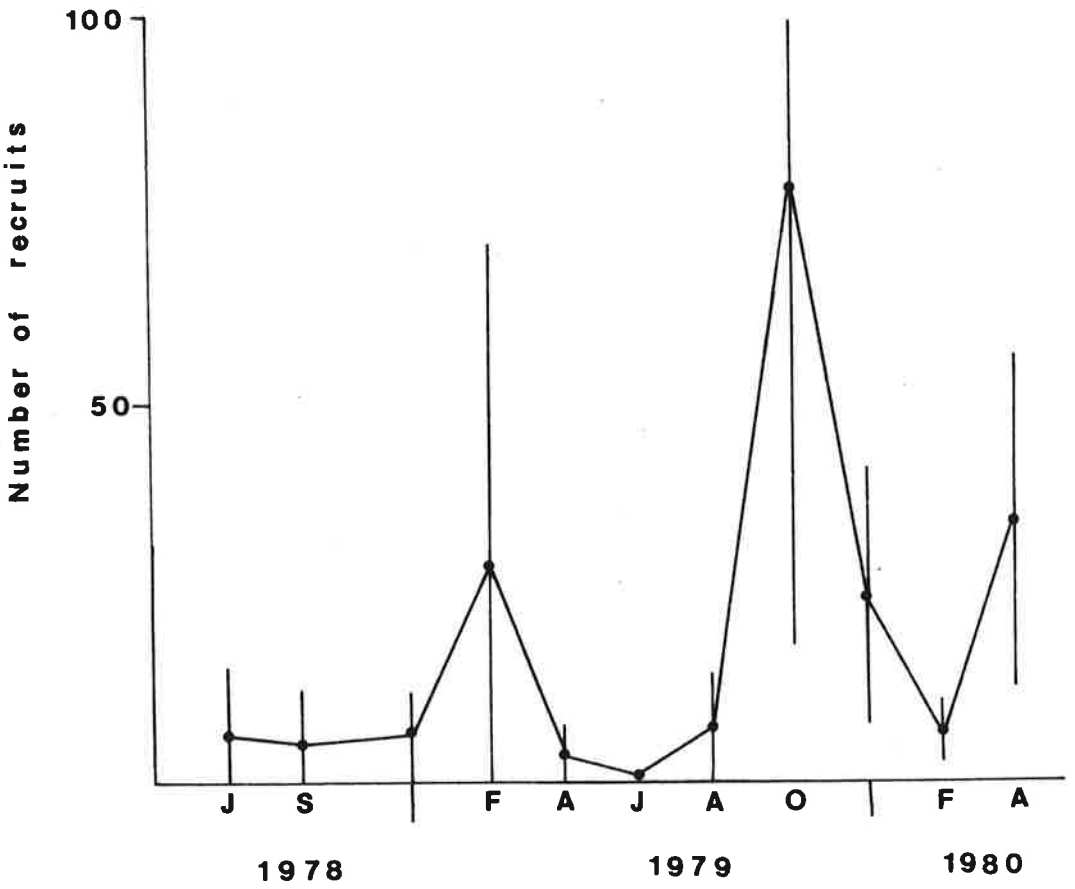

100
50
Number of recruits
J
S
F
A
J
A
O
F
A
1978
1979
1980

Figure 3.9 Variation in number of species colonizing per panel per 60 days with time for three panel sizes at West Lakes. Means and S.D. bars are shown.

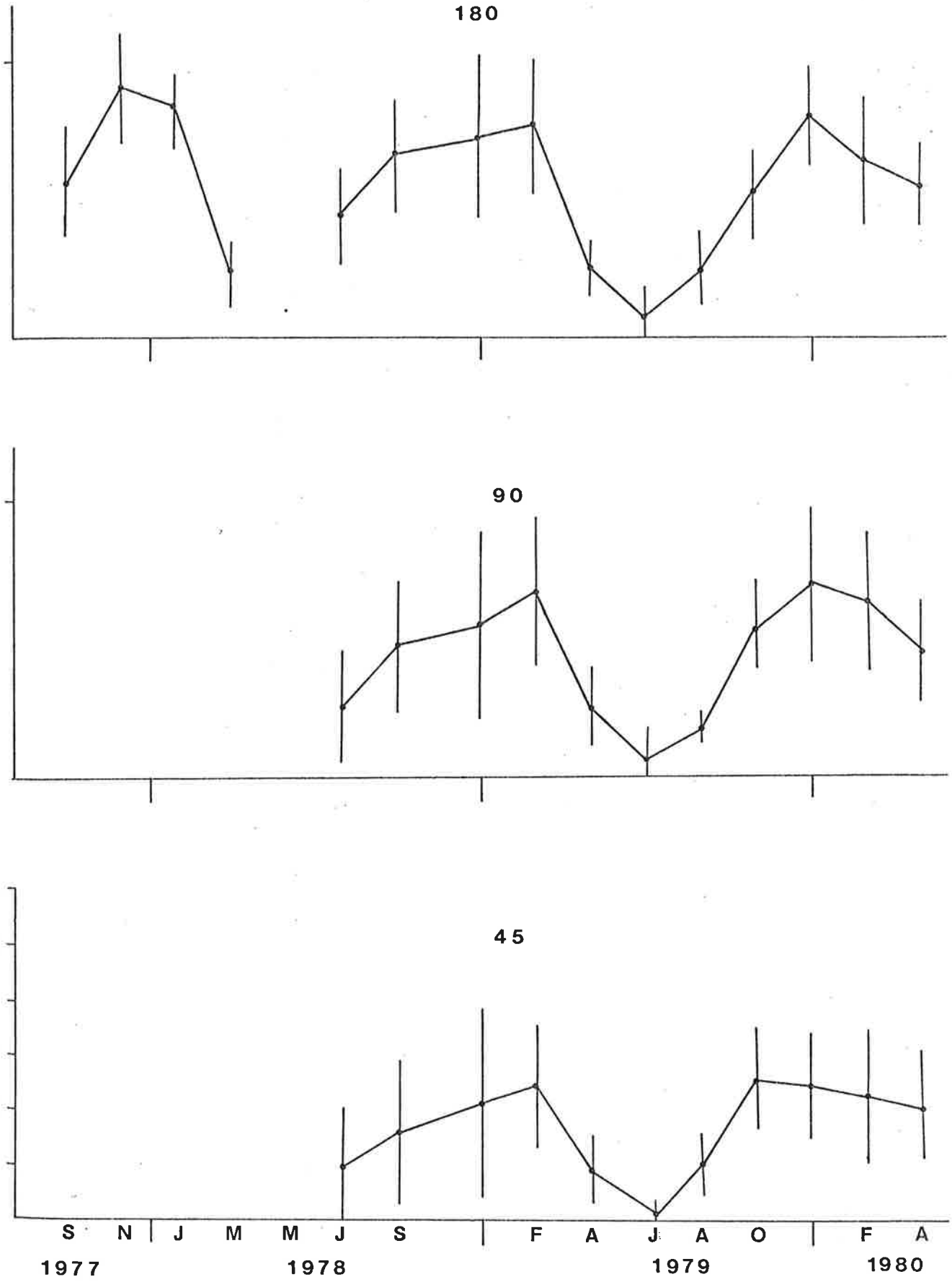

180
90
45
6
5
4
3
2
1
S N J M M J S F A J A O F A
1977 1978 1979 1980

Figure 3.10 Variation in number of species colonizing per panel per 60 days with time for three panel sizes at Edithburgh. Means and S.D. bars are shown.

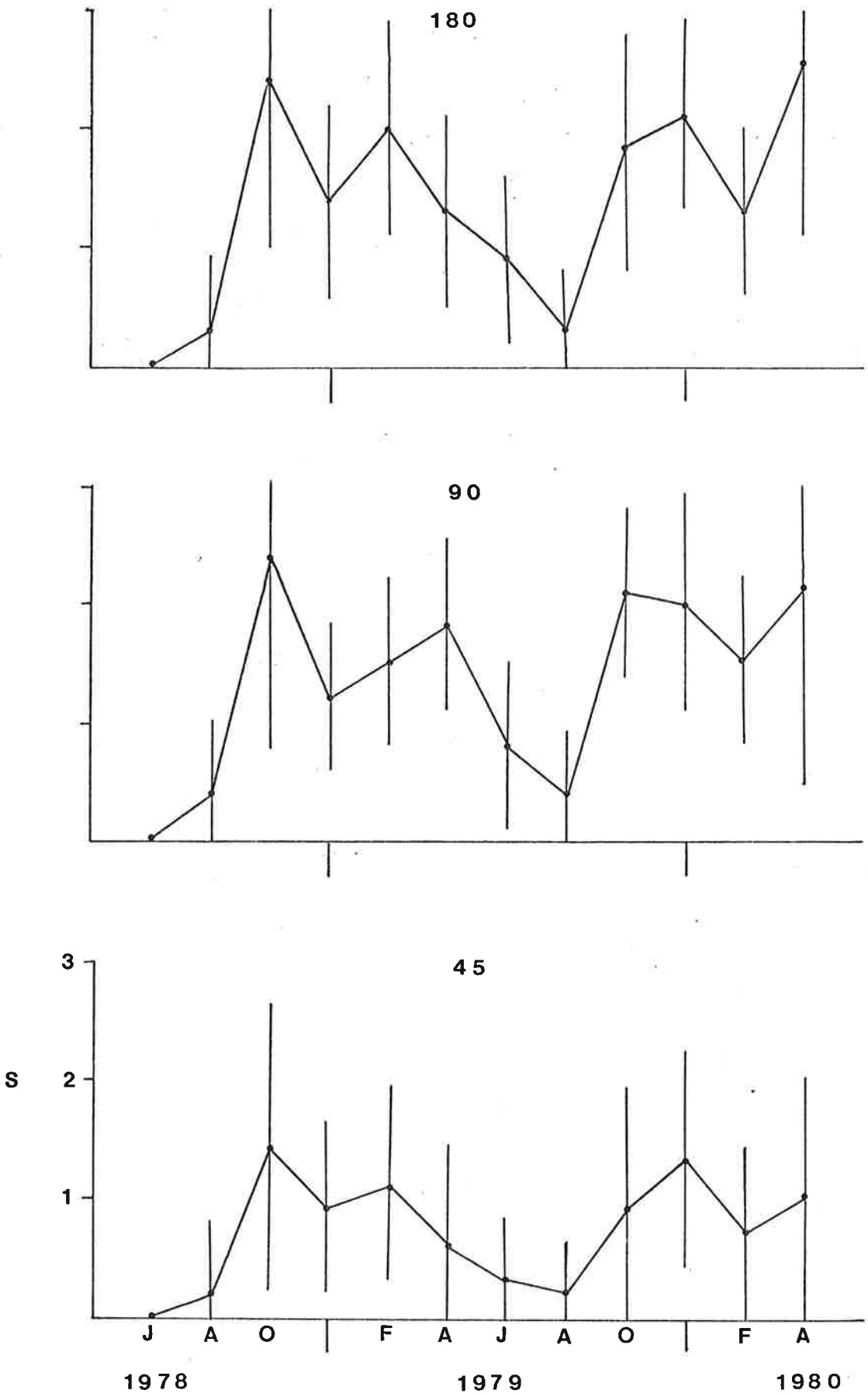

180
90
45
S
3
2
1
J
A
O
F
A
J
A
O
F
A
1978
1979
1980

Figure 3.11 Encounter between planktonic patch of Diameter D, and cluster of panels of diameter a, so that panel P1 intersects the patch at some point $D - \beta$ from the edge of the patch.

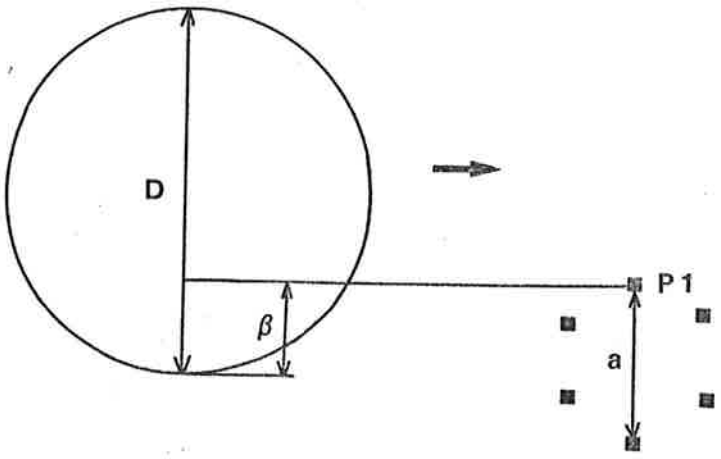
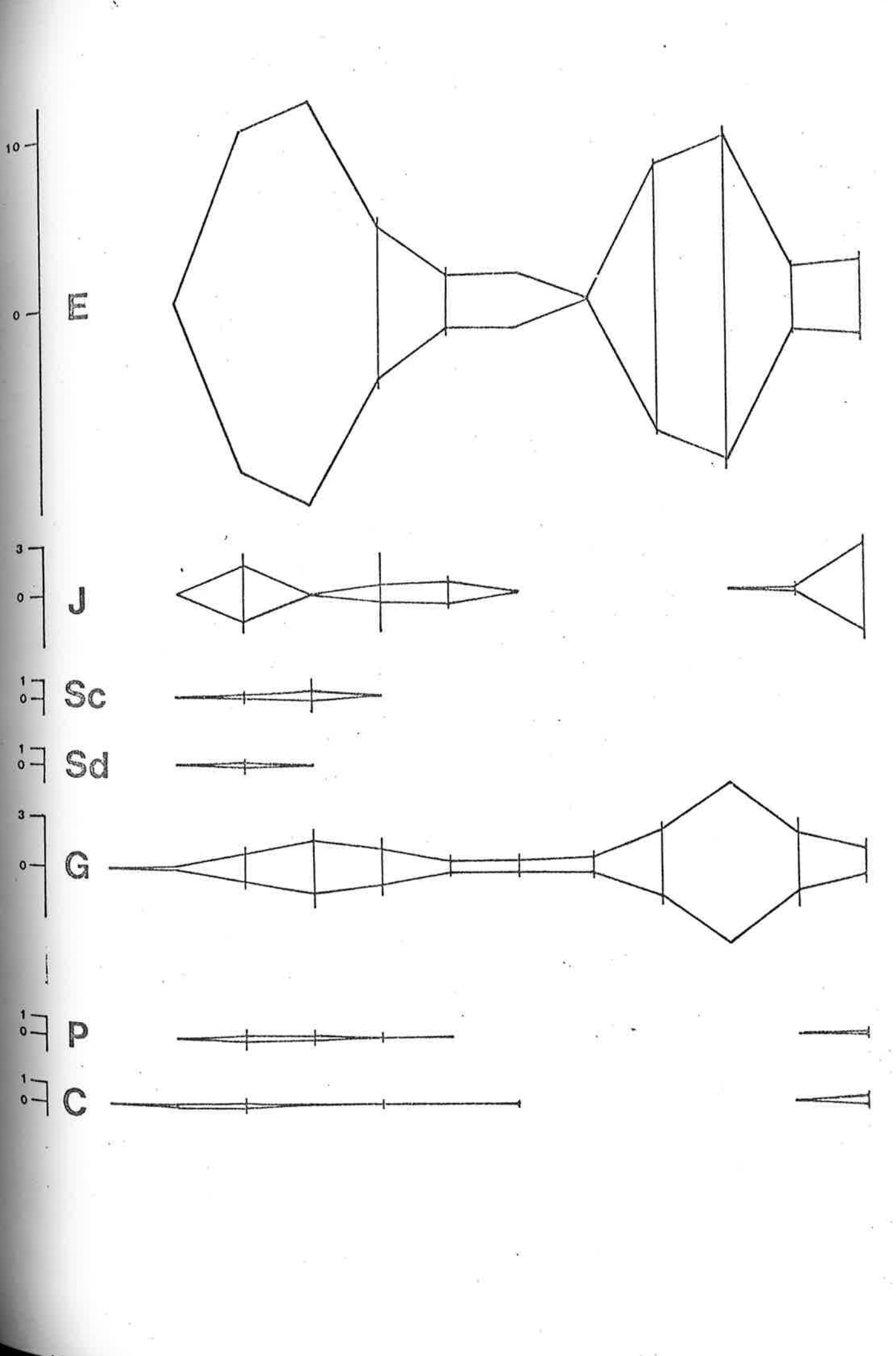

D
β
P 1
a

Figure 3.12 Variation in recruitment with time for individual species on 180cm^2 panels at Edithburgh. The mean number of recruits per panel per 60 days per 180cm^2 is plotted against the midpoint of the time period for which the recruitment was measured. The resulting curve is reflected in the "time" axis to produce the kites shown.

The following species codes apply to Figures 3.12 to 3.17.

A	Atapazoa fantasiana
Aa	Ascidia aspersa
Ar	Aplysilla rosea
As	Aplysilla sulphurea
B	Botrylloides leachii, Botryllus schlosseri
Ba	Bugula sp. A
Bal	Balanus amphitrite
Bb	Bugula sp. B
Bx	Bryozoan Bx 1
C	Celleporaria fusca
Ci	Ciona intestinalis
Cp	Cryptosula pallasiana
D	didemnid ascidians
E	Spirorbis (Eualospira) convexis
El	Electroma georgiana
Em	Elminius modestus
Es	Epopella simp ex
G	Galeolaria spp.
H	Hydroides norvegica
M	Monia ione
Pa	Parasmittina raigii
Pol	Polycarpa papillata
Por	miscellaneous sponges
S	Schizoporella schizostoma
Sc	Spirorbis sp.C
Sd	Spirorbis sp.D
Sp	Spirorbis (Janua) pagenstecheri

N.B. S.D. bars are shown where they exceeded means.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E
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0
J
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Sc
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0
Sd
3
0
G
1
0
P
1
0
C

Figure 3.12 - continued

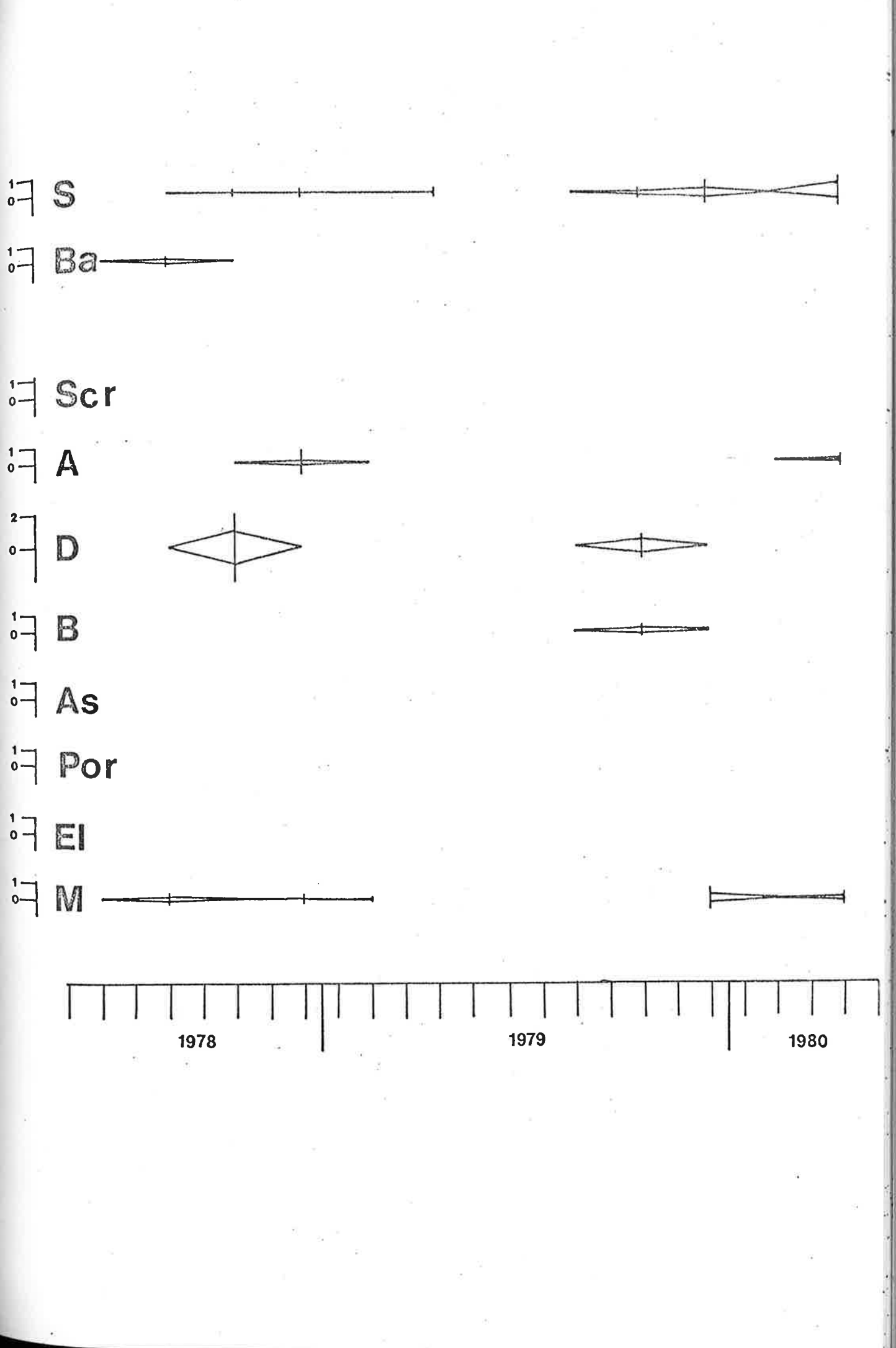
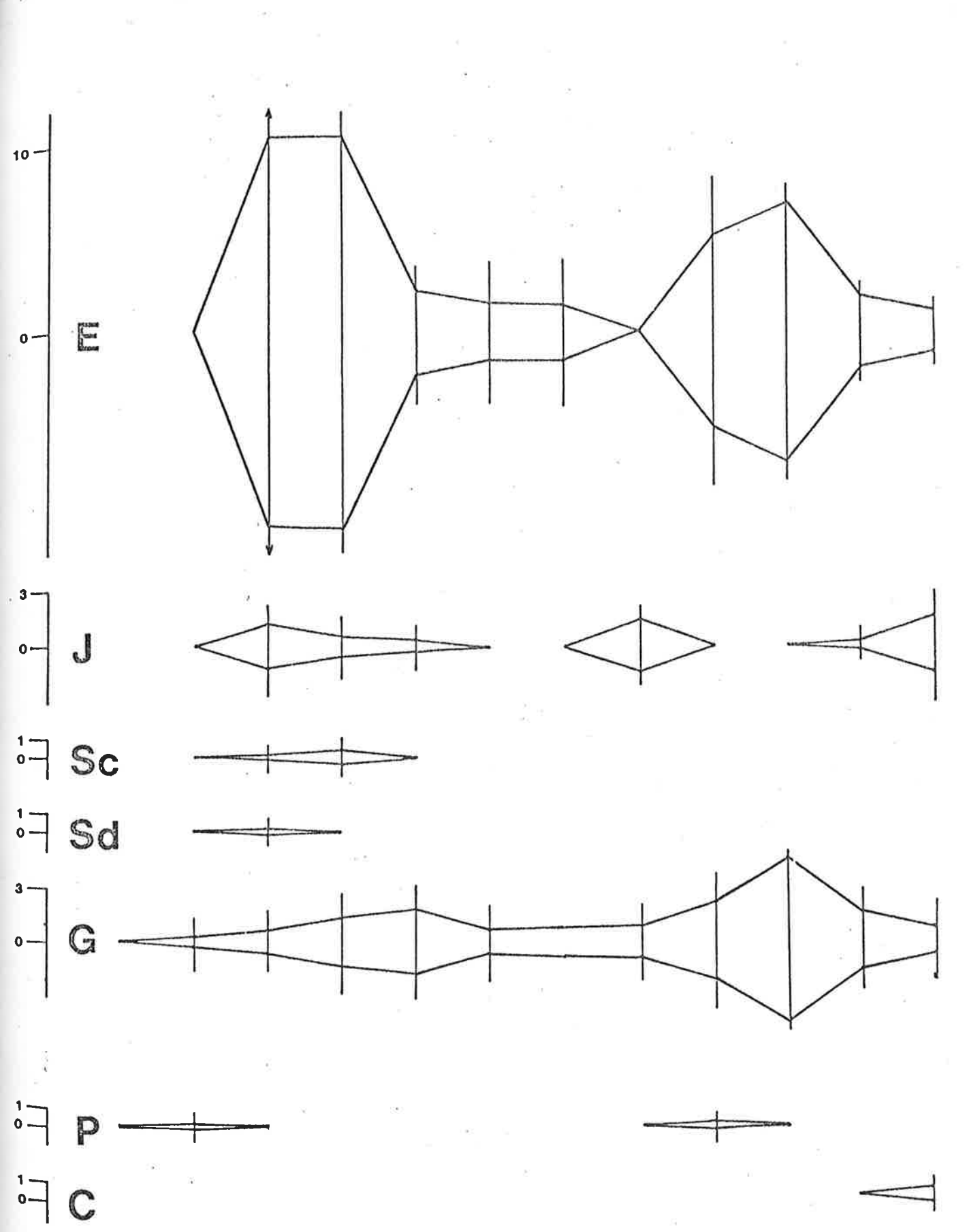

S
Ba
Scr
A
D
B
As
Por
El
M
1978
1979
1980

Figure 3.13 Variation in recruitment with time for individual species on 90cm^2 panels at Edithburgh. For explanation of figure, see caption for Figure 3.12.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J
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Sc
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0
Sd
3
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G
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0
P
1
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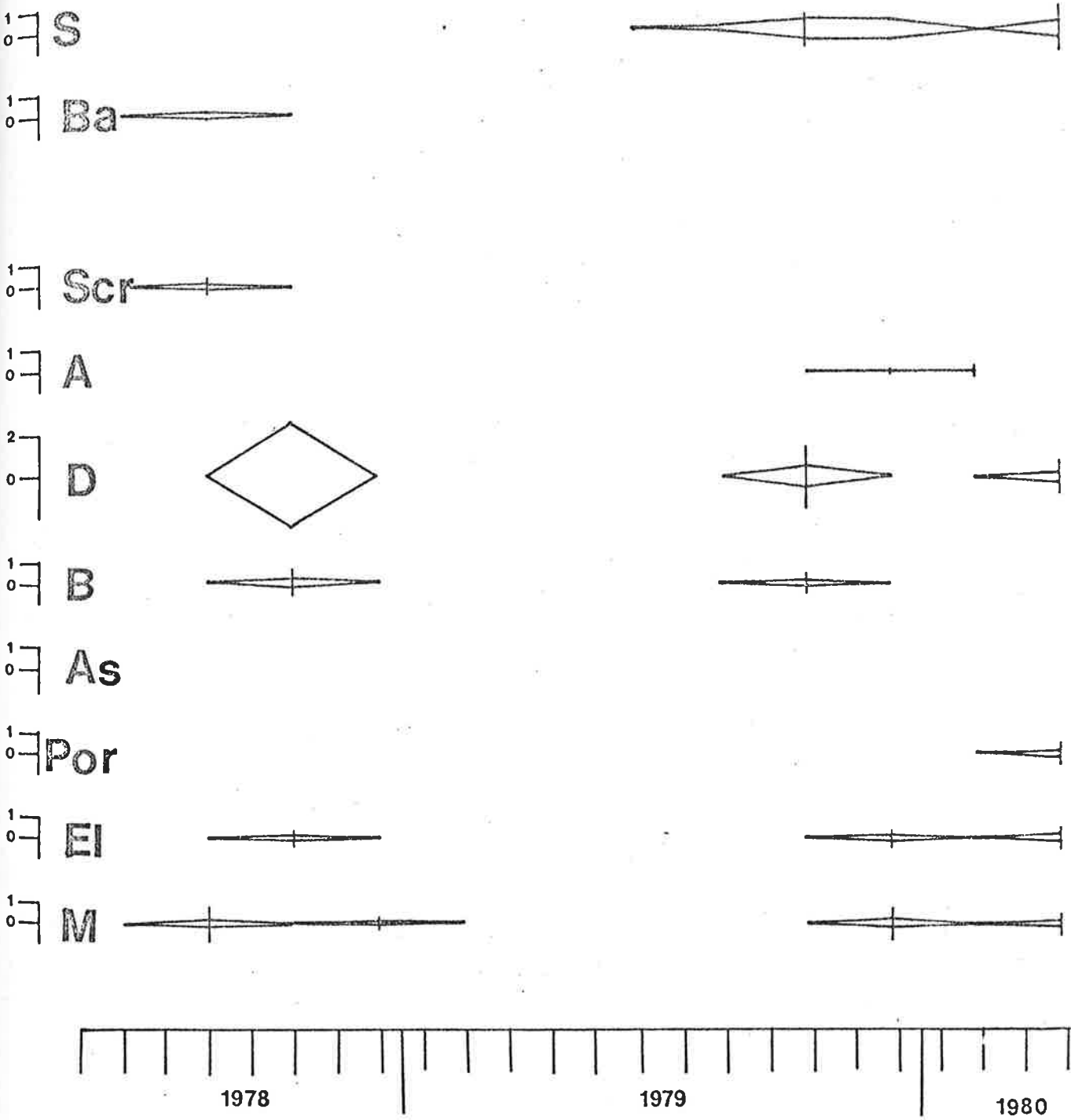
C

Figure 3.13 - continued.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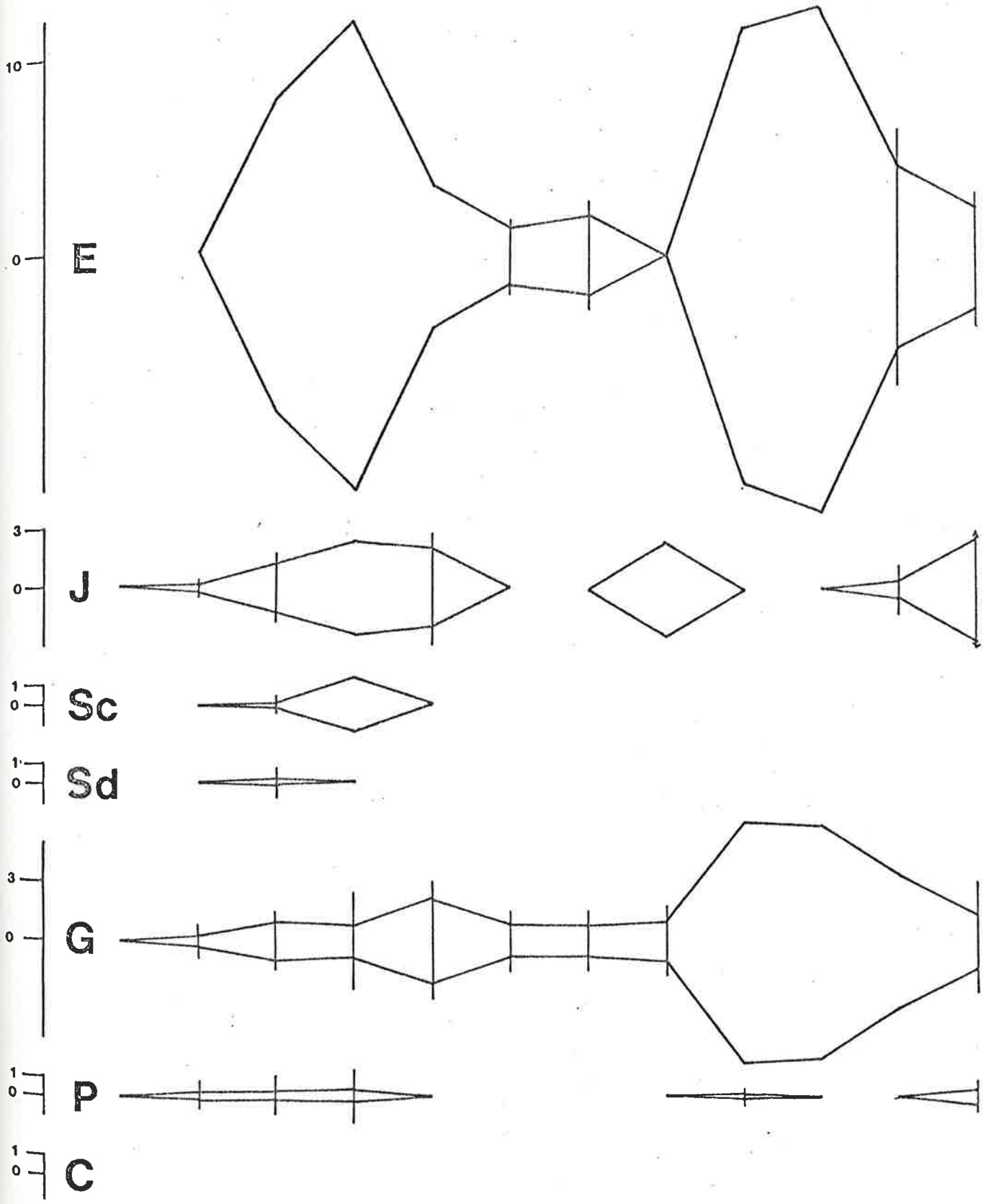
0
Ba
1
0
Scr
1
0
A
2
0
D
1
0
B
1
0
As
1
0
Por
1
0
El
1
0
M
1978
1979
1980

Figure 3.14 Variation in recruitment with time for individual species on 45cm^2 panels at Edithburgh. For explanation of figure, see caption to Figure 3.12.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0
E
3
0
J
1
0
Sc
1
0
Sd
3
0
G
1
0
P
1
0
C

Figure 3.14 - continued.

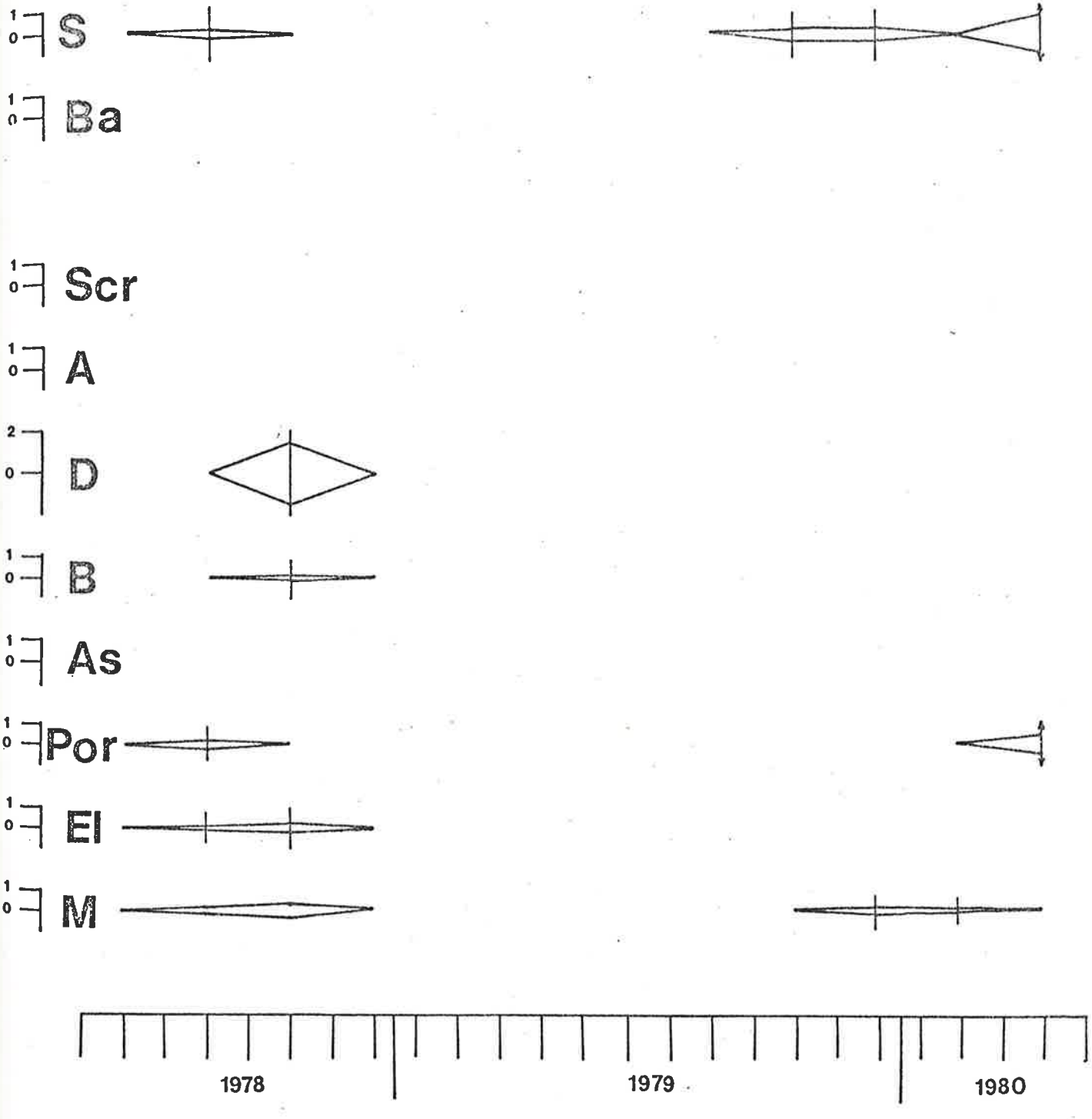
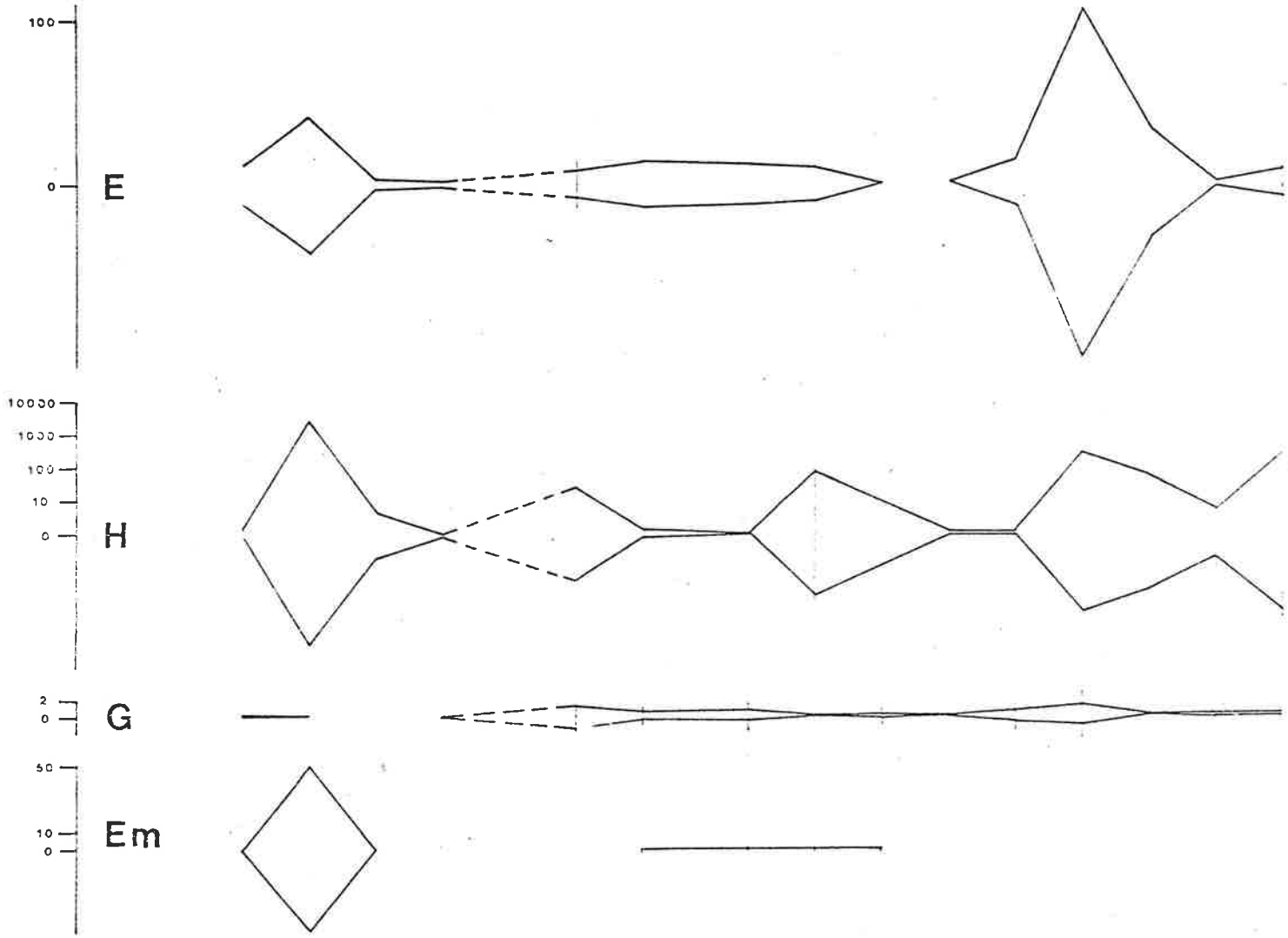

1
0
S
1
0
Ba
1
0
Scr
1
0
A
2
0
D
1
0
B
1
0
As
1
0
Por
1
0
El
1
0
M
1978
1979
1980

Figure 3.15 Variation in recruitment with time for individual species on 180cm^2 panels at West Lakes. For explanation to figure, see caption to Figure 3.12. Figure 3.15 is continued on the following page.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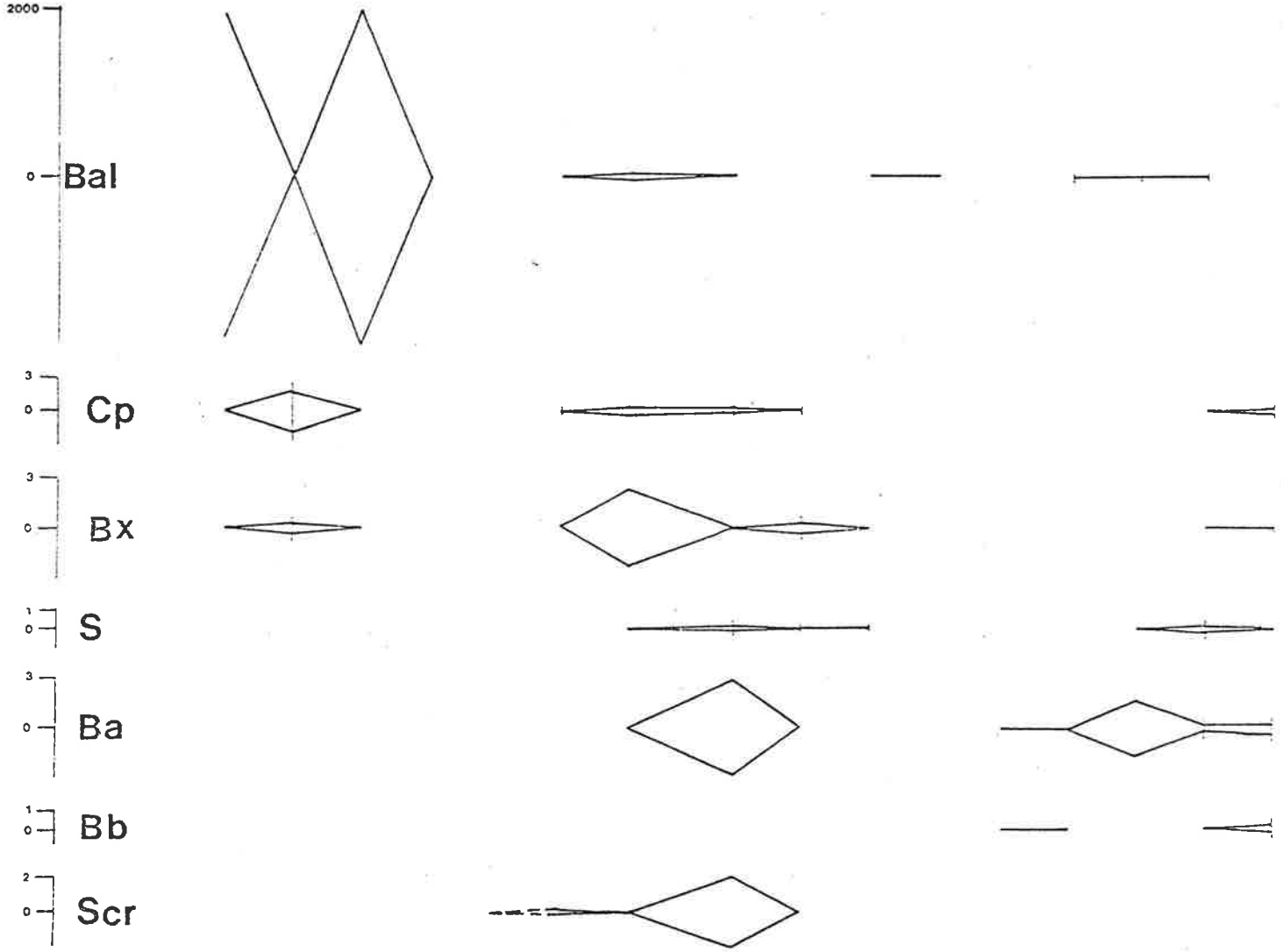
0
E
10000
1000
100
10
0
H
2
0
G
50
10
0
Em


2000
0
Bal
3
0
Cp
3
0
Bx
1
0
S
3
0
Ba
1
0
Bb
2
0
Scr

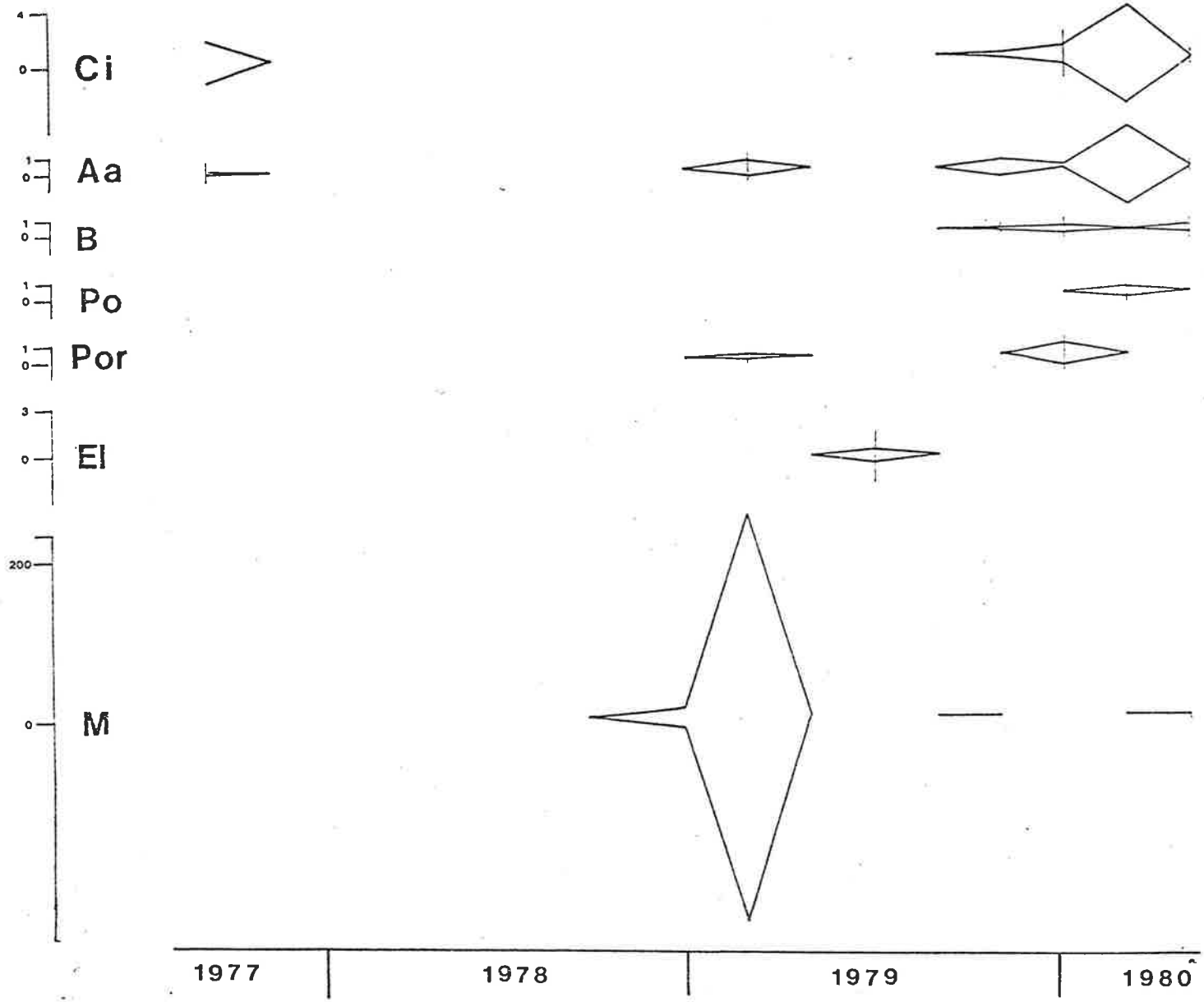
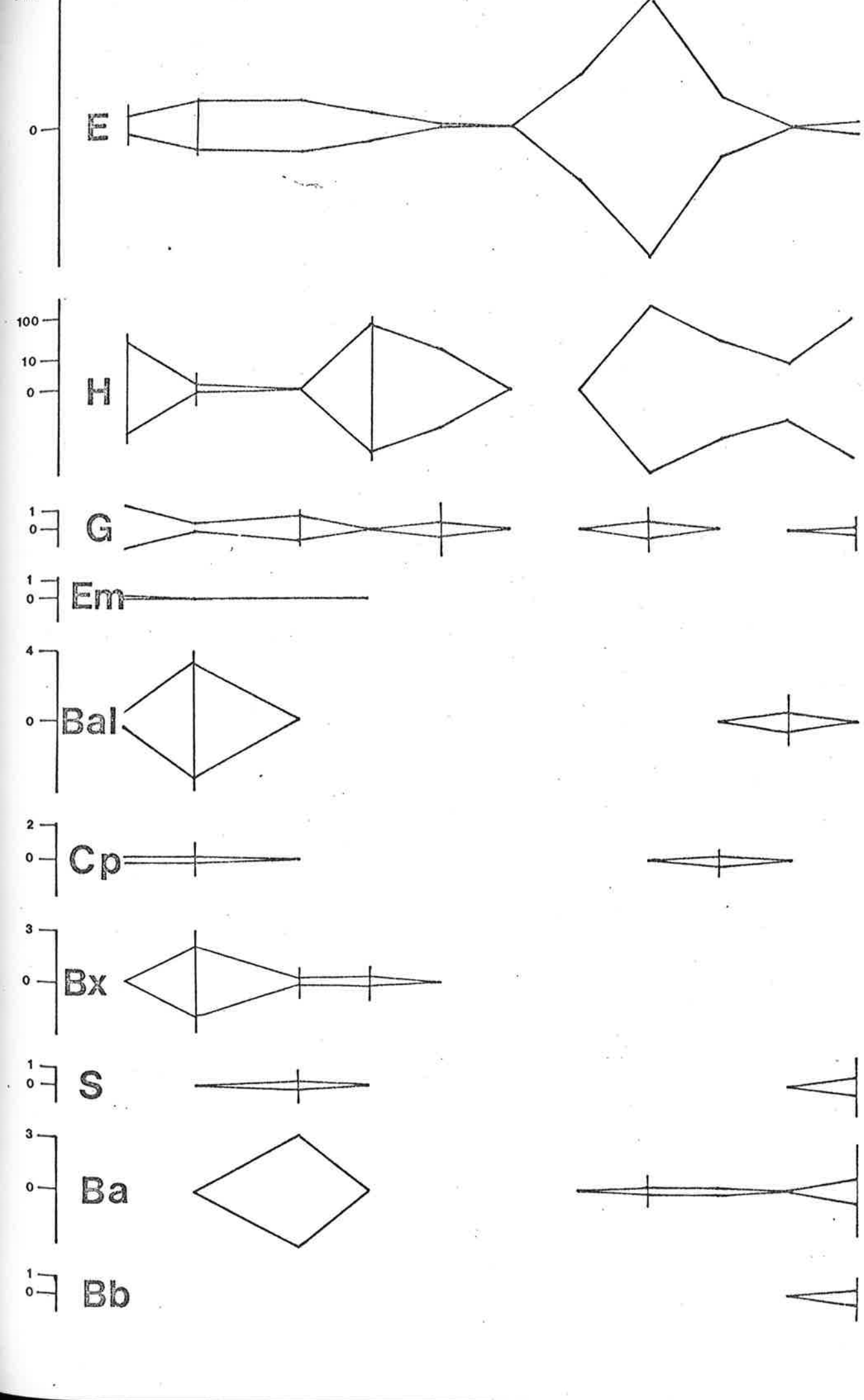

Ci
Aa
B
Po
Por
El
M
1977
1978
1979
1980

Figure 3.16 Variation in recruitment with time for individual species on $90cm^2$ panels at West Lakes. For explanation of figure, see caption to Figure 3.12.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10
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H
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0
G
1
0
Em
4
0
Bal
2
0
Cp
3
0
Bx
1
0
S
3
0
Ba
1
0
Bb

Figure 3.16 - continued.

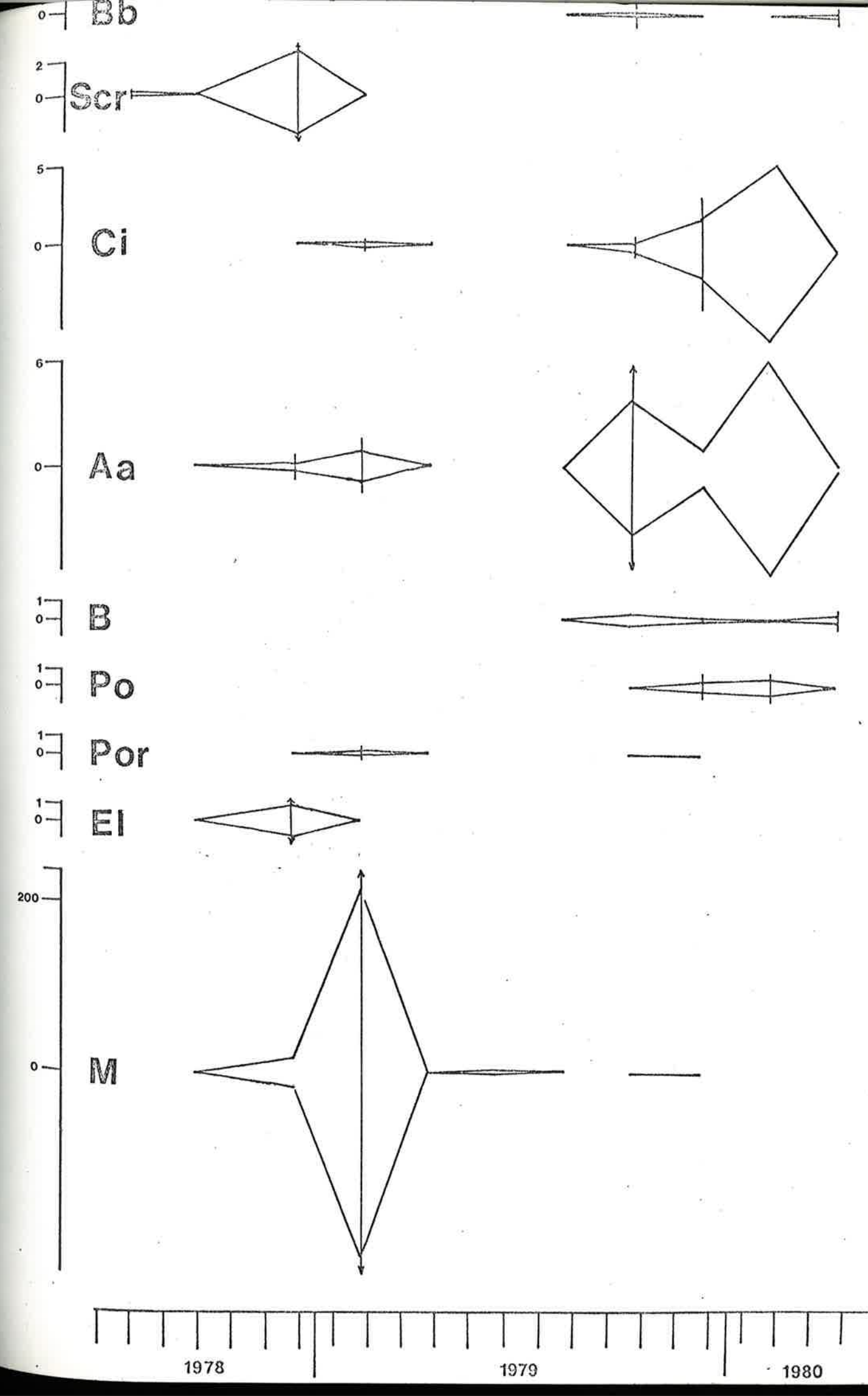
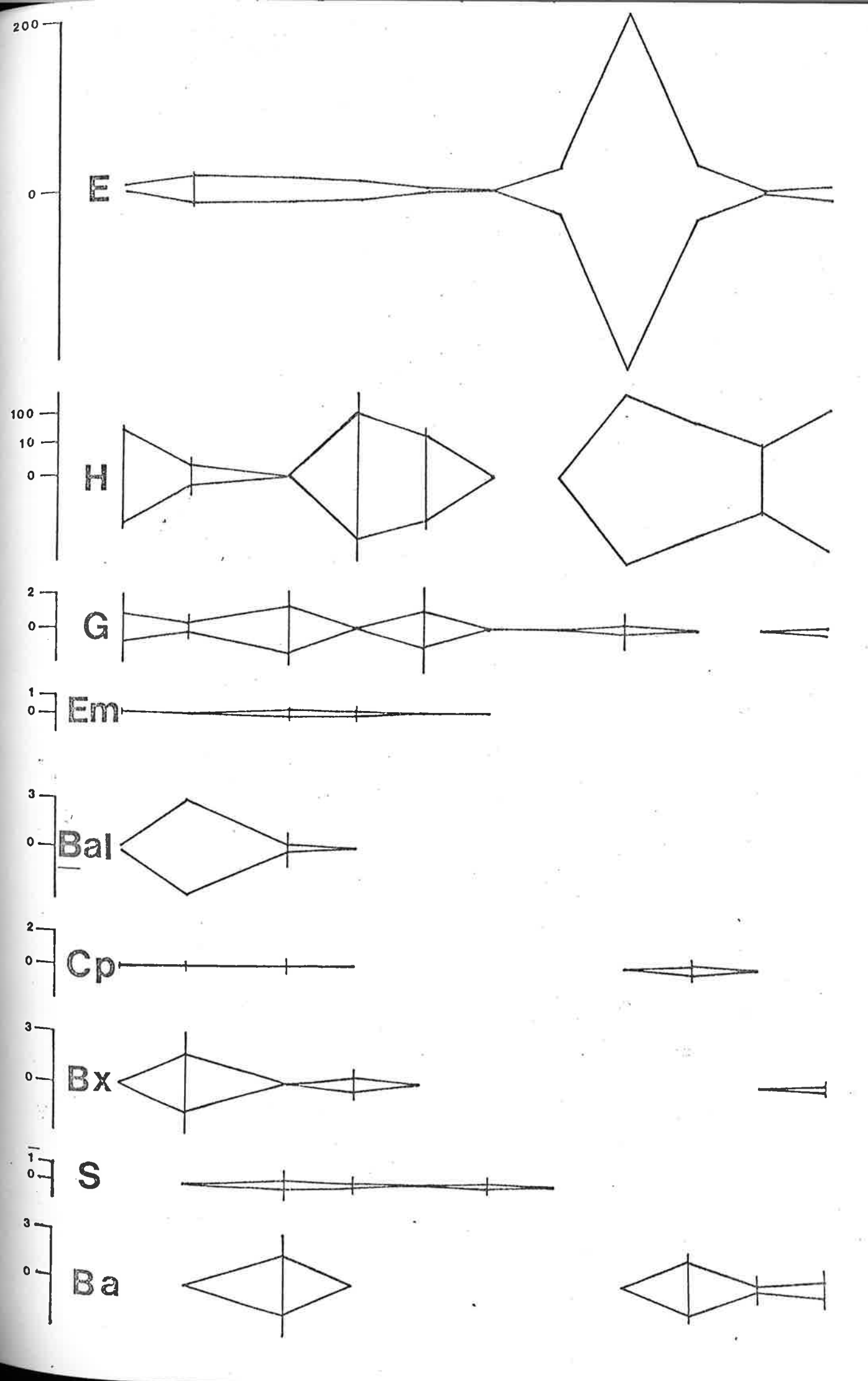

Bb
0
Scr
2
0
Ci
5
0
Aa
6
0
B
1
0
Po
1
0
Por
1
0
El
1
0
M
200
0
1978
1979
1980

Figure 3.17 Variation in recruitment with time for individual species on $45cm^2$ panels at West Lakes. For explanation of figure, see caption to Figure 3.12.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E
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10
0
H
2
0
G
1
0
Em
3
0
Bal
2
0
Cp
3
0
Bx
1
0
S
3
0
Ba

Figure 3.17 - continued.

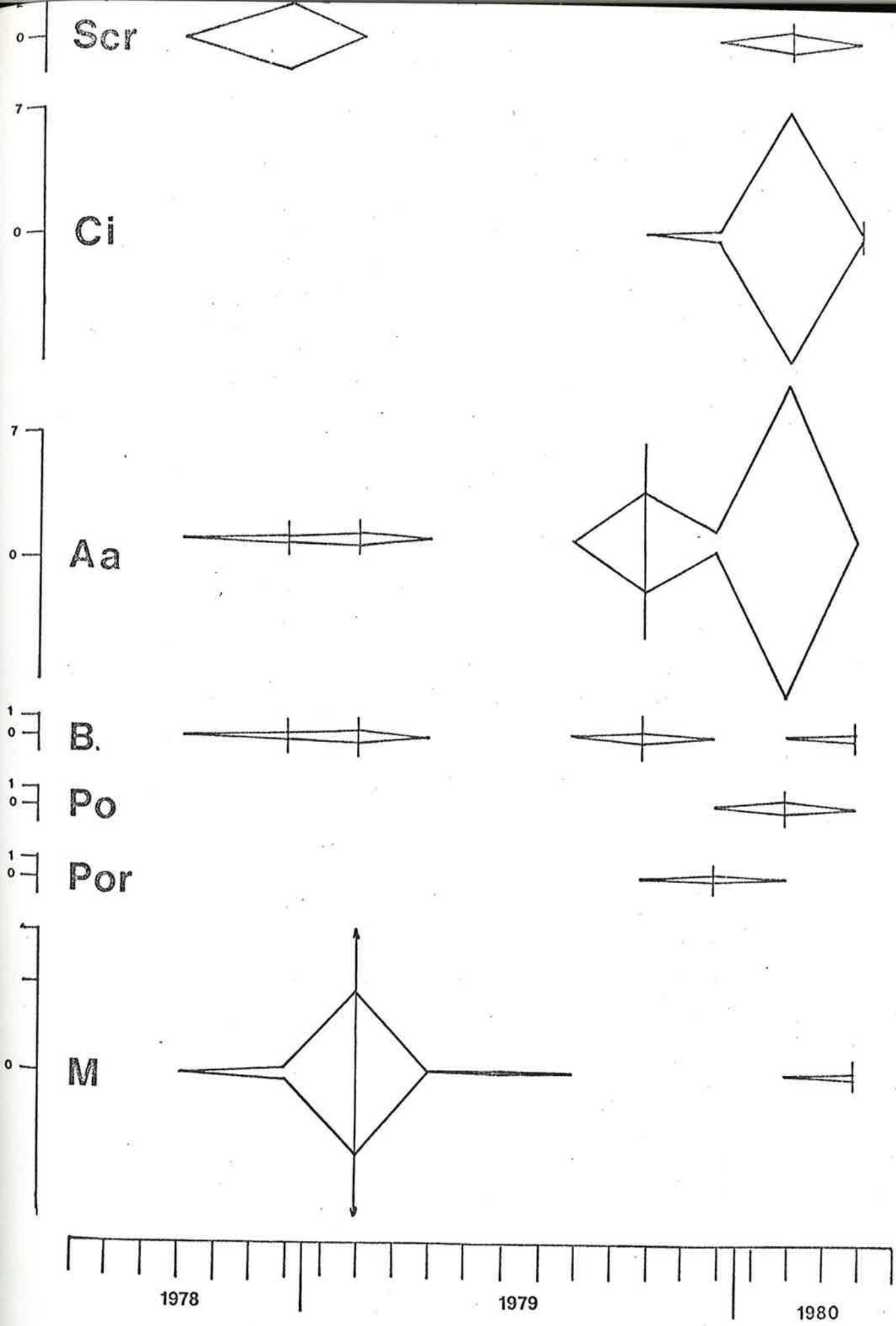
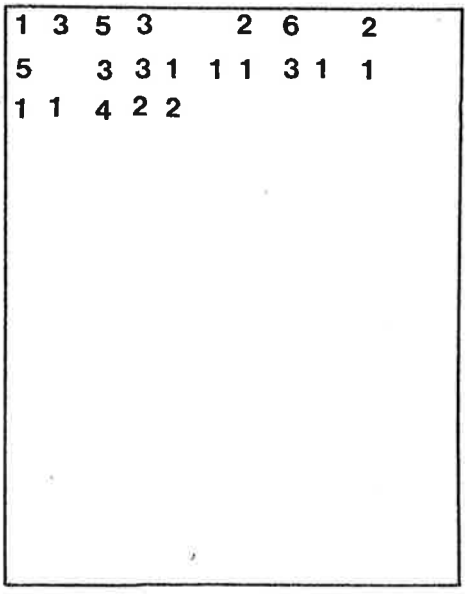
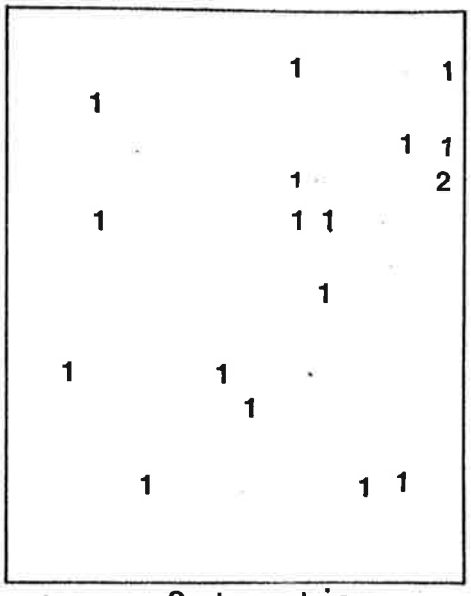

0
Scr
7
0
Ci
7
0
Aa
1
0
B.
1
0
Po
1
0
Por
0
M
1978
1979
1980

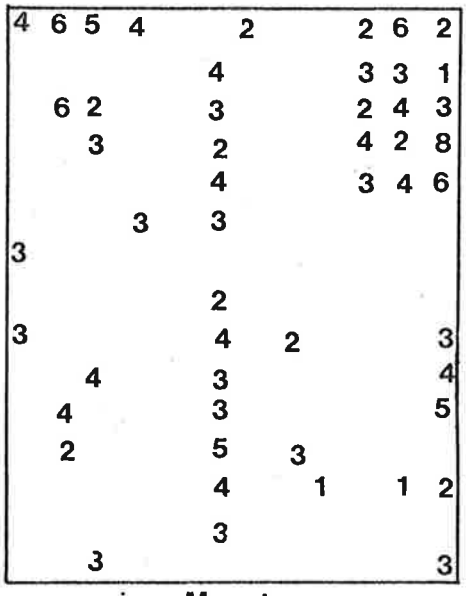
Figure 3.18 Within panel patterns of recruitment for four species. A representative panel is shown for each species, and the numbers represent the number of recruits of the species in a 1 cm^2 quadrat centred on the number.



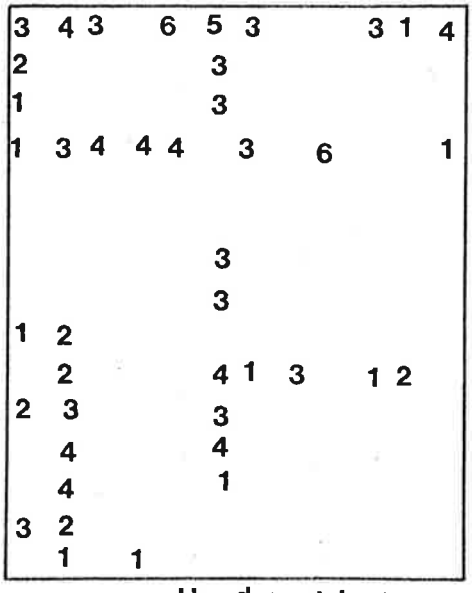
Elminius



Spirorbis



Monia



Hydrordes

4. POST-COLONIZATION EVENTS

Most of the *Pinna* shells in the study grid were at least 10 cm in height at the commencement of the experiment. They were therefore probably at least three years old (Butler and Brewster 1979). We would therefore expect that the initial burst of colonization would be over, and that the important interactions should involve adult organisms. Further, if an equilibrium exists, the fluctuations in S for individual patches should show low amplitude by this stage.

This chapter contains the tests for :

Hypothesis 1. Most patches show fluctuations in S which are narrowly bounded.

Hypothesis 3. Interactions between adult organisms influence the fluctuations in S more strongly than do colonization events.

Hypothesis 4 and 5 concerning the effect of predators and species which are good competitors.

The chapter is therefore a combination of experiments and observations. The dynamics of established *Pinna* epifaunal assemblages will also be described.

4.1 Fluctuations in S.

4.1.1 Methods

Fifty uncaged *Pinna* were tagged in the study grid (Figure 4.1), and photographed at bimonthly intervals for 24 months. During the course of the study, 6 shells were lost; a further 7 died and the shells degenerated, and 5 died towards the end of the study, but monitoring continued.

Testing for "narrow bounds"

For each uncaged *Pinna*, I then had records of S at two-monthly intervals for 22 months. Some shells could not be analysed at all sample periods, but I excluded from the analysis all *Pinna* shells that were not sampled at least five times. Thirty seven tagged *Pinna* remained. From these data, I could calculate a coefficient of variation (CV) for S. The definition of "narrow bounds" (Chapter 1, p 5) requires that the CV be less than 10.2%. The CV has a known standard error, and so we can then use a t-test to test whether the observed fluctuations in S are acceptably small.

The t-test is given by

$$t = (CV - 10.2)/\ s.e._{CV},$$

where $s.e._{CV} = (CV/(2n)^{\frac{1}{2}})\ (1 + (CV/100)^2)^{\frac{1}{2}}$

This is then compared with a t-distribution with n-1 degrees of freedom, n being the sample size for S. The test is one-tailed, since the null hypothesis is that C.V. < 10.2%.

In practice, critical values of CV could be obtained by rearranging the above equation as

$$(CV - 10.2)/s.e._{CV} = t_{0.1,n-1}, \text{ and hence}$$

$$t^2/10^4 n\ CV^4 + (t^2/2n - 1)\ CV^2 + 20.4CV - 104.04 = 0 \qquad (4.1)$$

This polynomial could then be solved to obtain a value for the CV, and this value used to compare quickly the observed S distribution for each *Pinna*.

The above method is applicable to individual patches, but it is necessary to have another criterion to determine whether a whole group of patches is generally narrowly bounded. This can be done as follows.

It is possible to vary w, and use equation 4.1 to calculate a set of critical values of C.V. for each value of w. The observed CV's can then be tested against these values, to find the smallest value of w which gives an envelope containing the observed fluctuations. As an

example, consider tagged *Pinna* no. 021. There were 11 censuses, and $\overline{S}$ = 2.73, s_S = 0.79, thus CV = 28.8%. This is significantly greater than 10.2% at p = 0.05 (i.e. w = 0.20), but does not differ significantly from 17.85% (i.e. w = 0.35). Thus a band of $\overline{S} \pm 0.35\overline{S}$ is necessary to contain the observed fluctuations in S for shell 021. This shell thus has 'critical w' of 0.35. This procedure is repeated for each patch, and a cumulative frequency distribution drawn up. The abscissa is w, and the ordinate the total number of patches whose critical w is less than or equal to this abscissa. This curve must increase monotonically, and will probably be approximately sigmoid, since there will be few extreme values of fluctuations in S.

The curve can then be made linear, and the value of w determined which would result in 95% of *Pinna* shells being bounded. Logit analysis was used, since it only assumes a logistic curve, rather than an underlying normal distribution, as is the case for probit analysis (Hewlett and Plackett 1979). As for individual patches, if the value of w is too high, then we conclude that the concept of "equilibrium" is not useful for the group of patches. I shall again use the criterion that if the 95% value, w_{95}, is greater than 0.2, then the patches are not narrowly bounded. Hewlett and Plackett (1979) do not give a method for calculating a standard error of a w_{95}, but as long as two sets of data give the same slope of logit vs log w, then the w_{95} values of caged and uncaged *Pinna* should differ by the same amount as the w_{50}'s, which have a standard error which can be calculated readily (formulae in Hewlett and Plackett (1979), p 25). Two groups of patches could then be compared by using a t-test on the w_{50}'s (Bailey 1959).

4.1.2 Results

Thirty seven *Pinna* shells were analysed. On only eight of these was S "narrowly bounded". A sample of the observed fluctuations is

shown on Figure 4.16. Fluctuations are shown which had w values ranging from 0.15 to 0.55.

Very few of the S curves could be classed as increasing; S had undergone its initial increase, and was fluctuating with no general trends apparent. The failure of S to be "narrowly bounded" was therefore not a consequence of the patches being relatively recently created.

When a curve of the number of shells bounded by a given value of w was plotted, the w_{95} was 0.5315. An indication of the precision of the w_{95} can be gained by examining the w_{50}. This was 0.275, with a standard error of 0.0001.

4.2 Good Competitors

In order to assess the effect of good competitors, it is first necessary to classify species according to their competitive ability. This has been done in the past in a number of ways. In the intertidal zone, manipulations of the relative abundance of gastropod species have been used to demonstrate the existence of competition and its effects (e.g. Underwood 1976, 1978). On subtidal marine hard substrata, competition amongst sessile organisms is assumed to be for space, and to occur generally by one colony overgrowing another. The results of these interactions are frequently assessed by observing the spatial positions of colonies in the field, and recording which colony is lying above the other. From this, it is possible to construct an n by n-1 matrix (or n by n if intra-specific encounters are included) showing the results of pairwise interactions between n species. This is known as a <u>contact matrix</u>.

The patterns of interspecific competition have been postulated either to be hierarchical (e.g. Osman 1977) or to form a network (Buss and Jackson 1979). Kay and Keough (1981) have criticised the interpretation and construction of contact matrices on a number of

grounds. Firstly, many of the studies have used data from point censuses; yet, there are records from Edithburgh of one species initially overgrowing another, but the final outcome being the opposite (Kay and Keough 1981). This result may also be produced if one species secretes allelopathic chemicals. Point censuses would therefore misclassify some of such interactions.

Secondly, many studies record that the outcome of competitive interactions between a given pair of species is not constant; rather, each species wins some encounters. Jackson (1979a) suggested that the outcome may be influenced by the angle at which two colonies meet, and Russ (pers. comm.) has found that differences in the relative sizes of the two colonies may influence the outcome - large colonies tend to overgrow small colonies regardless of species. It is possible that differences in food supply, such as one colony being up-current of the other, may modify the interaction between species.

Despite the variability of competitive interactions, contact matrices have been interpreted in an essentially deterministic manner. The spatial arrangement of colonies is likely to be difficult to predict, and differences in food supply will depend on very small scale planktonic patchiness and micro-current patterns. Both of these are likely to be difficult to measure, let alone predict accurately, and should therefore be treated as random variables. It therefore seems more appropriate when interpreting community-wide patterns of species abundance, to view competitive interactions in a stochastic manner. There is a need to regard interactions as having more than two outcomes (A wins, or B wins), and to acknowledge that the most appropriate view is that for each pairwise combination, species A has a probability p of winning an encounter with species B, i.e. A is expected to win mp of m encounters between the two. If a series of species pairs is considered, then we expect p to vary from 0 to 1.0. In discussing community structure, it is of course

convenient to summarize this continuum by recognizing discrete categories, but there must be more than two of them. Kay and Keough (1981) recognized three "average" outcomes to a given interspecific interaction; A wins most of the encounters, B wins most, or neither species wins consistently more encounters than another. These three outcomes were designated A dominant, B dominant, A and B competitively equivalent, respectively.

An interaction can be categorised by using the binomial test (Siegel 1956). Let p be the proportion of wins to the species which wins the greater number of encounters. Then we make a one-tailed test of the null hypothesis H_o: $p = 0.5$ against the alternative

and H_1: $p > 0.5$.

Russ (pers. comm.) and Harris (1978) report that for some competitive encounters, there are three outcomes; A wins, B wins, or neither win, with a static interface being formed between the two colonies. These are known as "ties". This necessitates some modification to the above procedure. Let r be the proportion of wins to species A, s the proportion of encounters which result in ties, and t the proportion of encounters which result in wins to species B.

Then $p = \max(r,t)$

and $q = s + \min(r,t)$

Then, H_o: $p = 0.5$

vs H_1: $p \neq 0.5$

This is tested using a two-tailed Binomial test, since there are more possible outcomes; if $p > 0.5$, one species is dominant; if $p = 0.5$, neither species wins the majority of encounters. Ties make up a variable proportion of the encounters. If $p < 0.5$, then ties are important, since p is the larger of r and t. In most cases, this will mean that ties are the most common outcome. A further category is therefore needed to allow for the situation when ties are common; Kay

and Keough (1981) labelled this competitively equal.

A consequence of using the above tests is that a reasonable number of replicates is necessary to categorise a given interspecific interaction; for a one-tailed binomial test, at least six observations are necessary. Kay and Keough (1981) suggested that most published studies in fact had too few replicates to distinguish between a network and a hierarchy. In view of the above arguments, discussion about which of networks or hierarchies are prevalent seems of little value. Indeed, Kay and Keough found that, on the pilings at Edithburgh, many sponges and tunicates are competitively equivalent, while sponges and tunicates almost always overgrow bryozoans, and sponges, tunicates and bryozoans all overgrow serpulids.

The patterns of overgrowth shown in their contact matrix could not be categorised as either a network or a hierarchy. Some groups of species could be found in which the patterns of overgrowth were not linear, but contained links of "competitive equivalence". The two examples of Kay and Keough (1981) are shown on Figure 4.15. The consequences of the patterns of overgrowth are important. Networks have been postulated to allow higher diversity to persist for longer than a hierarchical arrangement (Buss and Jackson 1979). With a hierarchy, the final composition of a patch is predictable when the initial composition is known. When the arrangement is a network, the final composition of a patch is not fixed when the initial composition is known, but is dependent on growth rates and spatial arrangement of colonies. Changes in either of these factors will change the outcomes, but once the spatial arrangement of the colonies and their growth rates are known, then the final patch composition is predictable. In any case, the rate of resource monopolisation is likely to be lower for a network than a hierarchy. Kay and Keough (1981) suggest that a large number of competitive equivalences may allow higher diversity than either

of these, regardless of spatial arrangement and growth rates of colonies. The final composition of a patch will not be predictable even when spatial arrangement etc. are known.

My method of assessing competitive interactions was as follows. Colonies were traced from bimonthly photographs of tagged *Pinna*. The positions of the colonies, especially the interface between them, were recorded at subsequent intervals. A colony was recorded as having been overgrown when approximately 25% of its area, or 2.5 cm^2, was covered. This distinction was arbitrary but, in practice, most colonies were more than 75% overgrown.

4.2.1 Results

The contact matrix for *Pinna* epifauna is shown on Figure 4.7. No data could be collected on the interactions between sponges and tunicates, as they rarely occurred together on a shell. On pier pilings, tunicates frequently overgrow sponges (Figure 4.8; Kay and Keough 1981) and so it seems likely that this is true on *Pinna* shells. There is circumstantial evidence to support this, tunicates frequently covered *Pinna* shells when they were present, but sponges did so much less frequently (Kay and Keough 1981). This suggests a much lower growth rate, and on the pilings the better competitors have higher growth rates than poor competitors (Kay 1980).

Bryozoans were almost always overgrown by sponges and tunicates, and serpulids were overgrown by all other species. The vermetid M48 frequently had other species growing over its shell, but only *Didemnum patulum* was observed to overgrow it completely. Similarly, *Polycarpa pedunculata* was never overgrown. When confronted with *D. patulum*, *P. pedunculata* became detached from the *Pinna* shell, and was thus not overgrown.

The same is most likely true of the coral *Scolymia australis*.

I was unable to observe interactions between this species and others during the experiments, because it was rare. I never observed a polyp which had been overgrown, however.

INTRA-SPECIFIC ENCOUNTERS

Bryozoans never overgrew conspecific colonies (see diagonal of contact matrix, Figure 4.7). The reaction to conspecific colonies could be divided into two categories; fusion and interface. An interface occurs when two colonies abut, and cease growing along the zone of contact. Growth frequently begins at other edges of the colonies. The presence of an interface is shown by a clear zone of contact between colonies.

Fusion occurs when the two colonies merge along the growing edge, forming one large colony. This is particularly well known for the tunicates *Botrylloides* spp. and *Botryllus schlosseri* (Mukai and Watanabe 1975). These are more difficult to observe in the field, since there is little evidence remaining after the fusion has occurred. For many bryozoans, it can be detected because the colonies are symmetrical when small, and after fusing, irregularly shaped colonies are formed where previously a series of small colonies were present.

The frequency of these two outcomes varied between species (Table 4.34). *Schizoporella* colonies usually fused, while those of *Celleporaria fusca* generally formed interfaces.

Similar data could not be obtained for sponges or tunicates, as they were too rare. On the pilings, interfaces form in *Botrylloides* and probably in *Didemnum* sp. A. Further data are being collected on this (Butler and Keough, unpubl. obs.). Sponges recruited too rarely for these data to be collected.

The species which could therefore be classed as good competitors are the sponge SP35 and the didemnid ascidians *Didemnum patulum* and

Didemnum sp. A.(T9) It is the impact of these that will be considered.

DIDEMNID ASCIDIANS

These were generally capable of monopolizing *Pinna* shells. Of the shells which had *D. patulum* present, the mean cover of the tunicate was 78% (Kay and Keough 1981). 62% of these patches were more than 90% covered by the tunicate. Indeed, three of the caged *Pinna* had a constant S of 1 for the duration of the experiment. These had *D. patulum* covering the shell for most of the experiment. The colonies are thus relatively long-lived. The time taken for monopolization of a *Pinna* shell could not be estimated accurately. Only a few caged *Pinna* acquired *D. patulum* recruits, and on these the times taken for monopolization were from two to six months. The curves of S vs time for these shells are shown on Figure 4.9. On some shells, the didemnids did not arrive until December 1979 or even February 1980. There was frequently too little time for S to be affected, since one valve of the shell reached high cover, but the second valve was free of tunicates. The S value was buffered by the two valves.

Only one example was found where the tunicate died, so that there was an opportunity to observe events after the tunicate died (Figure 4.9). No great change was observed initially, since again only one valve was affected initially. There was an initial rise in S, a subsequent fall as the tunicate colony recovered, and then a further rise after the colony had died completely.

SPONGE SP35

SP35 generally grew less quickly than *Didemnum patulum*. On the *Pinna* shells which bore SP35, mean cover of the sponge was 44% (Kay and Keough 1981). None of these shells were completely monopolized, and the effect of this species on S were correspondingly less dramatic

(Figure 4.10). Only five shells acquired sponges from all caged and uncaged *Pinna*. Of these, only two produced marked decreases in S (Figure 4.10). In both cases, the effect took more than twelve months. Better evidence concerning SP35 can be seen from those shells which bore high covers of the sponge initially, but where the sponge died. In each of these cases, S rose steadily (Figure 4.10).

4.3 Experiments to Assess Predation - A review and some observations.

The importance of predation is frequently assessed by manipulating the numbers of predators in a community and following the subsequent dynamics of the community. Exclusions may be of two kinds; manual removal of predators, or the construction of cages or barriers which restrict the access of predators to the organisms under study. The barriers may themselves affect the dynamics of the community, and so manual removal of predators appears preferable. This requires a considerable amount of time and either a large research budget, or a number of exploited friendships. More importantly, mobile predators such as fish can not be removed in this manner, and only asteroids (e.g. Paine 1966, 1971), echinoids (e.g. Kain and Jones 1967; Paine and Vadas 1969), and molluscs (e.g. Southward 1964) have been treated successfully in this way.

Fences have been used to exclude successfully echinoids (Ebert 1977; Karlson 1978) and asteroids (J. Harris, pers. comm.), but most studies have used cages, either to exclude predators (Day 1977; Kay 1980; Peterson 1979a; Russ 1980; Sutherland 1974) or to include predators and artificially increase their density (e.g. Keough and Butler 1979; Underwood 1978). Similarly, workers in soft-sediment environments have used caging studies extensively (Arntz 1977; Hulberg and Oliver 1980, Navqui 1968; Peterson and Andre 1980; Reise 1977;

Virnstein 1977, 1978; Woodin 1974; Young and Young 1976; Young *et al.* 1976; and see Peterson 1979a for a comprehensive review).

Some doubts have arisen recently about the usefulness of such experiments in soft sediments (Hulberg and Oliver 1980; Peterson 1979b; Virnstein 1978). It has been suggested that caging modifies the sediments and changes the water flow within the cages. Light is similarly affected. Peterson (1979b) suggested that many studies in such habitats had not controlled adequately for such effects, while Hulberg and Oliver (1980) suggest the possibility that sedimentary modification, rather than the absence of predators, causes changes in cages has rarely been addressed, let alone controlled for. The studies of Virnstein (1977, 1978) and Arntz (1977) are exceptions to this. Hulberg and Oliver (1980) concluded that the differences they observed between caged and uncaged areas were explicable simply in terms of sedimentary changes, although their "intuitive" feeling was that predators were important, despite the lack of evidence. Arntz (1977) labelled his results a "failed" experimental study, and Virnstein (1977) regarded his experiments as equivocal.

On subtidal hard substrata, caging has not been used quite as extensively, and critical accounts of the methods are less common. Caging experiments have generally used more controls in an attempt to assess caging effects. These controls have taken the form of roofs, or side-less cages, and topless cages. Underwood (1980) suggests that in the rocky intertidal zone of New South Wales, the roofs actually attract grazers because they shade the rock, reducing desiccation stress. Thus, roofs designed to measure the effect of caging actually manipulate the density of grazers, and must be regarded as an additional treatment rather than as a control. Russ (1980) used half-open cages to allow fish access while shading part of the settlement panels. He reported that fish move freely in and out of these enclosures, and in this case

the half-open cages provide some measure of the effect of caging.

Ayling (1981) used a variety of cages to exclude different types of predator; side-less cages excluded vertically feeding fish; large mesh walls excluded urchins and allowed access by the limpet *Cellana stellifera* and the monacanthid *Parika scaber*. Manual removal of *Cellana stellifera* allowed access by *Evechinus* and *Parika*. Although he did not address the question of caging effects specifically, the combination of caging treatments with estimates of the intensity of grazing by fish and urchins allowed the results to be interpreted as effects of predation, rather than artifacts.

Sammarco (1980) also used partly open cages, and reported no apparent change in predator behaviour in them. He did not measure light or water movement in cages.

Day (1977) used open-ended cages to control for caging effects, and also measured light intensity and water movement. Cages with algae growing on the meshes reduced significantly water movements, as measured by the percent weight loss of calcium sulphate blocks. He also found differences between sites in the degree of obstruction of water flow. Cages also reduced illumination significantly, although again the effect varied between sites within a single cave.

Marshall *et al.* (1980) used no caging controls and failed to consider the possibility of caging effects, despite their use of cages (screens) with a mesh size of only 1 mm.

Osman (1977) did only a pilot study, from which he concluded that predators were unimportant, although no caging controls were used. Sutherland (1974) used fishing net to exclude fish, but did not assess the effect of the net, although he concluded that predation by fish was important. Similarly, Peterson (1979a) did not include cage controls nor measurements of physical variables within cages.

Kay (1980) used open-ended cages to control for caging effects.

Her cages were longitudinally bisected cylinders with the long axes parallel to the pier pilings to which they were attached. The cage controls had no ends. She measured water movement inside clean and fouled cages, and cage controls and uncaged areas. She concluded that water movement did not differ between clean cages, cage controls and uncaged areas, but was reduced for fouled cages. Light intensity was also claimed not to be greatly reduced. However, I believe that her measurement techniques makes these conclusions suspect, for the following reasons.

Water movement was measured with plaster blocks, and analysed by two separate analyses. Fouled cages and cage controls were compared with unfouled cages by two-way ANOVA, and then t-tests were used to compare clean cages with uncaged areas. Means of percent weight loss were respectively: Fouled cages 24.08 ± 3.59 (S.D.), fouled cage control 25.52 ± 5.93, unfouled cage 32.57 ± 7.49, unfouled cage control 33.53 ± 6.97, uncaged areas 35.49 ± 6.37. Weight loss is directly proportional to water movement (Doty 1967; Muus 1971). Replicate numbers were four for the caging treatments and eight for the uncaged controls. There was no difference between cages and caged controls, but a significant decrease between fouled and unfouled cages. Most coefficients of dispersion are high (0.53, 1.37, 1.72, 1.45, and 1.14, respectively). Thus, there is a high probability of a Type II error with such small replicate numbers. It is likely that there is a difference in water movement between caged and uncaged areas, since Day (1977) found a difference using 1 cm mesh cages, while Kay used 5 mm mesh plastic netting.

The change in light is potentially more important. Kay used a photographic light meter to measure light inside and outside cages. She reported differences of one or two f-stops, but did not note that such meters use a logarithmic scale. It is unclear whether marine

animals are more sensitive to changes in light than this, i.e. whether their responses to light are on a linear scale or not. The fabric of her cages occupied approximately 54% of the total surface area, and substantial reductions in light intensity seem likely.

I attempted to get an impression of the degree of reduction in light intensity by measurements in my own cages. These will be described in detail in a subsequent section, but the essential dimensions were: 50 cm x 50 cm cages, 30 cm high, with plastic meshing, mesh size 12.5 mm and fabric diameter 2-3 mm. Measurements were made on a day of moderate sunshine, slight to choppy seas, and 7 metres visibility, on 9.viii.80. Light intensity was measured with a Li-Cor Model LI-185A Quantum/Radiometer/Photometer, and readings were in microeinsteins m^{-2} s^{-1}. The cages were embedded in the sand, and I measured the intensity of horizontal and vertical light, since some light may be reflected from the sand into the cage.

Sand level fluctuates, so that cages may be as much as 7 cm above the sand surface. I measured the light intensity in cages installed flush with the sand surface and in cages the edges of which were raised 5-7 cm above the sand. Two types of cages were used, fouled and unfouled; fouled cages had not been cleaned for three months, while unfouled cages had been thoroughly scrubbed ten minutes before the light recordings were taken. The ten minute period allowed any sediment to clear away after the cleaning.

Light levels fluctuated over short time intervals, and five replicate readings were taken, at fifteen second intervals. There were thus two factors, cage fouling, and cage position. Cage fouling had only two levels, fouled, and unfouled; cage position had three levels, flush, raised 5-7 cm, and completely removed, i.e. no cage. The no cage readings were taken immediately alongside each cage, to minimize any spatial variation in light intensity, so that for each cage, there

were three sets of readings; cage flush, cage raised, and a control.

The data for vertical and horizontal light levels were analysed separately, since the light readings were so different as to ensure heterogeneous variances. Each was analysed by a two-way ANOVA with replication (Tables 4.1, 4.2). Treatment means (Table 4.3) were transformed into the percentage of the no cage control value. Inspection showed that there were no consistent differences between raised and flush cages, but that fouling reduced light intensity by 75 to 85%. Unfouled cages reduced light to a lesser degree, but vertical light was reduced by 50 to 60%, and horizontal light by about 25%.

This appears quite important, as cages used by Kay (1980) contained over 50% more fabric than my own at Edithburgh. Examination of the literature shows many examples of mesh sizes far smaller than that used by Kay (Table 4.4), and even larger reductions of light are likely to be widespread in such cases.

The two modifying effects of cages have potentially serious consequences. Wilkinson and Vacelet (1979) and Velmirov (1976), for example, have shown that differences in growth form in sponges and octocorals respectively, are functions of different water movement. This effect can be measured readily in caging studies, but changes in light intensity may produce effects which are difficult to allow for when interpreting the results of such experiments.

Kay (1980), for example, ascribed the differences in percent cover of some species to the effect of caging, but claimed that exclusion of fish allowed solitary tunicates to increase in abundance. Many ascidians (including congeners of species found at Edithburgh) are known to have negatively phototactic larvae (see review by Buss 1979a). In Chapter 3, I suggested that *Ciona intestinalis* settles more densely in shaded areas. The possibility of such behaviour by larvae, and the presence of cages which reduce light intensity by 50%, make it imperative

to distinguish between settlement and recruitment. Underwood (1979) reviewed the caging studies on intertidal gastropods, and noted that this distinction has rarely been made for the rocky intertidal zone. The same is true for experiments on subtidal hard substrata.

Duration of experiments

Table 4.4 shows the duration of various caging studies. Most were of the order of twelve months or more, but major fluctuations in many such communities take place on an annual time scale, and in view of the considerable between-year variation in recruitment, experiments of longer duration seem desirable (e.g. Ayling 1981; Kay 1980). There are of course logistic problems with such experiments; cages become fouled or damaged by storms, boats, etc. Hulberg and Oliver (1980) provide a good example of such problems.

Caging controls

Many caging controls are open-ended or open-sided cages. The implicit assumption in doing this is that the abundance of potential predators does not differ between cage controls and uncaged control areas. This has rarely been examined, except by Underwood (1980), who found that intertidal gastropods aggregated under "roofs". Workers in soft sediments have sometimes reported that cages allow settlement and increase survival of some predators (Arntz 1977; Virnstein 1977), or that large fish may use cage controls as homes (Hulberg and Oliver 1980). On subtidal hard substrata, most people have inspected cage controls casually and reported no difference in predator activity. At Rapid Bay, the asteroid *Coscinasterias calamaria* shows preference for sheltered sites on the pilings when wave action is moderate (Keough 1981b) and, at both Rapid Bay and Edithburgh, I have observed small blennies, pempherids and the chaetodont *Chelmonops truncatus* in open-ended cages. Cages over

Pinna at Edithburgh similarly have raised densities of holothurians and some fish, such as *Echinophyryne crassispina*.

These observations suggest that controlling for cage effects may be very difficult, if not impossible. For a number of reasons, it is likely that caging effects are present (Hulberg and Oliver 1980; Kay 1980), and simple caging experiments may be insufficient to demonstrate unequivocally that a change in the community is due to predation and is not an artifact of the experimental method.

In some cases, knowledge of the behaviour of predators, as well as many other natural history observations, may allow specific cage designs to be used to exclude specific predators without side-effects (e.g. Ayling 1980; Choat pers. comm.), but where predators are unknown or poorly known, such designs cannot be used, and a different strategy is needed. Detailed observations of the natural history of the organisms under study are needed, especially their abundance in time, feeding, movements, etc. For all such studies, there must be an attempt to separate settlement and recruitment, and to show that differences arise by differential survival, not settlement.

4.4 "Biological Disturbance" at Edithburgh.

There existed little information about potential predators of *Pinna* epifauna. Casual surveys showed a few species to be common; the asteroid *Uniophora granifera*, the acmaeid limpet *Asteracmaea crebristriata*, and the small abalone *Haliotis cyclobates*. The latter two were likely to be algal grazers, but I believed it possible that they could damage newly-settled larvae by their movements, and chose to consider them. The sizes of the three varied considerably; the limpets are generally 10 to 15 mm long, *H. cyclobates* reaches a length of about 60 mm, while the diameter of *Uniophora* may reach 150 mm. Other

potential predators are relatively rare, but are listed in Appendix 1.2.

I knew very little about the abundance of fish or their effects. Kay (1980) ascribed an effect on the piling fauna to *Cheilodactylus nigripes* (= *Gonniistius vizonarius* in Kay (1980) and Scott *et al.* (1974)), with a possible extra effect due to *Chelmonops truncatus* and a small number of monacanthids. However, Cappo (1980), has shown that *C. nigripes* feeds mainly on infaunal organisms such as amphipods, polychaetes, and ophiuroids, and neither it nor *Chelmonops truncatus* is common in the study area. The most likely fish predators were the silverbelly *Parequula melbournensis* (Gerridae), and an unidentified odacid, probably a *Neoodax* sp.. Casual observations at Edithburgh and Rapid Bay suggested that monacanthids vary in abundance seasonally, and very few could be found when the study was being commenced. Russ (1980) has reported strong seasonality for the monacanthid *Penicipelta vittiger* (Castelnau); large schools of juveniles occur at Portsea pier from December to May. At Edithburgh, *Eubalichthys mosaicus* and *Brachaluteres jacksonianus* are the most common monacanthids.

Neoodax and *Parequula* are "horizontal" feeders, whereas many monacanthids may approach substrata from above.

The "predators" of most interest to me were *Asteracmaea* and *Haliotis, Uniophora*, and fish. Feeding methods varied, and I decided that no cage designs could efficiently exclude desirable combinations of these species. I had no data on their relative importances, and so opted for a multi-faceted experimental design.

1. Caging

Cages were constructed of 6 mm steel rods welded into a box 60 cm by 60 cm by 30 cm high, and plastic mesh (Nylex "Trical" mesh) used to cover the frame (Figure 4.11). Each corner of the cage had a leg 30 cm long. Meshes were listed as 12.5 mm, but actual size was 11 by 8 mm,

with the fabric between 1.8 and 2.5 mm wide. The cages were forced into the sand so that the bottom of the mesh was just below the sand level.

Twenty cages were used initially, divided into five treatments, each with four replicates. The treatments were:

(1) All predators excluded

(2) Fish and *Uniophora* excluded, but *Haliotis* and *Asteracmaea* included at normal density.

(3) Fish and gastropods excluded, *Uniophora* included.

(4) Fish excluded, all others allowed access. These cages were covered by mesh, but only part of each side (15 cm) was covered. They were designed to allow access to crawling species.

(5) Caging control. Cages made from 12.5 mm mesh galvanised wire. The aim was to compare these with plastic mesh cages, which contained a higher area of fabric.

This experiment commenced in June 1978, but was destroyed totally by a storm between the time of commencement and 17.vii.78. The two weeks prior to this date had been notable for persistent north-easterly winds, which produced large swells of long wave-length. In addition, large masses of algal stems had been washed against the cages, and this had offered more resistance to waves, making cages easier to dislodge. The cages had been washed to the south-west, and were subsequently repaired. Treatment 5 cages were torn badly, and this treatment was discontinued.

Observations even over this very short time period showed that the sand level fluctuated considerably over very short intervals, so that even flush-fitted cages frequently allowed access to crawling predators. Treatment 4 thus seemed redundant. In addition, I observed that small fish, notably apogonids and pempherids, were often found in cages of this type, and so rather than being a roof, these cages modified the density of fish species about which I had no information. This treatment was

also dispensed with.

The modified treatments were as follows

(1) Uncaged *Pinna*.

(2) All predators excluded or with access restricted.

(3) Starfish included, all others excluded.

(4) Gastropods included, all others excluded.

The cages were positioned by swimming through a band 15 metres wide and dropping them haphazardly along this band. The bottom topography was the main determinant of cage position, since I was seeking trios of *Pinna* where I could install the cages with minimal trouble. Cages were further anchored by hammering two 1.7 metre stardroppers on two sides of each cage, and attaching an elastic ("octopus") strap between them, level with the cage top. This was sufficient to prevent the cages being dislodged for the duration of the experiment. The positions of the cages are shown on Figure 4.1. Twenty-four cages were used, eight to each of Treatments 2, 3, and 4. After the cages had been positioned, they were assigned randomly to treatments. Cages contained between two and five *Pinna* (Table 4.5), with a mean of 3.13 ± 0.95 (S.D.) per cage.

Uncaged *Pinna* were five to fifteen metres away from caged *Pinna*. I anticipated that the cages would become fouled and need cleaning. I planned to do this in situ, and the degree of clumsiness of cold divers was such that I considered the potential damage to uncaged *Pinna* alongside the cages to be too great. I set up a small grid in the North-West quadrant of our study grid (Figure 4.1). It was 12.5 metres square, and jarrah stakes were positioned at 2.5 metre intervals to form a grid. Fifty uncaged *Pinna* were selected randomly within this area, and tagged.

All caged *Pinna* were also tagged. Tagging was done using heavy duty rubber bands with "Dymo" labels attached. The tags were placed on the shell just above sand level, so that only part of the tag was visible. These tags last for at least 2-3 years (A.J. Butler pers. comm.).

All of the tagged *Pinna* were then photographed at bimonthly intervals for 22 months, finishing in June 1980. At each visit, cage meshes were scrubbed inside and out using scrapers and scrubbing brushes. The low recruitment rates at Edithburgh, especially in the grid, made such a routine viable, but I believe that cage cleaning should be done more frequently where recruitment rates are higher.

Photographs were taken as detailed in Chapter 2, and percent covers calculated for each species.

2. Settlement vs recruitment

In studying the effect of predators, it is imperative to show that differences in abundance result from differential survival, not settlement. I thus ran three series of recruitment panels over a six-month period, from July 1979 to December 1980. Six panels of each size were suspended in randomly chosen cages, and the recruitment for those panels was compared with recruitment on the panels analysed in Chapter 3. This method should underestimate settlement for the uncaged panels, since some larvae, may have been eaten by the time the panels were collected. The caged panels should not be affected by predators, and recruitment should more nearly reflect settlement in the cages. Thus, by comparing the recruitments on the two panel types, I hoped to show that recruitment did not differ markedly between the two types, and considering that recruitment onto uncaged panels is being underestimated, it would then appear likely that there is no preferential settlement into the relatively sheltered, shaded cages.

3. Predator abundance

I wished to estimate the frequency with which *Pinna* shells are visited by predators. Fish are mobile, and feeding observations were difficult to make without the presence of the diver modifying the behaviour of the fish, especially when visibility was poor and the diver

needed to approach the fish closely. Accordingly, I recorded the number of monacanthids, *Pareguula*, and odacids in a 5 metre by 40 metre band simply by recording the numbers seen while swimming along the strip. I made all observations myself so as to keep biases constant. Even so, these observations must be regarded as semi-quantitative only, since the efficiency of searching was not known. These data were collected at approximately monthly intervals through 1979.

The gastropods and *Uniophora* are less mobile, and therefore it was possible to estimate the important variable, which is not the density of such animals, but rather the frequency or probability of a *Pinna* shell being visited. I marked off another small grid, 7.5 metres by 12.5, in which I tagged 125 *Pinna* (Figure 4.1). The area was then searched at intervals ranging from a few hours to a few months between 4.ii.79 and 10.iv.79. Each tagged *Pinna* was located, and the numbers of *Asteracmaea*, *Haliotis*, and *Uniophora* recorded for each shell. Occasionally, crabs, or the muricid *Pterynotis triformis* were found. These were noted when seen. Details of survey frequencies are given in Table 4.5.

It was impossible to mark limpets and the abalone individually, and so an alternative method of estimating their movements was needed. I used the following:

Consider a set of *Pinna* shells with limpets on them at some time, t_j. The limpets are distributed in a Poisson fashion. Consider now two extreme cases of movement.

1. None or very little between-patch movement. The limpets will be distributed as a Poisson at all times, but individual shells will have consistent numbers of limpets, in fact the same limpets through a period of time, although random mortality and occasional movements (immigrations and emigrations) mean that numbers of limpets on individual shells vary slightly, and over a long time, these differences should accumulate by random walks.

2. Animals move around frequently over short time periods, for example at night. Numbers of limpets on individual shells would be expected to fluctuate over relatively short periods of time, so that the number of limpets on a given shell would quickly become different from the number at time t_j. There is a limit to the possible numbers of limpets on a shell, and although differences quickly accrue, we would expect them to random walk around the mean number of limpets over all shells.

Therefore, we would expect the degree of similarity between the number of limpets on a given shell at time t_j and the numbers on the shell at time t_k to decrease as the time between t_j and t_k increases. In case 1, the rate of decrease should be slow, whereas for case 2, we expect the numbers to quickly become dissimilar, and then to be no more similar than two different, randomly chosen shells are to each other. The question of how to measure this change in similarity can be solved if the variable "number of limpets on a shell" is distributed as a Poisson.

With a large sample size, the Poisson distribution tends towards a normal distribution (Sokal and Rohlf 1969), and Bailey (1959) suggests that the approximation to the normal is good when $n\bar{x}$ is large, e.g. greater than 30. We can thus regard the number of limpets on a shell as a normal deviate, as long as we have many such shells. It is then possible to calculate a parametric correlation coefficient between the tagged *Pinna* at time t_j and t_k, as follows:

Let y_{ji} be the number of limpets on *Pinna* shell i at time t_j, and y_{ki} the number of limpets on the same shell at time t_k. The product-moment correlation coefficient can then be calculated using all tagged *Pinna* for which data were collected at times t_j and t_k. r_{jk} is then the correlation between y_j and y_k and will be donoted the auto-correlation.

We can similarly generate a baseline correlation by selecting random pairs of shells at a single time, so that y_{ji} is the number of limpets on shell i at time j, and y_{jl} is the number of limpets on shell l at time j. We can calculate r_{il} using a large number of such pairs, so that these "random correlations" will be estimated with the same precision as the autocorrelations.

The two cases above entail rather different predictions about the behaviour of r_{jk} as the time $T_{jk} = t_j - t_k$ increases.

Case 1. y_{ji} will remain highly correlated with y_{ki} through a long period of time, i.e. for large values of T_{jk}, since there are few movements. Random changes will cause the correlation coefficient to decline as T_{jk} increases, until r_{jk} finally reaches the value of the random correlation.

Case 2. With increasing time interval T_{jk} between surveys, the correlation between y_{ji} and y_{ki} will quickly approach the level of random correlations.

The correlation coefficient r_{jk} should decline at a rate which reflects the amount of movement. Correlation coefficients are assumed to be distributed normally, and since the distribution of limpet numbers approximates a normal distribution, it is reasonable to analyse the correlation coefficient itself parametrically. The rate at which the correlation coefficient declines can be measured by calculating a regression using the autocorrelation r_{jk} as the dependent variable, and T_{jk} as the independent variable. We can then use the statistics of the regression equation in a comparative sense to gain an idea of how much the animals move.

Three measures could be used from this regression equation as an index of movement: the y- intercept, which is the correlation between surveys separated by a time interval of 0. This is in some ways a measure of diver error, as well as the movement over very short time

intervals, and so is not satisfactory for the purpose. Secondly, the slope, b, which is the rate at which the correlation coefficient declines with time. Thirdly, the correlation between random pairs can be substituted for r in the equation

$$r_{jk} = a + b\ T_{jk}$$

to solve for T_r, the time required for the number of limpets on a *Pinna* shell at time t_k to be no better correlated with the same shells at time t_j than they are with any randomly selected *Pinna* shells. Either of the latter two alternatives should give consistent results.

I thus analysed the limpet data in the following way. Firstly, from the seventeen surveys (j = 1,17, k = 1,17), there are $\binom{17}{2} = 136$ correlations r_{jk}; all of these were calculated, together with the corresponding time intervals T_{jk} (see Table 4.5), and an equation of the form $r_{jk} = a + b\ T_{jk}$ was fitted by least squares regression.

Secondly, for each survey, 125 pairs of shells were selected randomly, and a correlation coefficient r_{il} calculated. The mean of the seventeen values for r_{il} was calculated: call it r_r (for the correlation between randomly chosen shells).

Data for *Haliotis cyclobates* were treated in the same way.

4.4.1 Results - Caging Experiment

The data were analysed in one of two ways. For common taxa, two-way ANOVA was used. Data from four time periods were analysed; October 1978, February 1979, December 1979, and June 1980. These formed the four levels of the first factor, time. The second factor was caging, with four levels; uncaged (Control), *Uniophora* inclusion (U), *Haliotis* and *Asteracmaea* inclusion (A) and "complete" exclusion (C). The four time periods were chosen as being likely to be important stages of the experiment, and so both factors can be regarded as fixed. Replicate numbers varied as *Pinna* shells died, or were occasionally missed. The

death of animals was as high as 7 in some treatments. I considered that the between-shell variation in percent cover of most species was so high that removal of replicates would have reduced replicate numbers by too much, and so an unbalanced analysis was done. It was possible to regard the *Pinna* within cages and cages within treatments as nested factors, but I did not for the following reasons. Firstly, there is no ready analysis for such an experimental design. Secondly, the clustering of *Pinna* shells under cages was a logistic convenience, and there is *a priori* no reason to expect them to have an effect. The data from Chapter 3 suggest that recruitment onto clustered *Pinna* will not be markedly more similar than that on widely separated *Pinna*, and so it is probably not important not to have created the design as nested. The ANOVA's were performed on untransformed data, since variances were not significantly heterogenerous, with one exception, and in this case the arc-sine transformation did not homogenize the variances.

If taxa were uncommon, so that 0 percent covers were the most common "score", a different analysis was used, because with many zeroes and occasional large numbers, variances would be very large, and so with an ANOVA, Type II errors would be more likely. The data for these species were analysed as follows.

Two aspects of a given taxon were of interest: (a) the total abundance, and (b) the proportion of shells which it occupied. For each shell, the taxon was scored as present or absent. These presences and absences were then compiled into a 4 x 4 x 2 table (Time x Caging x Presence/Absence), and a G-test for independence performed (Sokal and Rohlf 1969).

The abundance of the taxon was assessed by calculating the total number of cm^2 on *Pinna* shells in a given treatment, and the total number on which the taxon in question was present. This again gave a 4 x 4 x 2 table, and a G-analysis was performed.

Two individual species were sufficiently common to be analysed by ANOVA, *Schizoporella* and *Parasmittina*. The same analysis was performed using total bryozoan cover and total percent cover of all species.

The G-analysis was used for *Celleporaria fusca*, sponges and tunicates.

Schizoporella

The ANOVA table is presented on Table 4.23. There was no difference between caging treatments, but a significant effect due to time. In the three caged treatments mean percent cover rose until December 1979, after which it fell. In the control treatment, the rise continued throughout the experiment.

Parasmittina

The only significant effect was that due to caging (Table 4.24), and the lack of an interaction effect shows that there were consistent differences between caging treatments. Therefore, differences were a result of chance when the *Pinna* were allocated to treatments or had become established by October 1978. There was, however, a marked decrease in abundance from December 1979 to June 1980 in two of the caged treatments (Gastropods and complete exclusion).

Celleporaria fusca

The G-analysis is shown on Table 4.25. The abundance of *C. fusca* showed heterogeneity between times and treatments. The C x T term is trivial; it shows simply that when *Pinna* were not photographed for some reason, they were not always from the same treatment. The P x T partition shows that the proportion covered by *C. fusca* varied with time. More importantly, it increased in all treatments (Table 4.25). This was mainly due to settlement of *C. fusca* in late 1979, but not

during the same period in 1978 (Chapter 3; Figure 3.13).

The P x C term indicates heterogeneity between treatments in the abundance of *C. fusca*. Again, there were initial differences in abundance, but in this case, the interaction term indicates that the increase in abundance with time was not uniform across all caging treatments. Inspection of percent cover shows that the percentage increase was least in the uncaged controls, but the absolute increases showed no pattern.

The G-analysis of the frequency of occurrence of *C. fusca* (Table 4.26) shows that the percentage of shells which bore *C. fusca* increased with time in the three caging treatments, but not in the control. The difference between cages and controls may be investigated by partitioning the C x P term in Table 4.26. I used two partitions; the first excluded the control treatment and compared the three caged treatments. Again, the P x T component was significant (Table 4.27), and the C x P term was even smaller, indicating similarity between caged treatments. The second partition pooled all caged treatments and compared this with controls (Table 4.27). The C x P term was also significant indicating that the frequency of occurrence of *C. fusca* increased in cages, but not on control *Pinna*.

Thus, *C. fusca* increased in abundance on caged *Pinna*, and the mechanism was an increase in the number of shells on which the species occurred. Unfortunately, the species did not settle heavily during the time in which *C. fusca* recruits were recorded, and so it is impossible to state whether this was the result of increased settlement in cages, or increased survival of recruits.

Total Bryozoans

The ANOVA (Table 4.28) shows that the abundance of bryozoans showed heterogeneity between times and caging treatments and there was an interaction between time and caging. Examination of means (Table

4.28 and Figure 4.13), showed that there were initial differences between caging treatments in the abundance of bryozoans, but abundance increased steadily in all treatments until December 1979. After this, percent cover of bryozoans rose in controls, but fell in all three caged treatments.

Sponges

The G-analysis for abundance of sponges (Table 4.29) showed significant effects for all partitions.

Inspection of total percent covers (Table 4.29) shows consistent differences between treatments, and fluctuations with time. These fluctuations are not uniform across treatments, as shown by the P x C x T interaction term, and the data show no clear pattern at all.

Sponges remained at low abundances throughout the experiment, and similarly, examination of the proportion of shells bearing sponges (Table 4.30) shows no heterogeneity at all, so that the frequency of occurrence of sponges remained approximately constant across all treatments.

Tunicates

All partitions of the G-statistic for tunicate abundance were significant (Table 4.31), and inspection of total abundance for each treatment combination (Table 4.31) showed that for caged *Pinna*, the cover of tunicates was approximately steady up until December 1979, and increased in all three treatments between then and June 1980. In the control treatment, abundance was low initially, but fell after February 1979. This was due to a single colony of *Didemnum patulum*, which covered shell M009, and then died. No further tunicates became established.

Analysis of the frequency of occurrence of tunicates was difficult, since the G-test uses the quantity $f \ln f$, where f is the frequency of observations in a given cell. Therefore, both 0 and 1 give the same value, 0. When a table contains modest numbers of 0's and 1's, the analysis is flawed, because row or column totals for a row of 1's, compared to a row of 0's will differ, but the sum of the $f \ln f$'s will not. The tunicate presence in a treatment frequently was 0, and in some caged treatments only one tunicate colony was recorded. I therefore inspected the data visually and the three caged treatments did not appear to differ greatly (Table 4.32). I pooled these data, and compared them with uncaged controls (Table 4.32). This analysis showed that the two differed.

The increase in tunicate abundance within caged treatments was thus due to an increase in the number of *Pinna* shells colonized by tunicates, and the subsequent growth of these recruits. No new recruits were observed on control *Pinna*.

Serpulids

No analysis was done on these species, since it was difficult to determine whether they were dead or alive. Two estimations of the number of serpulids were made for uncaged *Pinna* during October 1978 and February 1979, and the percent cover measured (Kay and Keough 1981). This was extremely time-consuming and I did not have much confidence in the distinction between live and dead individuals. They will not be discussed further.

TOTAL Percent Cover (all species pooled)

The ANOVA (Table 4.33) showed that there was significant heterogeneity between both caging treatments and time periods. Inspection of treatment means (Table 4.33) showed that total cover rose

steadily in caged treatments, but did not change in the controls. In caged treatments, the results of the previous analyses suggest that the initial rise was the increase in bryozoans, mainly *Schizoporella* and *Parasmittina*. Later, *Celleporaria fusca* and colonial tunicates recruited and grew, the latter often at the expense of bryozoans. On control *Pinna*, the initial cover of tunicates decreased, and bryozoans increased, resulting in no net change. These events were coincident, rather than linked.

4.4.2 Results . Recruitment in cages.

Data (number of recruits per 180 cm^2 per 60 days) were analysed by two-way fixed-factor ANOVA. In this case, sample sizes were sufficient to allow random removal of replicates to give unequal but proportional subclass sizes. For each time period, I analysed total recruits (all species pooled), individual species, and species number. Results of the ANOVAs are shown on Tables 4.6 to 4.19. Only two ANOVAs showed a significant effect due to caging. Calculation of the probability of Type II errors for 14 tests with $\alpha = 0.05$ shows that the probability of two or more significant F-ratios in this number of tests is 0.153. Accordingly, there is no reason to reject the null hypothesis that recruitment does not differ significantly between caged and uncaged panels.

Only four groups recruited at levels sufficient for analysis; *Galeolaria, Spirorbis convexis, S. pagenstecheri,* and didemnid ascidians, and the conclusion is that recruitment over periods of two months does not differ between the two panel types. Monacanthids were often observed browsing over uncaged panels, and since panels were immersed for two months at a time, it seems likely that some had been removed from uncaged panels before they were collected and censused. Thus, it is likely that the settlement of, say, didemnids, was actually higher on

uncaged panels, with the cages acting as a filter for larvae. The essential point is that none of the species settled preferentially in cages due to photonegative behaviour etc. The importance of this will become apparent with respect to didemnid ascidians when the result of the caging experiment are to be interpreted.

4.4.3 Results . Movement of predators.

1. *Uniophora*

On no occasion were more than two *Uniophora* found feeding on *Pinna* shells, and the mean number of starfish per survey was 0.67 ± 0.82 (S.D.). Even when surveys were close together, a *Pinna* shell which bore a *Uniophora* on one survey never bore one on the following survey. *Uniophora* are moderately common in the grid study area, but visits to *Pinna* shells are clearly rare.

2. *Asteracmaea* - density

The mean number of limpets per shell varied between 1.4 and 2.0, but was generally about 1.6 (Figure 4.2). My impression was that the limpets were more abundant at night, when some which had been attached to shells below sand level moved up to feed. It was difficult to test this, since night surveys were confounded by decreased efficiency of divers (Figure 4.3). Generally, over ninety percent of tagged *Pinna* were found. The few days after the experiment began show low efficiencies, of the order of 80%. This is probably an artifact of the method, in fact an example of learning by an assistant. The same assistant helped survey the tagged animals on surveys 2, 3, 4, 5, 6, and 10, and I suggest that the curve shows increased efficiency in performing the task.

A frequency distribution of limpets per shell was compiled for each survey, and compared to a Poisson distribution by calculating expected numbers of *Pinna* shells with x limpets for a Poisson with the

observed mean, and testing the fit of the observed distribution to this by χ^2. Results are shown in Table 4.20. Only two significant results were obtained, and calculation of the expected number of significant results assuming that the data do not deviate from a Poisson distribution gives a probability of 0.21 of obtaining two or more significant results in seventeen tests. It is clear that the limpets are distributed randomly over *Pinna* shells.

3. Abalone - density

This fluctuated between 0.1 and 0.3 per *Pinna* shell (Figure 4.4), and although few *Pinna* shells had more than one *Haliotis*, comparison with a Poisson was possible for most surveys. Again, only two significant deviations from a Poisson distribution were obtained (Table 4.21), and with a significance level of 0.05, the probability of at least two significant results is 0.21. *Haliotis cyclobates* also appear to be distributed randomly with respect to *Pinna* shells. This species appears to be nocturnal, and individuals are often seen moving about at night.

Relative movements of *Asteracmaea* and *Haliotis*

Figure 4.5 shows the regressions or r_{jk} against T_{jk} for both species. The mean correlation between random pairs of shells, r_r, was 0.0200 ± 0.0205 (S.E.) for *Asteracmaea* and 0.0574 ± 0.0331 (S.E.) for *Haliotis*. These were substituted into the relevant regression equations, and a time, T_r, was estimated for the autocorrelation to reach this level. This time was 338 days for *Asteracmaea* and 105 days for *Haliotis*.

The study area was revisited after 607 days, and the remaining tagged *Pinna* were surveyed. The previous surveys were only separated by 65 days, and so I calculated the auto correlations r_{18k}, which was the auto-correlation between survey 18 and each of the previous seventeen. T_{18k} was thus always greater than 500 days. The resultant set of 17 auto-correlations was tested against the null hypothesis $H_0 : \mu = 0.0200$,

this being the value of r_r for *Asteracmaea*. There was no significant difference between the mean of the r_{18k}'s and 0.0200 ($t = 0.6275$, $df = 16$, $p > 0.2$). Thus, after more than 500 days, the limpet numbers on individual *Pinna* had indeed changed so that they bore no more resemblance to the numbers at earlier time than to those on a randomly selected *Pinna* shell.

Analyses of variance for the two regressions are shown on Table 4.22. The regression slope was much greater for *Haliotis* than for *Asteracmaea* (Figure 4.5).

The above analysis suggests that *Asteracmaea* moves about very little, and that most shells bear limpets (Figure 4.6). In contrast, few shells bear abalone at any one time. *Haliotis* remain on one shell for a much shorter period of time than *Asteracmaea*, and we can view the individual *Pinna* shells as almost constantly having a few limpets, and receiving occasional short visits by *Haliotis*, and rare and very short visits from *Uniophora*.

4. Fish

Monacanthids

Two species were common, the mosaic leatherjacket, *Eubalichthys mosaicus*, and the pygmy leatherjacket, *Brachaluteres jacksonianus*. Only juveniles of the former were recorded, and Coleman (1980) reports that juveniles tend to inhabit shallow reefs and bays, while large males are found near offshore reefs. At Edithburgh, I have never seen large *Eubalichthys* in the study grid, although they are not uncommon near the pier. The juveniles are usually no more than 80 mm long. *Brachaluteres jacksonianus*, on the other hand, is a very small species, reaching no more than 80 mm in length (Coleman 1980). The two species are frequently orange-brown, but can be distinguished by the distended belly of *Brachaluteres*.

Eubalichthys showed marked seasonal fluctuations in abundance. Individuals were never seen for most of the year, and appeared in September of each year in moderate numbers (Figure 4.12). By late December, few animals were seen.

Brachaluteres also showed seasonal changes in abundance (Figure 4.12), but these were not as marked as for *Eubalichthys*. The former were seen for more of the summer months.

Both species were often seen browsing both on settlement panels and over *Pinna* shells.

Parequula melbournensis

Coleman (1980) records this species as carnivorous, and individuals of this species almost invariably appeared when sediment was disturbed. They were seen swimming around *Pinna* shells, but were not obviously feeding, while they could be seen taking particles from stirred-up sediment.

They also showed seasonal changes in abundance, but could be seen all year round, although less frequently during winter (Figure 4.12). Scott *et al.* (1974) claim that the species is solitary, but this is not the case. They are most frequently seen in pairs or small groups of up to six fish.

Neoodax sp.

Again, was most abundant during summer months (Figure 4.12). Individuals are often seen browsing over rocks and *Pinna* shells.

4.5 Effects of Predators on S

The critical w was used as a measure of the degree of fluctuations, and the two distributions of critical w's were compared by the logit analysis detailed previously. The previous sections give cause for

believing that fish are the important predators, and so all caged *Pinna* were pooled, and curves of the number of *Pinna* shells whose critical w was less than or equal to a given w were plotted (Figure 4.14).

Logit curves were plotted, and the slopes did not differ (uncaged : $f = 10.2745$; caged: $f = 10.344$, $t = 0.359$, $p > 0.05$). The calculated w_{50}'s were 0.275 (± 0.0001) for uncaged *Pinna* and 0.313 (± 0.0001) for caged *Pinna*. These differed significantly ($t = 537.4$, $p < 0.001$). The w_{95}'s were 0.5315 (uncaged) and 0.6024 (caged).

Thus, I conclude that the fluctuations in S are in general greater on *Pinna* from which fish are excluded, or more specifically, for a given w, fewer caged *Pinna* are contained within the region $\bar{S} \pm w\bar{S}$ than uncaged. The most likely explanation for this is the increased incidence of colonial tunicates, which were shown to have dramatic effects on S.

The effect of fish is relatively minor, since even the uncaged *Pinna* fluctuate widely in species number.

4.6 Discussion

Dynamics of the Epifauna of Uncaged Pinna

Total percent covers were consistently below 40%, and tunicates and sponges were rare (see also Kay and Keough 1981). The contact matrix (Figure 4.7) contains relatively few interactions, especially when it is realised that it was compiled from observations on an original 130 tagged *Pinna* (105 by the end of the experiment) over two years. Thus, with the exception of interactions between serpulids and other species, interactions between adult organisms occurred relatively infrequently. On the uncaged *Pinna*, most of these interactions were between bryozoan colonies, and some of these resulted in "ties".

Even when an interaction resulted in a "win", the overgrown species was often able to grow along a colony edge which was away from the site of overgrowth, and so the colony was not completely eliminated. In any event, there was frequently more than one colony of the common bryozoan species on a given shell, and they were never all overgrown. The competitive equivalences mean that even on a given shell, each species is likely to win some encounters, and thus neither will be eliminated.

The species which are good competitors, the sponges and colonial tunicates - especially the latter - could be shown to have dramatic effects. These species are rare but, if they colonize, other species are excluded. The immigration or extinction of these species produces fluctuations in S, and it is tempting to postulate that those *Pinna* shells which show wide fluctuations do so because of these species. However, examination of the raw data for those *Pinna* shells which showed high w values (i.e. S fluctuated widely) showed that only in some cases were the fluctuations due to tunicates or sponges. The fluctuations in S are not narrowly bounded, and this is not because of the behaviour of sponges or tunicates.

We can characterize the uncaged *Pinna* as having low percent cover, with almost all shells bearing *Schizoporella* and *Parasmittina* colonies, as well as serpulids, *Geleolaria* spp. and *Spirorbis* spp. Many shells also have other species of bryozoans and solitary forms, and occasional *Pinna* bear sponges or tunicates. Interactions between adult organisms are relatively rare, and the variation in recruitment detailed in Chapter 3 is sufficient to explain the level of between-patch variation, evidenced by the large standard deviations for almost all measurements. It is only on occasional patches that interactions between resident organisms are important.

The wide fluctuations in S are thus due mainly to the highly variable recruitment rates and extinctions.

4.6.1 The impact of Predators

Two taxa showed increased abundance in caged treatments, *Celleporaria fusca* and colonial tunicates, mostly didemnids. The increase in *C. fusca* could not be ascribed to predation, since there were no data on recruitment inside and outside cages.

Evidence regarding tunicates is stronger, however. They were settling while the panels were in the cages, and so data could be obtained on their recruitment. After two months, the number of recruits did not differ between caged and uncaged panels. It is possible that the cages had an effect, in this case physically screening larvae so that settlement was lower inside, and some recruits were eaten outside the cages. The important point is that, at two months, both types of panel had didemnid recruits.

Thus, the increase in tunicate presence after two months can be ascribed to differential survival of recruits. The increase in tunicate abundance was due to the growth of these recruits. All caged treatments showed a similar increase in tunicate abundance, and the factor common to all three treatments was the exclusion of fish. It is most likely that predation by fish accounts for the low frequency of occurrence of tunicates on uncaged *Pinna*. Supporting evidence was gained during the experiments which are detailed in Chapter 5. The experiment was monitored at monthly intervals and, in September 1979, large numbers of didemnid recruits were observed. Most of these did not survive, and indeed of the 41 recruits observed, only 6 survived. Monacanthids are common around the pier, and the chaetodont *Chelmonops truncatus* may also be important.

Monacanthids were most abundant in the study grid just when the didemnid recruits reached "countable" size (2-3 mm diameter), and the observations of their feeding suggest that they, rather than *Neoodax* or *Parequula* are important.

Haliotis, Asteracmaea and *Uniophora* produced no marked effects on the abundance or presence of any taxon, and their impact appears small.

The bryozoans *Schizoporella* and *Parasmittina* showed a decrease in abundance towards the end of the experiment. This was not directly due to predation, since they had increased in abundance for 18 months in the presence of gastropods and *Uniophora*, and continued to increase in abundance on uncaged *Pinna*. The decrease in bryozoan abundance was a direct result of overgrowth by tunicates.

The frequency of overgrowth interactions was greater on caged *Pinna* and adult-adult interactions were important on a greater number of *Pinna* shells. The tunicates were capable of overgrowing all other species, and their effects were dramatic when present.

S fluctuated even more widely on caged then uncaged *Pinna*, so that on few shells was S "narrowly bounded". The wider fluctuations were due to the increased presence of tunicates. These effects were not fully manifest, since on some shells the tunicates had not completely overgrown all other species. If monitoring had continued until this occurred, then the values of w for these *Pinna* would have been increased, and the difference between caged and uncaged *Pinna* would have been even greater.

Thus, the fish are a cause of the scarcity of tunicates on uncaged *Pinna*, and from the caging results, without the fish, the composition of the epifauna on a given *Pinna* shell would be more likely to be determined by adult-adult interactions, rather than larval interactions in the plankton or interactions between adults and larvae. Similarly, they exert a damping effect on the fluctuations in S, or,

more accurately, they prevent tunicates from causing S to fluctuate more widely. It should be stressed that even with most larval tunicates being removed, S still fluctuates too widely for the concept of equilibrium to be useful. This is mainly due to variation in recruitment, and chance extinction.

The behaviour of individual taxa is thus important in explaining the dynamics of this community and it is the interaction of two such taxa which is crucial; the monacanthids are only present in great numbers for a short time each year, and this coincides with the time of recruitment of colonial tunicates.

The question arises of how strong an influence the interaction between these species really is, on the abundance of, say, bryozoans. The two main tunicates were *Didemnum patulum* and *Didemnum* sp. A. Of these, *D. patulum* lives for a number of years. This study observed colonies for two years. They had covered the shells by this stage, and so settled the previous summer at the latest. They are still alive now, so they can live at least 3 years. *Didemnum* sp. A is an annual species at Edithburgh (Kay 1980; Kay and Keough 1981), settling in early summer, and dying off the following spring.

Most of the tunicates which recruited were *Didemnum* sp. A, and so they could be expected to die off by spring of this year. Their effect would thus show seasonal variation. In addition, there were no new recruits at all during the summer of 1978-9, and so even without fish, the effect of tunicates would show between-year variation. The cause of this is difficult to determine, since recruitment of most species was heavier in 1978 than late 1979. It is possible, of course, that in 1979 settlement was heavier but fish were more abundant so that the observed recruitment was lower. This must remain speculation, however, in the absence of data on fish abundance or tunicate settlement, in 1978.

The abundance of sponges could not be investigated, because they

did not recruit at all during the experiment. Their abundance will be considered in greater detail in Chapter 5.

In summary, the *Pinna* shells at Edithburgh have numbers of epifaunal species which fluctuate widely, so that they can not be considered to be narrowly bounded. The fluctuations in S are due to a number of causes, such as large variation in recruitment, extinctions of rare species. Species which are good competitors have the capacity to influence strongly the composition of a given patch, and hence S, but their effect is ameliorated by the action of one or two species of mobile predator. Interactions between adult organisms are of minor importance, except when good competitors become established. The important interactions concern larvae, either in the plankton or at the surface of the *Pinna* shells, or newly metamorphosed juveniles and their predators.

Chance events and the properties of a few (individual) species are thus major causes of the large fluctuations in S. There is thus no support for the concept of an equilibrium, and we are left with the question of whether there are better approaches, which take into account chance and the properties of individual species.

Chapter 5 contains an attempt to develop such a model and to test it.

TABLE 4.1 Analysis of variance table for vertical light intensity in cages at Edithburgh.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Cage fouling	1	340.04	340.04	5.68 *
Cage position	2	21040.87	10520.43	175.68 ***
Interaction	2	965.26	482.63	8.06 **
Residual; error	24	1437.2	59.88	
Total	29	23783.37		

F-max = 68.82; $0.05 > p > 0.01$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Means for various treatments (microeinsteins m^{-2} s^{-1})

	Fouled	Unfouled
Flush	21.6	30.2
Raised	14.0	33.6
No cage	85	77

TABLE 4.2 Analysis of variance table for horizontal light intensity in cages at Edithburgh.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Cage fouling	1	5.46	5.46	1.69
Cage position	2	1129.27	564.63	174.27 ***
Interaction	2	554.58	277.29	85.58 ***
Residual; error	24	77.77	3.24	
Total	29	1767.08		

'F-max = 19.81, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Treatment means (microeinsteins $m^{-2} s^{-1}$)

	Fouled	Unfouled
Flush	5.10	12.40
Raised	5.44	12.00
No cage	27.40	16.10

TABLE 4.3 Cage light intensities recast as percentages of "no cage" or control value (means shown).

(a) Vertical light

	Fouled	Unfouled
Flush	25.41	39.22
Raised	16.47	43.64

(b) Horizontal light

	Fouled	Unfouled
Flush	18.61	77.02
Raised	19.85	74.53

TABLE 4.4 Cage details and durations of experiments for caging experiments on subtidal hard substrata.

Source	Site	Mesh size	Duration
Sammarco (1980)	Discovery Bay	2.54 cm	12 months
Osman (1977)	Woods Hole	0.75 cm^2	12 "
Peterson (1979a)	Barngate, N.J.	6 mm	13 "
Marshall *et al.* (1980)	Sydney	1 mm	$\leq$ 6 "
Russ (1980)	Portsea	12.5 mm	7 "
Ayling (in press)	Leigh, N.Z.	30 mm	22 "
Kay (1980)	Edithburgh, Rapid Bay	20 mm^2	24 "
Sutherland (1974)	Beaufort	6 mm	9 "
Day (1977)	Heron Island	12.5 mm	3 "
Keough & Butler (1979)	Rapid Bay	12.5 mm	6 "

TABLE 4.5 Details of examination of tagged *Pinna* at Edithburgh to assess frequency of predator visits. A.M. denotes a survey done between 9 a.m. and 11 a.m.; P.M. from 3 p.m. to 8 p.m. Night surveys were commenced at about midnight.

Date	Time of Day	Time since previous survey	
4.ii.79	P.M.	-	1
6.ii.79	P.M.	48 h	2
7.ii.79	A.M.	12 h	3
7.ii.79	early afternoon	4 h	4
8.ii.79	P.M.	24 h	5
9.ii.79	A.M.	12 h	6
10.ii.79	A.M.	24 h	7
11.ii.79	P.M.	30 h	8
12.ii.79	night survey	30 h	9
13.ii.79	A.M.	8 h	10
14.ii.79	P.M.	30 h	11
28.iii.79	A.M.	42 days	12
29.iii.79	P.M.	30 h	13
30.iii.79	P.M.	12 h	14
30.iii.79	night survey	12 h	15
10.iv.79	A.M.	11 days	16
20.iv.79	P.M.	10 days	17

TABLE 4.6 Analysis of variance table for effect of caging on numbers of recruiting species at Edithburgh. Time period 9/79-11/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	2.01	2.01	2.89
Panel size	2	4.35	2.18	3.14 *
Interaction	2	4.12	2.06	2.96
Residual; error	134	93.14	0.70	
Total	139	103.62		

F-max = 7.75, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.7 Analysis of variance table for effect of caging on numbers of recruiting species at Edithburgh. Time period 5/79-7/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	4.41	4.41	9.39 **
Panel size	2	10.12	5.06	10.77 **
Interaction	2	0.28	0.14	0.30
Residual; error	114	53.56	0.47	
Total	119	68.37		

F-max = 6.41, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.8 Analysis of variance table for effect of caging on numbers of recruiting species at Edithburgh. Time period 7/79-9/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	0.89	0.89	1.56
Panel size	2	3.58	1.79	3.14
Interaction	2	0.00	0.00	0.00
Residual; error	132	75.15	0.57	
Total	137	79.62		

F-max = 2.40, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.9 Analysis of variance table for effect of caging on recruitment of *Spirorbis pagenstecheri* at Edithburgh. Time period 9/79-11/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	5.21	5.21	1.18
Panel size	2	18.36	9.18	2.07
Interaction	2	6.17	3.09	0.70
Residual; error	134	593.74	4.43	
Total	139	623.48		

F-max = 5.43, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$.

TABLE 4.10. Analysis of variance table for effect of caging on *Spirorbis pagenstecheri* at Edithburgh. Time period 5/79-7/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	1.35	1.35	0.81
Panel size	2	28.72	14.36	8.65
Interaction	2	8.91	4.46	2.68
Residual; error	114	189.36	1.66	
Total	119	228.34		

F-max = 17.30, P< 0.01.

* p < 0.05, ** p < 0.01, ** p < 0.001.

TABLE 4.11 Analysis of variance table for effect of caging on recruitment of *Spirorbis pagenstecheri* at Edithburgh. Time period 7/79-9/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	2.59	2.59	0.24
Panel size	2	21.58	10.79	0.99
Interaction	2	7.99	4.00	0.37
Residual; error	132	1434.66	10.87	
Total	137	1466.82		

F-max = 5.14, p > 0.05

* p < 0.05, ** p < 0.01, *** p < 0.001.

TABLE 4.12 Analysis of variance table for effect of caging on *Galeolaria* recruitment at Edithburgh. Time period 9/79-11/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	7.61	7.61	0.69
Panel size	2	35.12	17.56	1.59
Interaction	2	17.89	8.95	0.81
Residual; error	134	1480.61	11.05	
Total	139	1541.23		

'F-max = 9.13, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.13 Analysis of variance table for effect of caging on *Spirorbis convexis* at Edithburgh. Time period 5/79-7/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	0.17	0.17	0.09
Panel size	2	54.46	27.23	14.41 ***
Interaction	2	3.04	1.52	0.80
Residual; error	114	215.66	1.89	
Total	119	272.33		

F-max = 8.48, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.14 Analysis of variance table for effect of caging on total recruitment at Edithburgh. Time period 9/79-11/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	16.01	16.01	0.75
Panel size	2	75.61	37.81	1.77
Interaction	2	25.32	12.66	0.59
Residual; error	134	2856.31	21.32	
Total	139	2973.25		

F-max = 8.61, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.15 Analysis of variance table for effect of caging on recruitment of *Didemnid ascidians* at Edithburgh. Time period 9/79-11/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	2.05	2.05	3.83
Panel size	2	3.45	1.73	3.23 *
Interaction	2	3.02	1.51	2.82
Residual; error	134	71.77	0.54	
Total	139	80.33		

F-max = 8.71, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.16 Analysis of variance table for effect of caging on recruitment of *Galeolaria* at Edithburgh. Time period 5/79-7/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	3.17	3.17	5.31 *
Panel size	2	3.22	1.61	2.71
Interaction	2	2.13	1.07	1.80
Residual; error	114	67.85	0.60	
Total	119	76.37		

F-max = 7.54, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.17 Analysis of variance table for effect of caging on recruitment of *Galeolaria* at Edithburgh. Time period 7/79-9/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups				
Caging	1	14.21	14.21	1.20
Panel size	2	30.64	15.32	1.30
Interaction	2	8.91	4.46	0.38
Residual; error	132	1562.13	11.83	
Total	137	1615.89		

F-max = 6.31, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.18 Analysis of variance table for effect of caging on total recruitment at Edithburgh. Time period 5/79-7/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	5	65.13	13.26	
Caging	1	8.53	8.53	2.80
Panel size	2	47.45	24.23	7.94 ***
Interaction	2	9.16	4.58	1.5
Residual; error	114	347.2	3.05	
Total	119	412.34		

F-max = 9.5, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.19 Analysis of variance table for effect of caging on total recruitment at Edithburgh. Time period 7/79-9/79.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	5	72.11	14.42	0.68
Caging	1	17.62	17.62	0.82
Panel size	2	47.52	23.76	1.11
Interaction	2	6.97	3.49	0.17
Residual; error	132	2819.89	21.36	
Total	137	2892.41		

F-max = 2.89, $p > 0.05$

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TABLE 4.20 Results of χ^2 for goodness-of-fit of observed distribution of limpets on *Pinna* shells to a Poisson distribution. Survey numbers correspond to those on Table 4.5.

Survey number	χ^2	d.f.[1]	P
1	3.11	4	>0.50
2	1.82	4	>0.50
3	0.63	4	>0.90
4	6.89	4	>0.10
5	4.62	4	>0.10
6	0.41	4	>0.975
7	0.54	4	>0.90
8	2.59	4	>0.50
9	1.041	4	>0.90
10	2.88	4	>0.50
11	4.97	4	>0.10
12	10.14*	4	0.05 > P > 0.01
13	5.19	4	>0.10
14	8.84	4	>0.05
15	6.01	4	>0.10
16	7.89*	3	0.05 > P > 0.01
17	0.39	4	>0.975

[1] degrees of freedom varied according to how many classes required pooling to get sufficiently high expected number for analysis.

TABLE 4.21 Results of χ^2 test for goodness-of-fit of observed distribution of *Haliotis cyclobates* to a Poisson distribution. All surveys had df = 1.

Survey number	χ^2	P
1	0.98	>0.10
2	0.26	>0.50
3	insufficient degrees of freedom	
4	0.95	>0.10
5	3.40	>0.05
6	0.16	>0.90
7	1.12	>0.10
8	1.25	>0.10
9	0.35	>0.50
10	0.04	>0.50
11	0.88	>0.10
12	5.23*	0.025 > P > 0.01
13	2.28	>0.10
14	0.05	>0.50
15	2.10	>0.10
16	1.57	>0.10
17	5.54*	0.025 > P > 0.01

TABLE 4.22 Analysis of variance for regressions of autocorrelation on time. (a) *Asteracmaea*, (b) *Haliotis*. Regression is of the form r = a + b T

(a) a 0.64200 r -.44288

b -0.00184 S_b .00032 r^2 0.19614

ANOVA

Source	df	SS	MS	F
Regression	1	0.293	0.293	32.696 ***
Residual	134	1.201	0.009	
	135			

(b) a = 0.38147 r = -.39457

b = 0.00306 S_b = .00062 r^2 = 0.15568

ANOVA

Source	df	SS	MS	F
Regression	1	0.811	0.811	24.527 ***
Residual	134	4.430	0.033	

TABLE 4.23 Analysis of variance table for percent cover of *Schizoporella*. The table below shows means and standard deviations of percent cover.

ns, non significant, *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	15	4259.76	283.98	3.25**
Caging	3	286.91	95.64	1.10 ns
Time	3	3493.2	1164.4	13.33 ***
Interaction	9	479.65	53.29	0.67 ns
Residual; error	282	24626.32	87.33	
Total	297			

F-max = 10.84, $p > 0.05$

Caging treatment		Time			
		10/78	2/79	12/79	6/80
Control	$\bar{x}$	4.9	7.85	12.3	12.9
	S.D.	5.42	7.27	7.91	9.54
U	$\bar{x}$	6.19	7.83	17.96	11.7
	S.D.	7.02	9.42	13.62	9.42
A	$\bar{x}$	5.42	6.98	13.32	9.05
	S.D.	5.66	4.42	8.64	6.83
C	$\bar{x}$	8.2	8.7	16.35	9.43
	S.D.	12.3	7.67	13.82	14.55

TABLE 4.24 Analysis of variance table on percent cover of *Parasmittina*. The second table shows means and standard deviations of percent cover.

ns, non significant; *, p <0.05; **, p <0.01; ***, p <0.001

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	15	3391.67	226.11	1.4 ns
Caging	3	2178.73	726.24	4.51 **
Time	3	325.8	108.6	0.61 ns
Interaction	9	887.13	98.57	0.61 ns
Residual; error	291	46908.06	161.2	
Total	306			

F-max = 7.35 , p < 0.01.

Caging Treatment		Time 10/78	2/79	12/79	6/80
Control	$\bar{x}$	10.62	9.68	13.86	12.66
	S.D.	13.94	13.92	15.44	14.11
U	$\bar{x}$	7.28	7.98	8.36	8.12
	S.D.	13.37	13.76	10.46	15.51
A	$\bar{x}$	4.18	6.13	6.85	1.08
	S.D.	5.41	8.63	10.9	2.12
C	$\bar{x}$	7.77	11.18	7.20	2.41
	S.D.	15.9	13.48	15.16	6.87

TABLE 4.25 Results of G-analysis for abundance of *Celleporaria fusca* in the caging experiment. The G for heterogeneity and its partitions are shown. The lower table shows total percent covers for each treatment and time.

Source of variation	df	G	p
Caging x Time	9	115.8	<0.001
Presence x Time	3	485.2	<0.001
Presence x Caging	3	143.36	<0.001
P x C x T interaction	9	135.63	<0.001
P x C x T independence	24	879.99	<0.001

	Time			
Treatment	10/78	2/79	12/79	6/80
Control	2.9	1.6	4.4	6.1
U	0.05	0.7	1.9	3.9
A	0.2	0.3	2.5	4.3
C	1.0	2.0	2.4	10.3

TABLE 4.26 G-analysis for the proportion of *Pinna* shells bearing *C. fusca*. The lower table shows the percentage of shells in each treatment which bore *C. fusca* each time period.

Source of variation	df	G	P
Caging x Time	9	0.92	>0.05
Caging x Presence	3	4.58	>0.05
Presence x Time	3	18.11	<0.001
P x C x T interaction	9	13.73	>0.05
P x C x T independence	24	37.33	<0.05

	Time			
Treatment	10/78	2/79	12/79	6/80
Control	45	33	33	46
U	6	11	38	44
A	6	17	45	35
C	13	13	38	62

TABLE 4.27 Frequency of occurrence of *C. fusca*. The table in 4.26 was partitioned, and resulting G-statistics are shown.

(a) Caged treatments only.

Source	df	G	P
Caging x Time	6	0.27	>0.05
Caging x Presence	2	0.32	>0.05
Presence x Time	3	13.99	<0.005
P x C x T interaction	6	1.19	>0.05
P x C x T independence	17	15.78	>0.05

(b) All caged treatments pooled and compared with controls.

Source	df	G	P
Caging x Time	3	0.37	>0.05
Caging x Presence	1	3.94	<0.05
Presence x Time	3	18.11	<0.005
P x C x T interaction	3	11.34	<0.01
P x C x T independence	10	33.76	<0.005

TABLE 4.28 Analysis of variance table on percent cover of all bryozoans. The lower table shows means and standard deviations of percent covers for each treatment and time period.

ns, non significant; *, p <0.05; **, p <0.01; ***, p<0.001.

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	15	18143.73	1209.58	23.81 ***
Caging	3	11830	3943.33	77.64 ***
Time	3	5193.09	1731.03	34.08 ***
Interaction	9	1120.64	124.52	2.45 **
Residual, error	280	14221.58	50.79	
Total	295			

F-max = 15.5, p < 0.01

Caging Treatment		Time 10/78	2/79	12/79	6/80
Control	$\bar{x}$	25.6	23.0	33.1	36.8
	S.D.	11.7	21.4	18.8	23.6
U	$\bar{x}$	12.59	15.67	23.25	19.14
	S.D.	13.88	17.99	16.55	14.35
A	$\bar{x}$	8.14	10.3	19.51	15.46
	S.D.	5.9	7	15.44	11.11
C	$\bar{x}$	13.61	19.84	23.61	17.22
	S.D.	16.68	15.2	17.95	16.67

TABLE 4.29 G-analysis on total abundance of sponges. The lower table shows the total percent cover of sponges for each caging treatment and time period.

Source	df	G	P
Caging x Time	9	115.8	<0.005
Caging x Presence	3	143.5	<0.005
Presence x Time	3	155.0	<0.005
P x C x T interaction	9	135.7	<0.005
P x C x T independence	24	775.2	<0.005

Caging Treatment	Time			
	10/78	2/79	12/79	6/80
Control	6.9	7.9	3.6	3.9
U	2.3	5.5	2.4	1.7
A	2.7	4.0	7.0	5.6
C	0.5	0.6	0.9	0.7

TABLE 4.30 Analysis of frequency of occurrence of sponges.

Source	df	G	P
Caging x Time	9	0.93	>0.05
Caging x Presence	3	7.15	<0.05
Presence x Time	3	1.15	>0.05
P x C x T interaction	9	6.03	>0.05
PxCxT independence	24	15.25	>0.05

TABLE 4.31 Analysis of tunicate abundance. The lower table shows the total percent cover of colonial tunicates for each treatment and time period.

Source	df	G	P
Caging x Time	9	115.98	<0.005
Caging x Presence	3	610.38	<0.005
Presence x Time	3	237.62	<0.005
P x C x T interaction	9	629.34	<0.005
P x C x T independence	24	1593.32	<0.005

	Time			
Caging Treatment	10/78	2/79	12/79	6/80
Control	2.9	2.3	0	0
U	3.7	4.0	3.7	9.5
A	0	0	4.5	7.0
C	6.7	5.4	4.6	14.7

TABLE 4.32 Percentage of *Pinna* shells bearing tunicates in four caging treatments at four times. The G-analysis to compare caged and uncaged treatments is also shown.

Caging Treatment	Time 10/78	2/79	12/79	6/80
Control	0	3.9	0	0
U	12.5	11.1	14.3	38.9
A	0	0	13.6	23.5
C	6.7	6.7	4.8	30.8

G-analysis

Source	df	G	P
Time x Caging	3	1.657	>0.05
Presence x Time	3	11.742	<0.01
Presence x Caging	1	22.301	<0.005
P x C x T interaction	3	11.607	<0.01
P x C x T independence	10	46.307	<0.005

TABLE 4.33 Two-way ANOVA on total percent covers. The lower table shows means and standard deviations of total percent cover for each treatment combination.

ns, non significant; *, p <0.05; **, p <0.01; ***, p <0.001

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Sub groups	15	20669.73	1377.98	6.61 **
Caging	3	5963.42	1987.81	9.54 ***
Time	3	11148.02	3716.01	17.83 ***
Interaction	9	3558.29	395.37	0.90 ns
Residual; error	290	60440.98	208.42	
Total	305			

F-max = 7.73, p > 0.05

Caging Treatments		Time 10/78	2/79	12/79	6/80
Controls	$\bar{x}$	39.47	34.08	35.24	39.7
	S.D.	19.98	15.8	20.05	25.54
U	$\bar{x}$	19.9	25.7	31.9	33.8
	S.D.	17.4	20.79	16.66	23.96
A	$\bar{x}$	12.0	12.5	27.3	30.3
	S.D.	10.67	12.81	24.39	29.43
C	$\bar{x}$	22.5	29.0	30.2	38.5
	S.D.	27.86	22.1	23.44	29.67

TABLE 4.34 Frequencies of fusions and interfaces between colonies of *Schizoporella schizostoma*, *Parasmittina raigii*, *Celleporaria fusca*, or B7.

Species	Fusions	Interfaces
Schizoporella	32	4
Parasmittina	14	5
Celleporaria	0	8
B7	3	1

G for independence = 26.46, df = 3, $p < 0.005$

Figure 4.1 Plan of Northern half of study grid, showing location of caging experiment and predator monitoring.

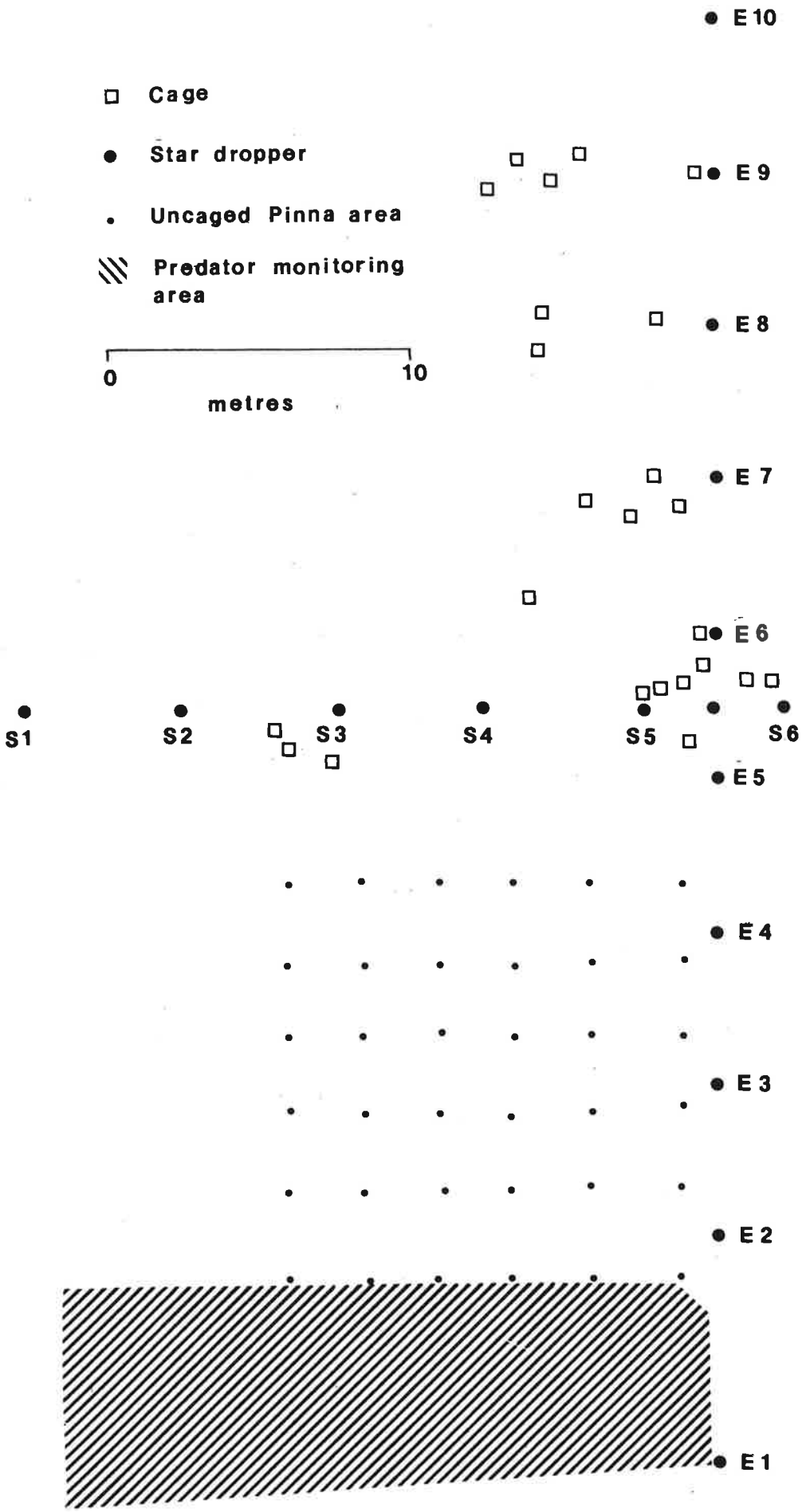

E10
Cage
Star dropper
Uncaged Pinna area
Predator monitoring area
0
10
metres
E9
E8
E7
E6
S1
S2
S3
S4
S5
S6
E5
E4
E3
E2
E1

Figure 4.2 Variation in mean ($\pm$ S.D.) number of limpets per *Pinna* shell during predator monitoring.

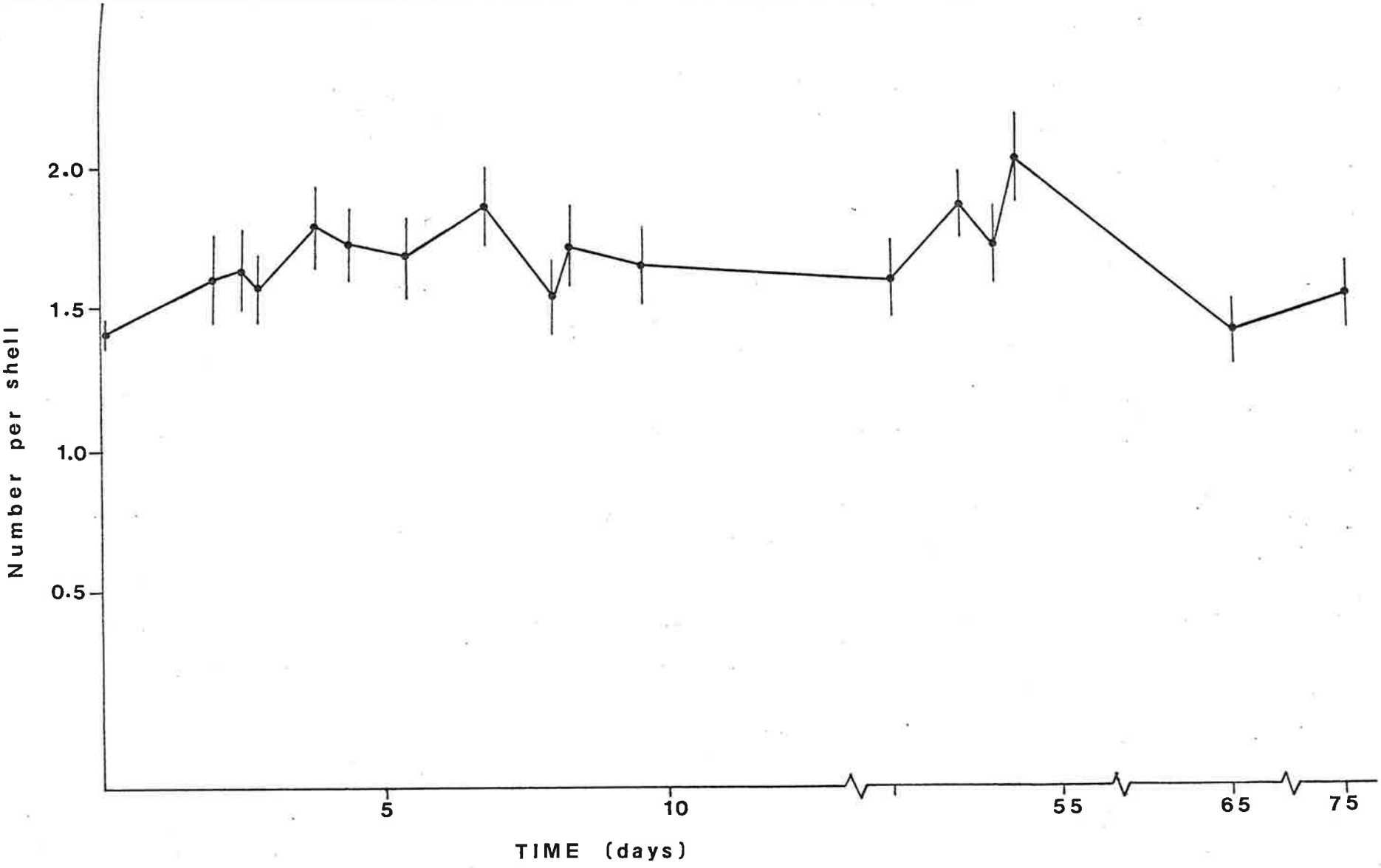

2.0
1.5
1.0
0.5
Number per shell
5
10
55
65
75
TIME (days)

Figure 4.3 Numbers of tagged Pinna which were relocated successfully on each dive during predator monitoring.

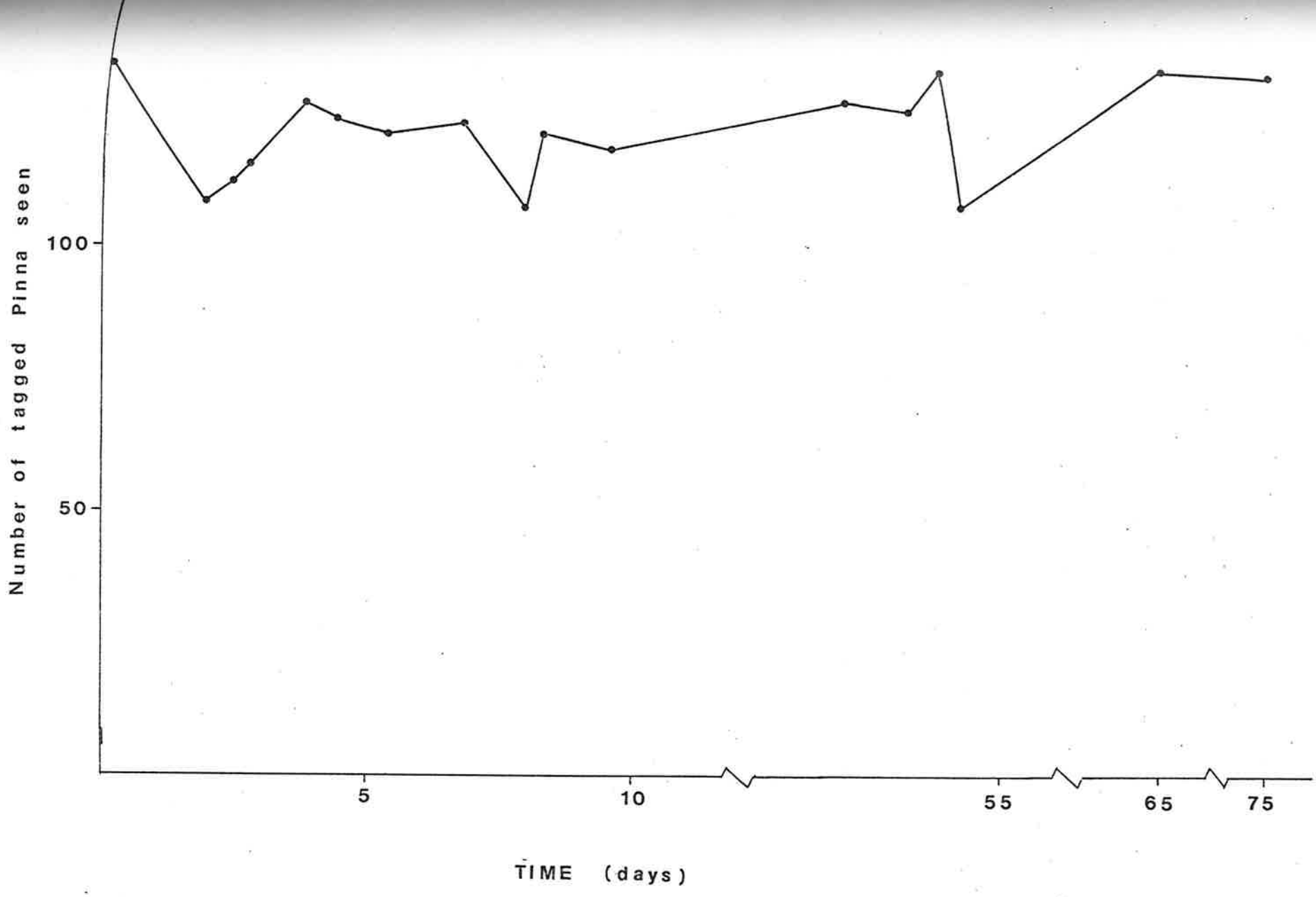

Number of tagged Pinna seen
100
50
5
10
55
65
75
TIME (days)

Figure 4.4 Variation in mean ($\pm$ S.D.) number of Haliotis per Pinna shell during the predator monitoring.

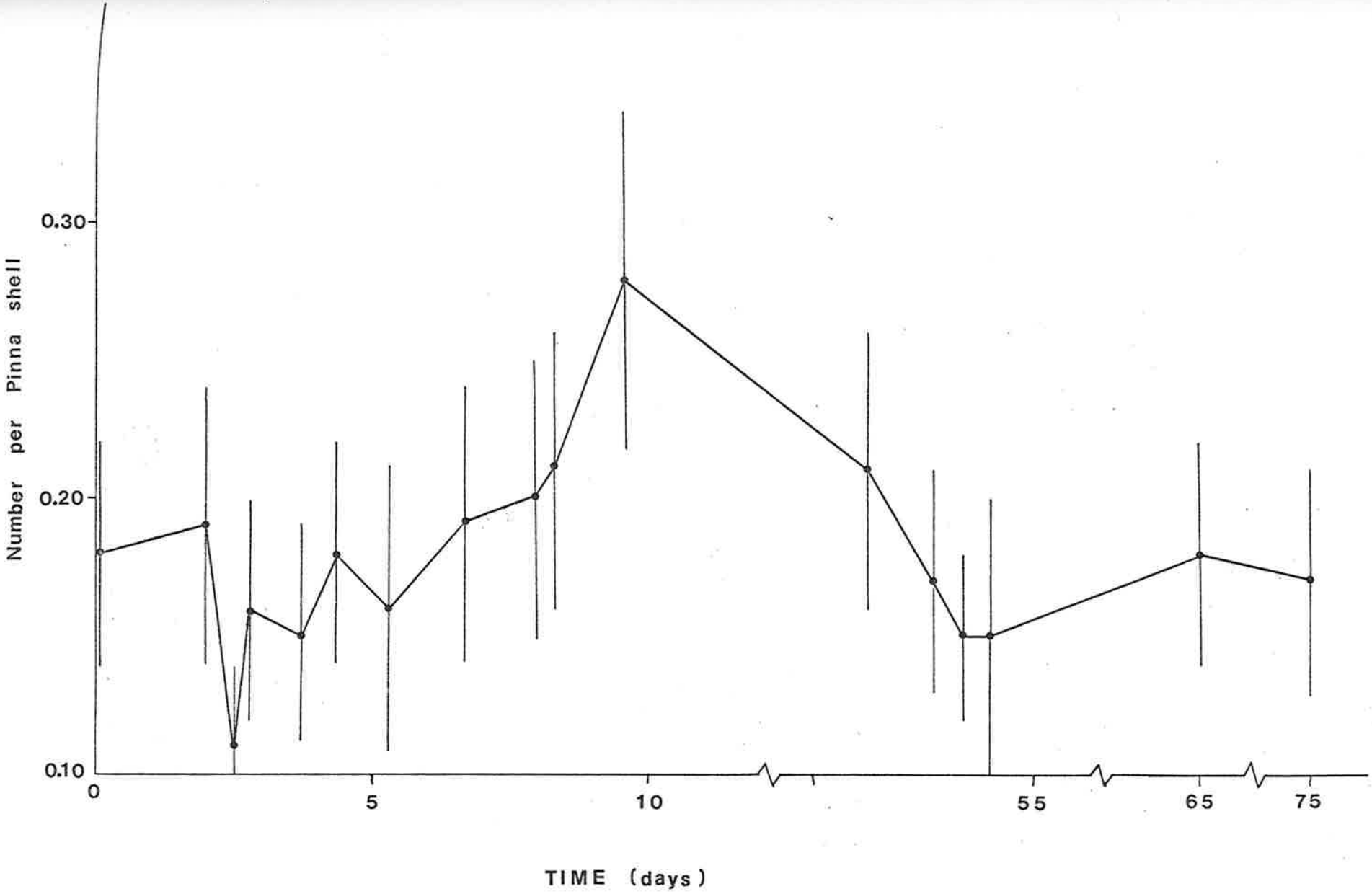

Number per Pinna shell
0.30
0.20
0.10
0
5
10
55
65
75
TIME (days)

Figure 4.5 Decline of r_{jk} with time for *Asteracmaea* and *Haliotis*. For details of symbols, see text, page 120ff.

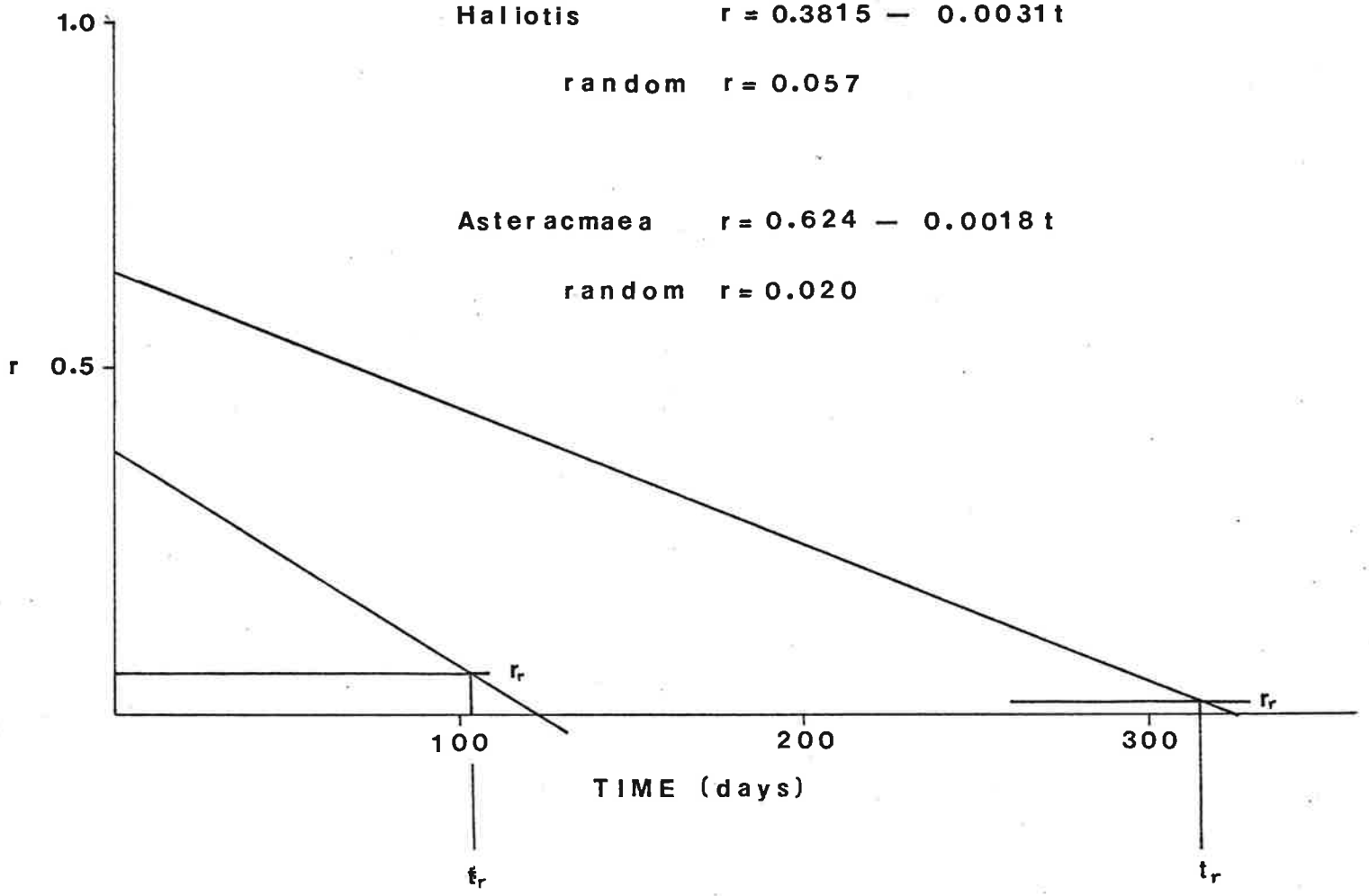

Haliotis r = 0.3815 — 0.0031t
random r = 0.057
Asteracmaea r = 0.624 — 0.0018t
random r = 0.020
1.0
r 0.5
r_r
r_r
100
200
300
TIME (days)
t_r
t_r

Figure 4.6 Percentage of tagged Pinna shells bearing Asteracmaea (●) and Haliotis (△) during predator monitoring.

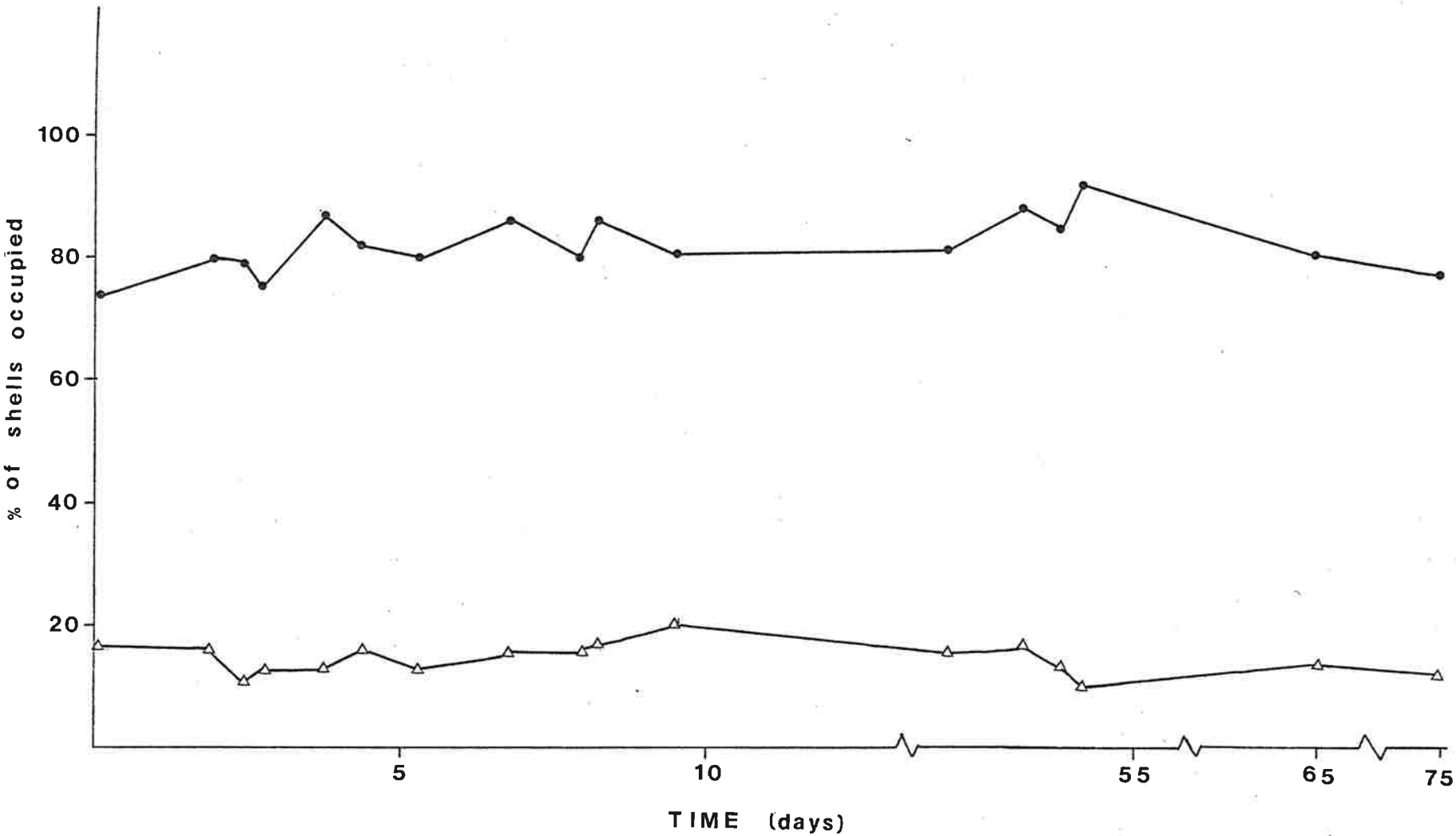

100
80
60
40
20
% of shells occupied
5
10
55
65
75
TIME (days)

Figure 4.7 Contact matrix for competitive interactions on Pinna shells for those species pairs where the number of observations exceeded five. In each cell, the number on the left is the number of wins to the "row" species, the number on the right is the number of wins to the "column" species, and, where present, the number in the lower central position is the number of ties. Arrows indicate the direction of dominance, and an asterisk denotes competitive equivalence.

Key to species symbols:

S Schizoporella schizostoma
Pa Parasmittina raigii
Cf Celleporaria fusca
B7 bryozoan species B7
SP35 sponge species SP35
Dp Didemnum patulum
T9 Didemnum sp.A
G Galeolaria spp.
Sp Spirorbis spp.

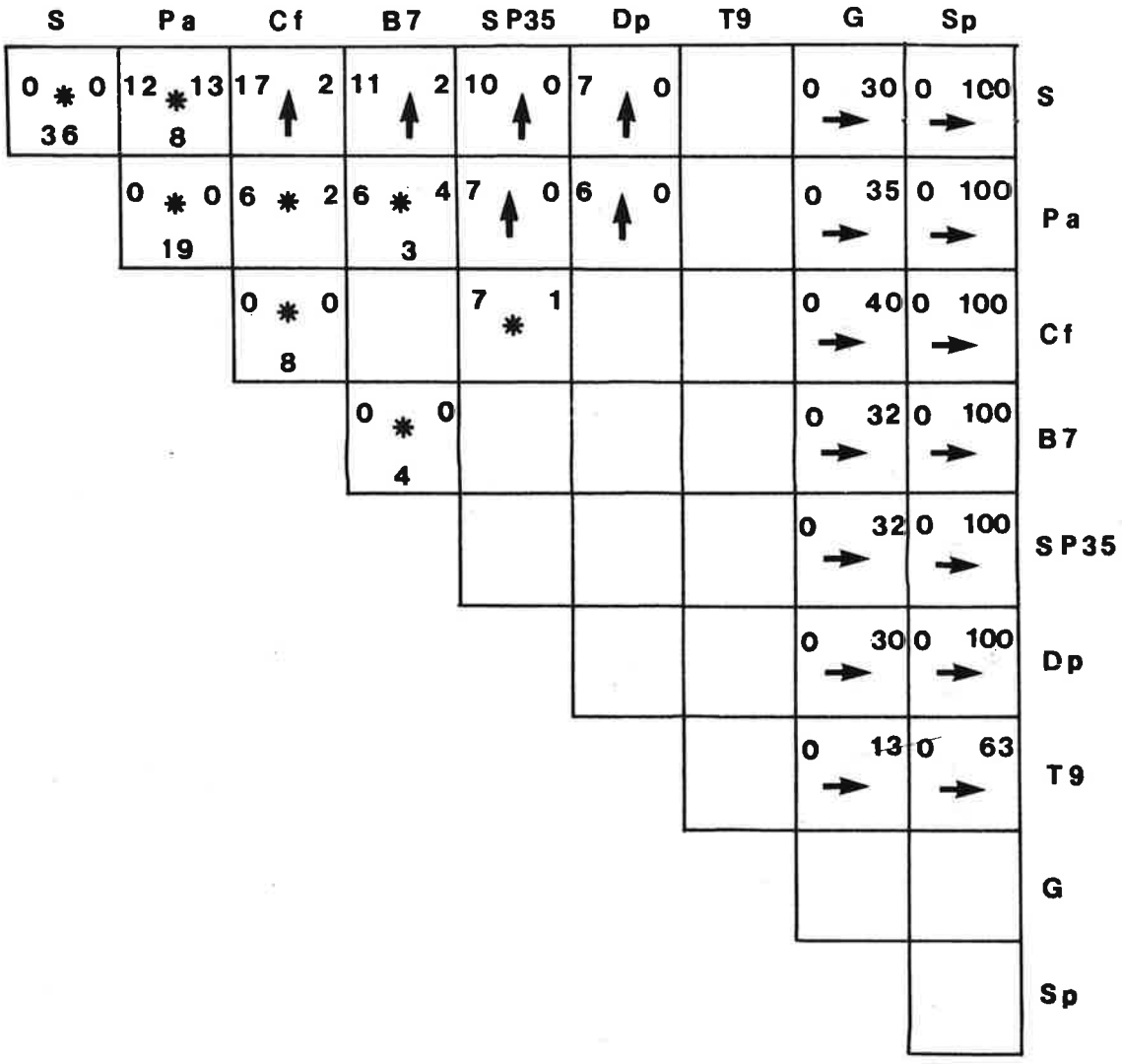

S
Pa
Cf
B7
SP35
Dp
T9
G
Sp
0 * 0
36
12 * 13
8
17 2
11 2
10 0
7 0
0 30
0 100
S
0 * 0
19
6 * 2
6 * 4
3
7 0
6 0
0 35
0 100
Pa
0 * 0
8
7 * 1
0 40
0 100
Cf
0 * 0
4
0 32
0 100
B7
0 32
0 100
SP35
0 30
0 100
Dp
0 13
0 63
T9
G
Sp

Figure 4.8 Pier piling contact matrix of competitive interactions for species pairs where the number of observations > 6. In each cell, the left-hand number is the number of wins to the "column" species, the right-hand number is the wins to the "row" species. Arrows point in the direction of the dominant of each species pair, and asterisks indicate competitive equivalences.

For further explanation, see Appendix 2, Fig.6.

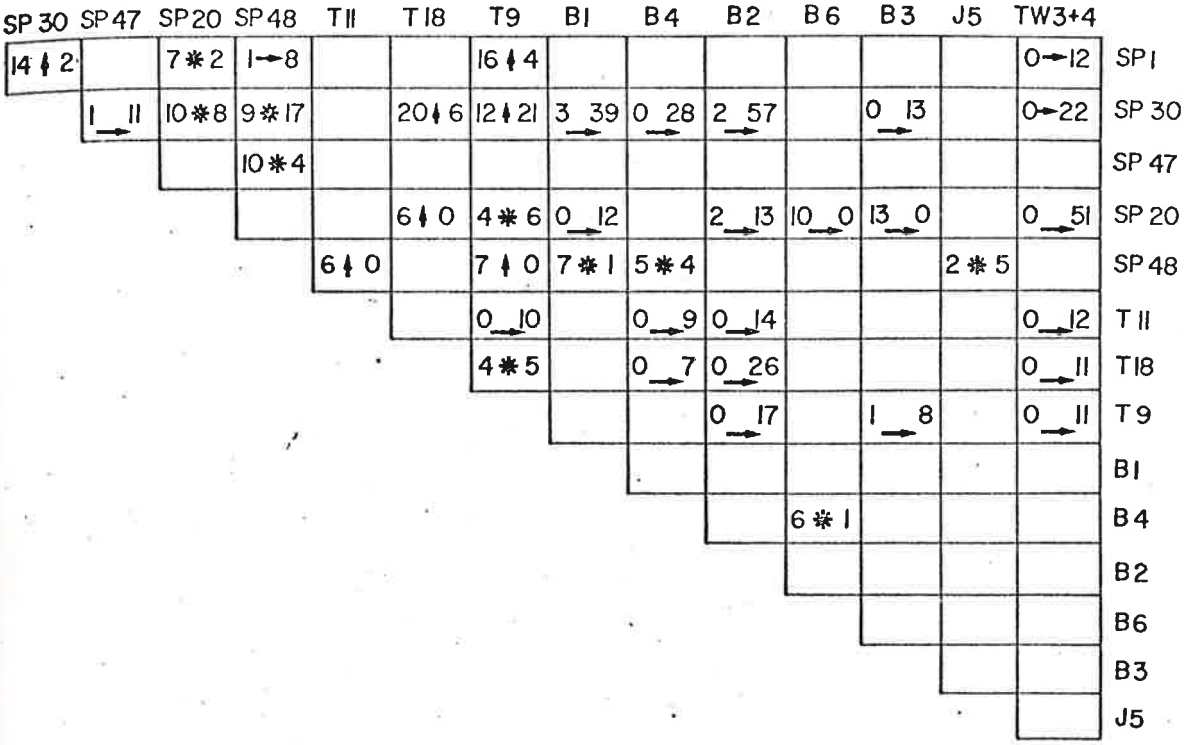

SP 30 SP 47 SP 20 SP 48 T 11 T 18 T 9 B 1 B 4 B 2 B 6 B 3 J 5 TW3+4
14 ↓ 2
7 * 2
1 → 8
16 ↓ 4
0 → 12
SP 1
1 → 11
10 * 8
9 * 17
20 ↓ 6
12 ↓ 21
3 → 39
0 → 28
2 → 57
0 → 13
0 ← 22
SP 30
10 * 4
SP 47
6 ↓ 0
4 * 6
0 → 12
2 → 13
10 → 0
13 → 0
0 → 51
SP 20
6 ↓ 0
7 ↓ 0
7 * 1
5 * 4
2 * 5
SP 48
0 → 10
0 → 9
0 → 14
0 → 12
T 11
4 * 5
0 → 7
0 → 26
0 → 11
T 18
0 → 17
1 → 8
0 → 11
T 9
B 1
6 * 1
B 4
B 2
B 6
B 3
J 5

Figure 4.9. Fluctuations in S with time on Pinna shells which bore tunicates at some stage of the experiment. A closed triangle denotes a point at which a tunicate recruited; an open triangle a point at which a tunicate died.

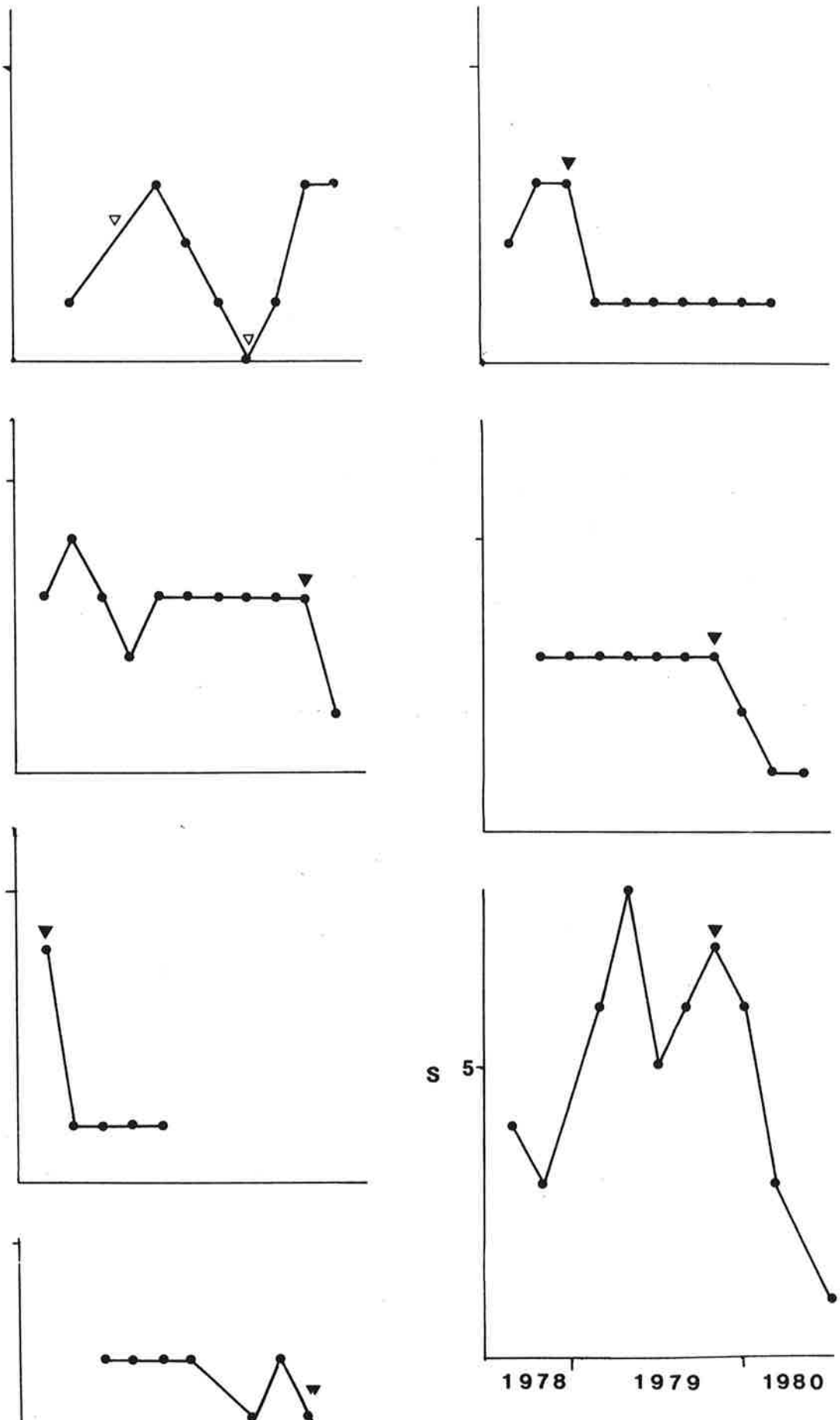

S
5
1978
1979
1980

Figure 4.10. Fluctuations in S with time on Pinna shells which bore sponges at some stage of the experiment. Closed triangles denote a point at which a sponge recruited; open triangles points at which a sponge died. Note that on one shell, the death of a sponge was followed by the recruitment of a tunicate colony (denoted by "T" on the figure).

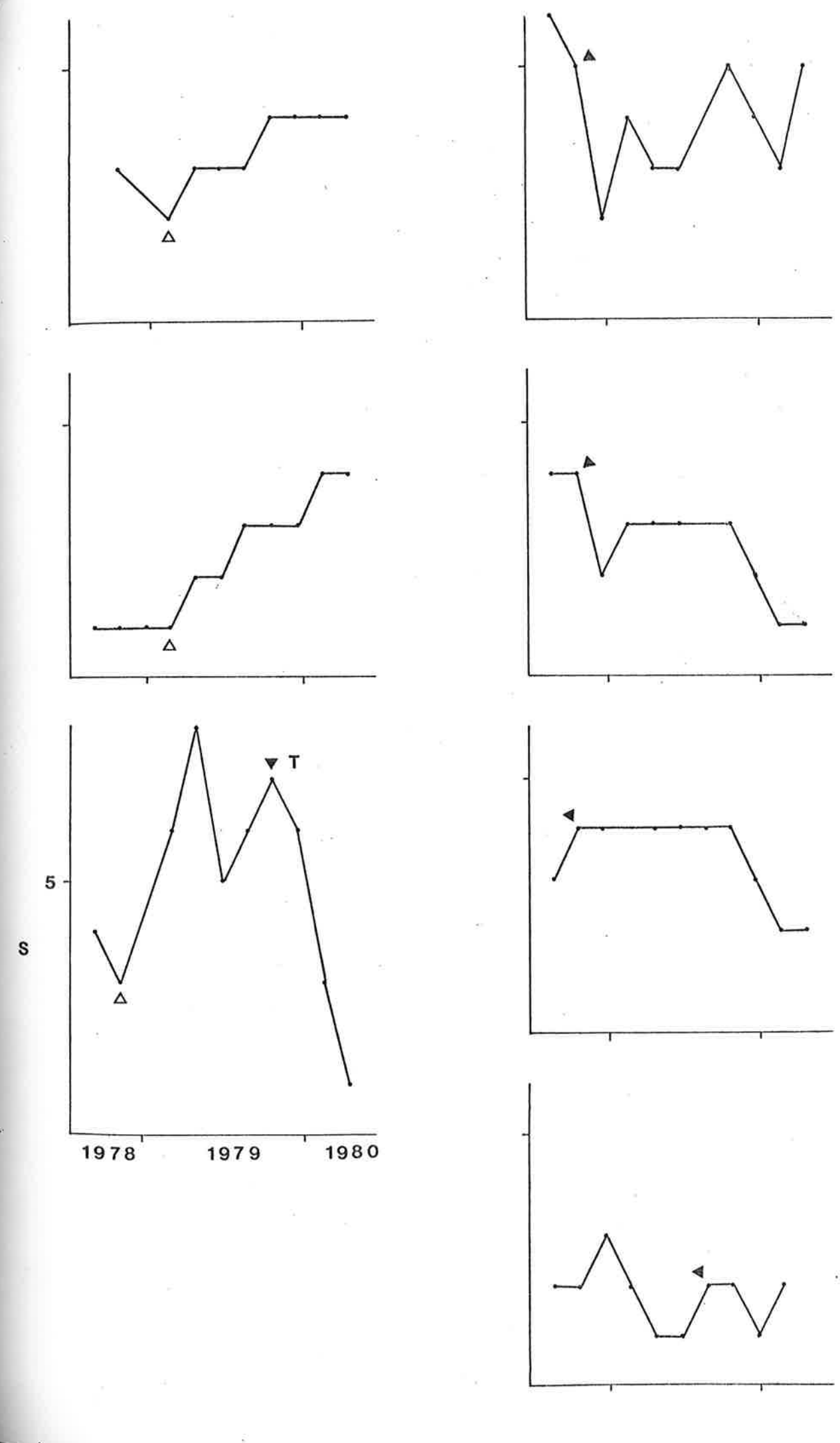

T
5
S
1978
1979
1980

Figure 4.11 Design of cages used in caging experiment. All dimensions are in centimetres.

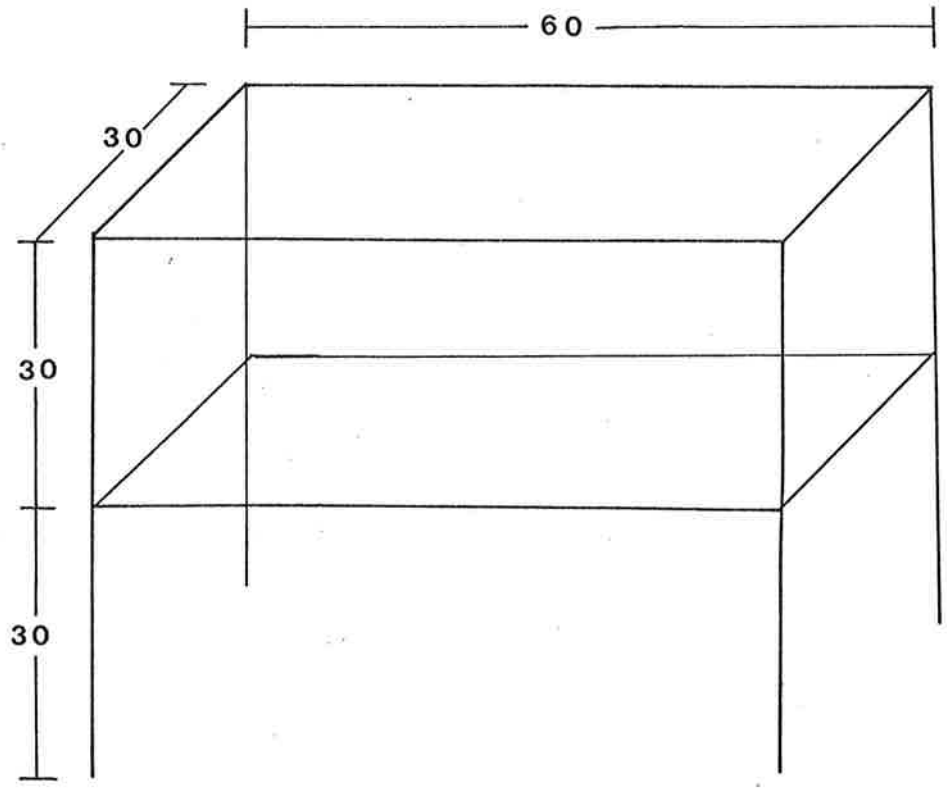

60
30
30
30

Figure 4.12 Number of fish seen along a transect through the Edithburgh study grid during 1979-80.

A - Eubalichthys mosaicus (●) and Brachaluteres jacksonianus (○)

B - Parequula melbournensis

C - Neoodax sp.

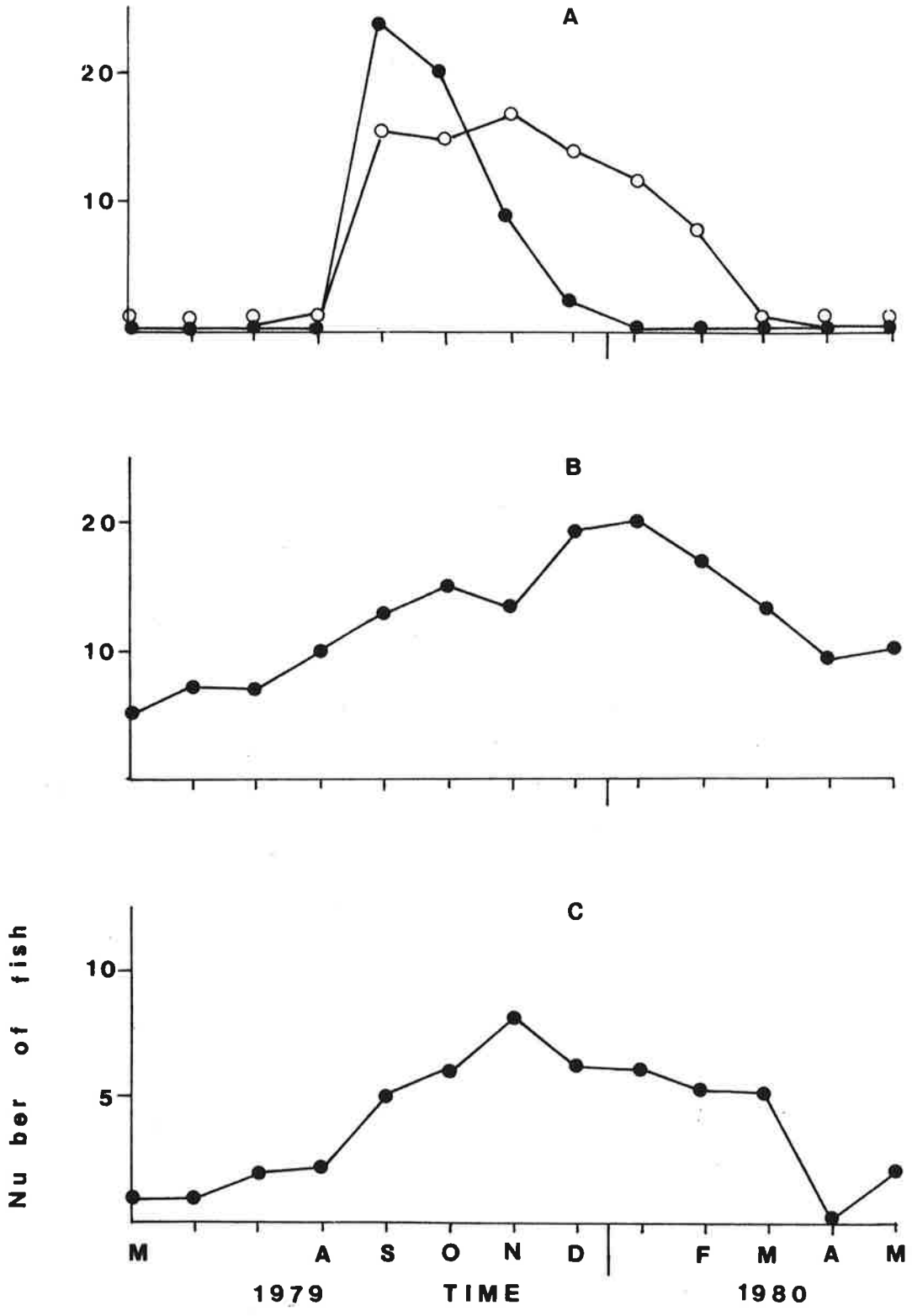

A
20
10
B
20
10
C
10
5
Nu ber of fish
M
A
S
O
N
D
F
M
A
M
1979
TIME
1980

Figure 4.13 Change in bryozoan abundance with time. Points are means ± s.e.. In all cases, s.d.s were approximately equal to means.

● - uncaged Pinna

○ - Uniophora included

■ - gastropods included

△ - all predators excluded

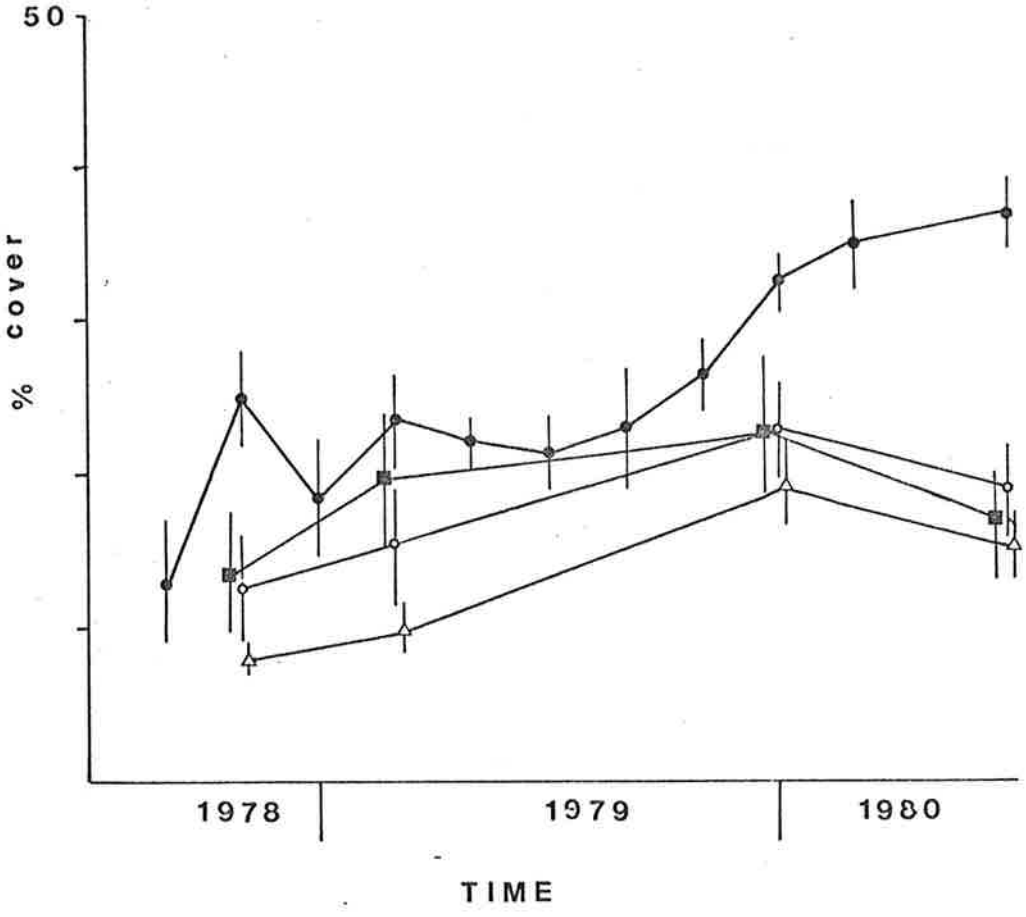

50
% cover
1978
1979
1980
TIME

Figure 4.14 Percentage of caged (■) and uncaged (□) Pinna shells on which the fluctuations in S have a critical w less than or equal to a given w, plotted against w.

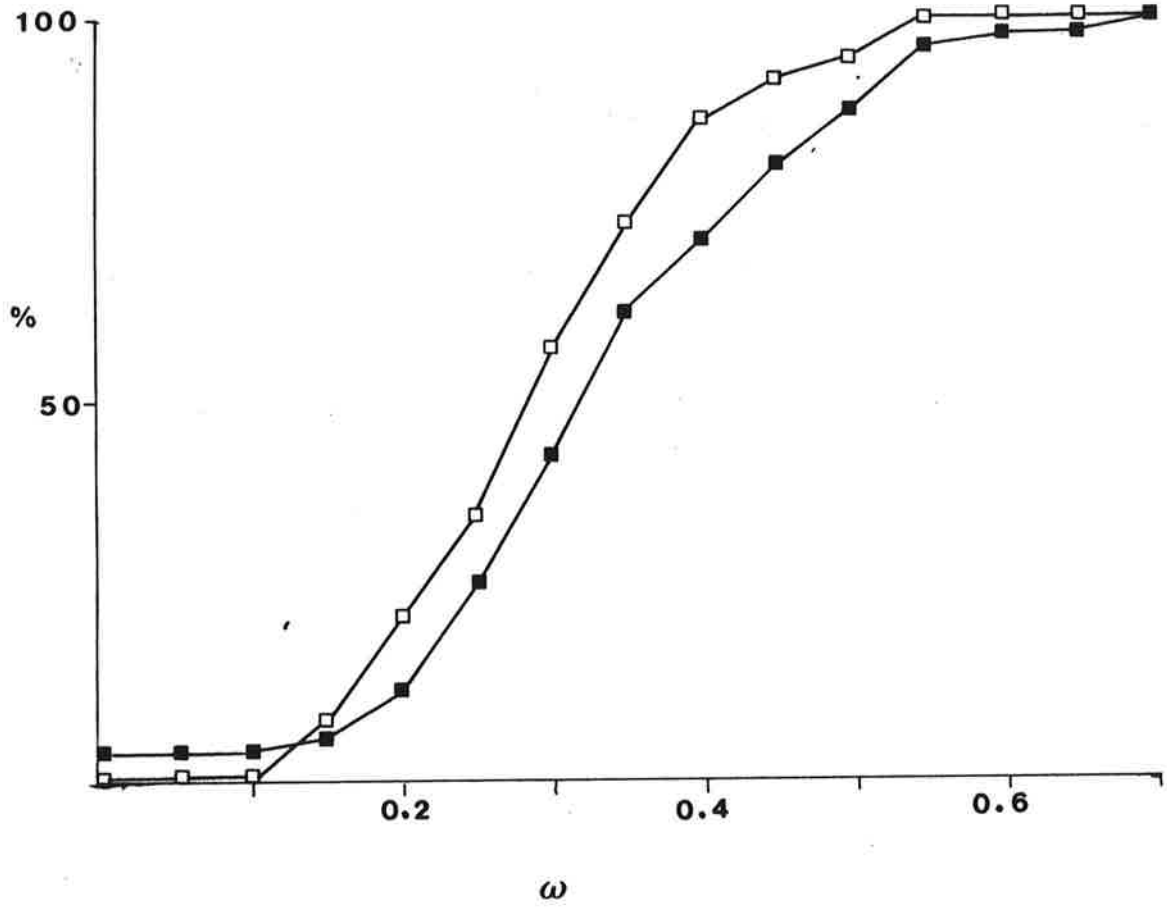
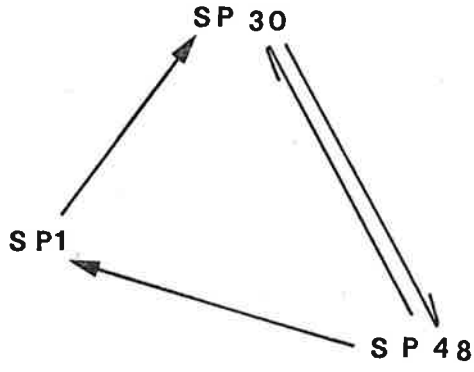

100
%
50
0.2
0.4
0.6
ω

Figure 4.15 Non-hierarchical overgrowth patterns. Arrows indicate the direction of dominance, half-arrows indicate competitive equivalences. SP1 is Aplysilla rosea, SP20 Mycale, SP30 Crella, and SP48 an unidentified sponge species. T9 is Didemnum sp. A, T18 is a didemnid species.


SP 30
SP1
SP 48

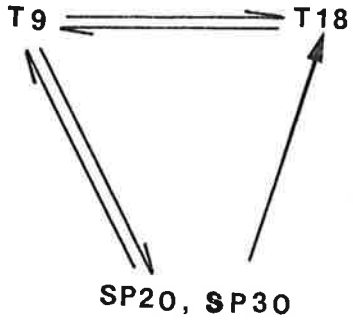
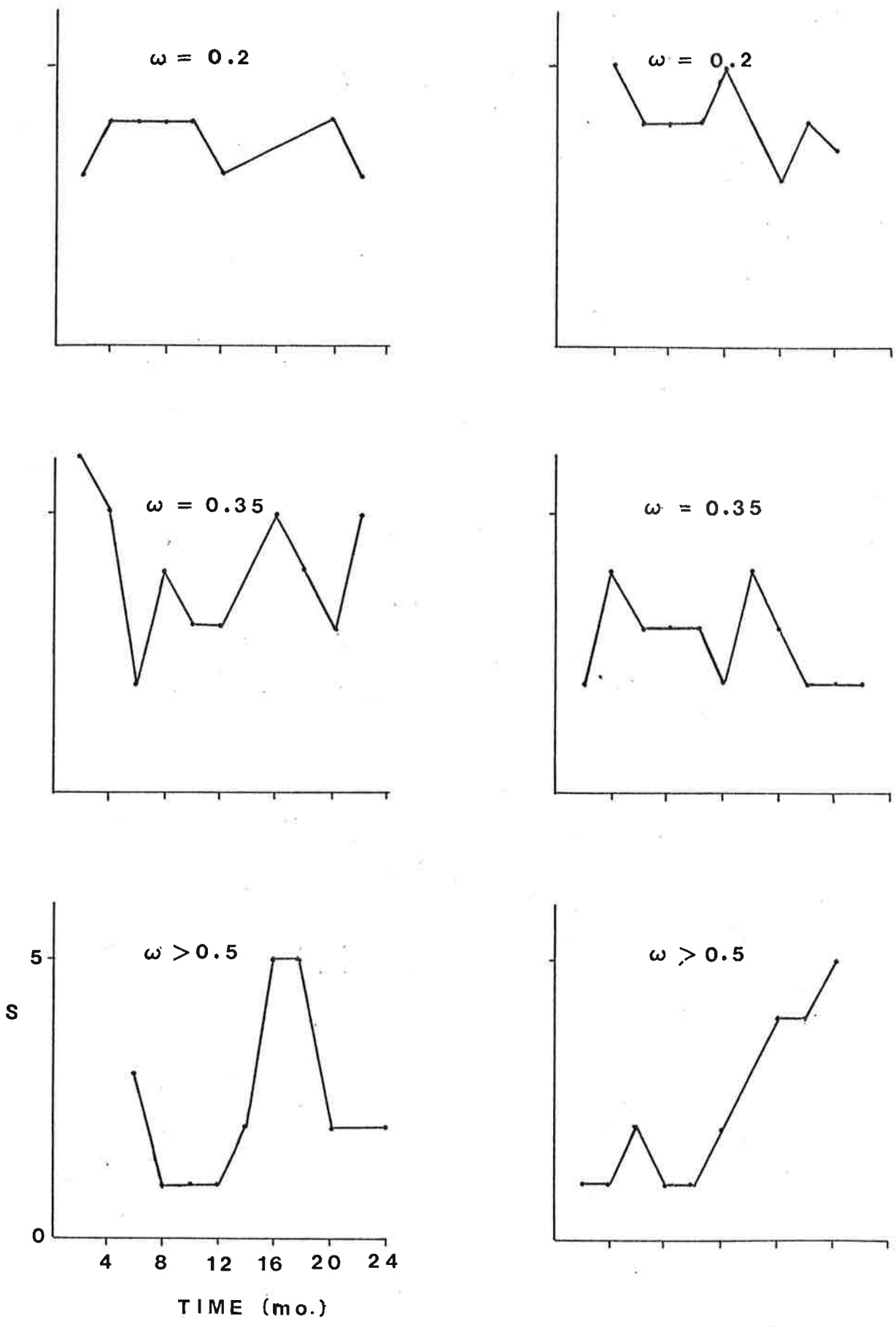

T9
T18
SP20, SP30

Figure 4.16 Samples of fluctuations in S for six uncaged Pinna, spanning a range of critical w values. The value shown on each graph is the value of the critical w.


ω = 0.2
ω = 0.2
ω = 0.35
ω = 0.35
ω > 0.5
ω > 0.5
S
5
0
4
8
12
16
20
24
TIME (mo.)

5. AN ALTERNATIVE MODEL FOR PATCH DYNAMICS AND A TEST OF IT

5.1 INTRODUCTION

The epifaunal assemblages on *Pinna* shells can be relatively easily understood. *Pinna* shells are not the only pieces of available substratum at Edithburgh, however. Hard substrata range in size from large rock walls and overhangs tens or even hundreds of square metres in area down to small rocks and mollusc shells a few square centimetres in area. Any theory which purports to explain the nature of species assemblages in patchy environments must consider a range of patch sizes, since most patchy environments have ranges of patch sizes of at least two orders of magnitude (see Connor and McCoy 1979 for examples). The numbers of species will differ between patches of different sizes (Chapter 1) and hence there will be differences in the frequency of encounters with other species. There is the possibility that biologically derived selective pressures may vary between patch sizes, so that changes in the behaviour of individual species may occur in evolutionary time. It is thus possible that larval behaviour, growth form, etc., may vary with patch size.

In conducting experiments on ecological time scales, we are only able to observe the end result of such evolutionary changes. Nevertheless, the selective pressures may still be operating, and it is possible that the events on a series of patches of a given size can only be understood fully by investigating the events on a wide range of patch sizes.

There is evidence that in some marine epifaunal communities the assemblage of species on a series of patches differs with patch size. Jackson (1977b) suggested that in a cryptic coral reef community, community structure varied with the size of coral heads to which the epifauna were attached. Kay and Keough (1981, see Appendix 2) reported marked

differences in the abundance of broad groups of sessile fauna. On pier pilings, sponges and tunicates are abundant, whereas *Pinna* shells bear what is mainly a bryozoan/serpulid assemblage (see Figure 5.1).

Jackson (1977b) suggested that on small substrata, the number of species is reduced, and so for a poor interference competitor, the probability of deleterious competitive interactions is reduced. Poor competitors could then monopolize a small substratum and prevent further invasion. He also suggested that the number of panels colonized by a given species increased with panel size, except for one species, the ascidian *Diplosoma macdonaldi*. There were no counts of the number of settling larvae, and it was thus impossible to know whether the differences resulted from aggregative settlement, low settlement rate, different settlement behaviour, or differential mortality of juveniles.

Jackson's data, however, showed that small isolated patches had higher initial percent cover than large, and this difference persisted, although to a lesser degree. If this is the case, a poor competitor would survive better by settling on a large substratum, since more free space is available. Data were only given for sponges and serpulids but sponges were most abundant on small to medium-sized patches. Sponges are superior competitors to serpulids, and so again, panels which have a high cover of sheet-like sponges would appear to be rather poor as refuges from competition! A possible explanation for his patterns of abundance can be found by considering within-patch patterns of settlement.

On a small patch, irrespective of where a larva of a colonial species settles, it will grow and occupy the patch quickly. On large substrata, larvae may settle gregariously (Chapter 3) so that 'bare' patches are present on the substratum. These will remain open for some time, so that percent cover will be lower.

Kay and Keough (1981) suggested that at Edithburgh the good competitors do not recruit in large numbers (see also Chapter 3), so that on *Pinna*, the probability of a shell being colonized by, for example, a tunicate, is about 0.01 yr^{-1}. When a patch is colonized by a good competitor, it will exclude most other species. Poor competitors generally produce more larvae and so the probability of their colonizing a *Pinna* shell is high. We would thus expect a series of small substrata to be occupied mainly by bryozoans, with occasional patches dominated by tunicates or sponges. Larger substrata have an increased chance of being colonized by a good competitor, say $\sim$0.7-1.0 yr^{-1}, so that most large patches will be dominated by good competitors.

The differences between the fauna of pier pilings and *Pinna* were consistent with this model, but differences in substratum type, light intensity, etc. made this a non-critical test of the model. The original model was not well defined, and only considered patches of the "habitat island" type. Clearly, patches will have varying degrees of isolation, and a model can be developed which incorporates patch isolation as well as patch size. In the following account, two types of patch will be considered; isolated patches, and those which are cleared in the sessile fauna. The model will be generalized to consider a continuum of patch sizes and isolations.

As mentioned in previous chapters, huge variations in species composition of individual patches make models make predictions about individual species difficult to apply. I intend to consider the abundance of higher taxa but it should be borne in mind that the identities of the individual species within any patch remain highly variable.

Consider the competitive and colonizing abilities of the major groups (Table 5.1). Consider also four types of patch:

(1) small and isolated

(2) large and isolated

(3) small, non-isolated patches (i.e. interconnected)

(4) large, non-isolated patches (i.e. interconnected)

The information in Table 5.1 can be used to make predictions about the events within individual patches of each of the above types. Predictions can similarly be made about the mean abundance (i.e. percent cover) of each of the major taxa over all patches of a given type, and qualitative statements can be made about the expected variances of these abundances.

Small, isolated patches

High probability of colonization by poor competitors (bryozoans and serpulids). Low probability of colonization by good competitors (sponges and tunicates).

Most patches of this type will be occupied by poor competitors, with a few occupied by good competitors, which have excluded the poor competitors. Between-patch variance will be relatively low. A more detailed treatment of between-patch variance is given in the methods section of this chapter.

Large, isolated patches

High probability of colonization by poor competitors. Also high probability of colonization by good competitors, since with larger area, the probability of encounter by a larva increases on passive sampling grounds (i.e. assuming no habitat selection) alone. All or almost all patches will be colonized by poor competitors, which will persist for some time. Most patches will also be colonized by good competitors, which will subsequently exclude the poor competitors. In time, most patches will be dominated by good competitors, and between-patch variance will be relatively low. Disturbance may overlay this

process, delaying the removal of poor competitors, and increasing between-patch variability.

Small, non-isolated patches

High probability of colonization by poor competitors. Invasion by adjacent adults is now allowed, so that there is a high probability of invasion by good competitors. In most patches, no colonists survive, so that poor competitors are quickly excluded and the patches are dominated by good competitors. Between-patch variance will be low.

Large, non-isolated patches

High probability of colonization by all groups. Invasion by good competitors is largely from the edge of the patch, and so some time is necessary for the patch to become completely occupied. Kay and Keough (1981) have shown that small non-isolated patches are occupied more quickly than are large. Poor competitors will persist for longer before being excluded. Again, with large patch size, events become more predictable, and so between-patch variance will be relatively low.

The above model deals only with extremes of patch types, and of course a continuum is more realistic. Patches will be isolated from each other by backgrounds which vary greatly in the ease of crossing. Similar arguments may be applied to any patch size. Using the above reasoning, it is possible to make predictions about the abundance of different groups of epifauna as a function of patch size (Figure 5.2).

Variances would be expected to be highest at intermediate patch sizes. The abundances of poor competitors will be influenced strongly by the abundance of good competitors, and so variances in abundance of poor competitors will be maximal when the between-patch variance of good competitors is highest. For isolated patches, this will be when patch size is intermediate, i.e. as the probability of

colonization by good competitors reaches 0.5. More details are given in the methods section.

For non-isolated patches, variances should also be maximized at intermediate patch sizes. The rate of patch occupation varies with the identities of adjacent species (Kay and Keough 1981); thus with increasing patch size, more species can abut the patch and so we would expect their growth rates to "average out" so that the amount of a large patch occupied in this way should become more predictable. Small patches are occupied relatively quickly, no matter which species abuts. At intermediate patch sizes, patch occupation rates should vary considerably, as few species abut each patch, and the rates of occupation should depend on the growth rate of these few species. Growth rates vary considerably between species (Kay 1980) and so we expect considerable between-patch variation in the abundance of good competitors, and the abundance of poor competitors should be negatively correlated in an individual patch. Thus the between-patch variance can also be plotted as a function of patch size (Figure 5.2). This has some importance with respect to the design and analysis of experiments.

An experiment to test these predictions was conducted using jarrah blocks and cleared patches on the pilings of the pier at Edithburgh.

The predictions about events within patches allow us to make predictions about the distribution of abundances over a range of patch types and sizes. This can be done separately for each major taxon.

Bryozoans

1. Should be more abundant on small isolated patches than large.
2. Should be more abundant on isolated patches than non-isolated.
3. Will be more abundant on large non-isolated patches than small.

Sponges

1. Will be more abundant on non-isolated patches than isolated.

2. Will be more abundant on large isolated patches than small.

3. There should be no strong trend with patch size for non-isolated patches.

Tunicates

Same three predictions as for sponges.

Serpulids

Same as for Bryozoa. Live and dead individuals are difficult to distinguish, and so they will not be considered further.

The Gulf of St Vincent has been present for about 5000 yr (Cook *et al.* 1977), and the family Pinnidae is an old family (Stanley, 1977). There have thus been small isolated substrata and large substrata (rocky reefs) available for settlement and growth by sessile organisms in this region for at least 5000 years, possibly longer. This would appear to be sufficient time for species to evolve habitat selecting behaviour as larvae which allows them to settle preferentially on substrata of different types. Jackson (1977b) mentioned the possibility of such habitat selection, but presented no data. An examination of settlement patterns would seem warranted, since the presence of habitat selection would suggest that small substrata are important for the persistence over long periods of species which are poor competitors.

Logistic problems prevented me from using large *Pinna* shell patches, and so I decided to test the hypotheses in the introduction on the pilings using jarrah blocks.

5.2 EXPERIMENTAL DESIGN

The patch size model makes predictions about the between-patch variances of the percent covers of different kinds of species. I had no *a priori* knowledge of the patch size at which variances could decrease (see Figure 5.2), and so with two or three patch sizes, there was the possibility that an experimental design incorporating analysis of variance on the data could not be significant since variances might be large relative to differences in mean cover.

To illustrate the problem, consider the following:

Let p = probability of colonization by a tunicate.

Consider n patches of each size. Let n = 100.

If a tunicate colonizes, it will monopolize the substratum i.e. 100% cover. All other patches have 0 cover of tunicate.

The mean abundance of tunicates on patches of a given size is then;

$\bar{X}_T = (E(0).0 + E(t).100) / 100$, where

E(0) is the expected number of patches not colonized by tunicates, and E(t) the number colonized by tunicates.

$= (n(1-p).0 + np.100) / 100$

$= np$

Similarly, variance is calculated by

$$V_T = \frac{1}{n-1} (E(0).0^2 + E(t).100^2) - (np^2).n$$

$$= \frac{1}{99} np.100^2 - n^3.p^2$$

$$= \frac{10^6}{99} (p)(1-p)$$

This is simply using E(t) = np, and not considering V_E, which is of the form 100p(1-p). The latter is superimposed on the variance of percent cover, and the following is applicable to both components.

A function of the form $f(p) = cp(1-p)$ is increasing up till $p = 0.5$, then decreasing from $p = 0.5$ to $p = 1$, since $df/dp = c(1-2p)$.

Thus, the mean abundance of tunicates, for example, will increase with patch size, since p should increase with patch size. Variance will also increase with patch size until a patch becomes sufficiently large to have p(T) greater than 0.5. p will not necessarily be a linear function of patch size, so that it is difficult to predict by extrapolation the patch size at which p reaches 0.5. More importantly, the relation between patch size and abundance of tunicates, may be non-linear, so that a graph of the form shown in Figure 5.2 may be obtained. In such a situation, the predicted increase in V_T may produce a violation of an ANOVA assumption (homoscedacity), or at least make rejection of a null hypothesis of no difference in tunicate abundance less likely.

I decided to use a hybrid experimental design. There were only two extreme patch types, namely completely isolated and completely surrounded by other animals, and so analysis of variance was appropriate for testing for differences in abundance between isolated and non-isolated patches. As has been shown, the variance of the abundance of a particular taxon on a particular size of patch is not independent of patch size. The hypotheses mentioned earlier lead to predictions about changes in mean abundances. I therefore used a range of patch sizes, with the knowledge that between-patch, within-size variances would probably preclude analysis of variance.

The hypotheses about differences between patch types were tested by ANOVA, and I included patch sizes so that the analysis was a two-factor ANOVA (patch type by patch size). If significant effects due to patch size were found, the analysis was terminated, since the differences between patch sizes were then of sufficient magnitude to overcome the bias in the data towards retention of a null hypothesis of

no difference between patch sizes. If the hypothesis involved differences in mean abundance with patch size, but no significant treatment effect was found in the ANOVA, I reanalysed the data, because of this *a priori* bias. I then calculated a regression of mean abundance of the taxon in question on patch size as the independent variable. This was done separately for each patch type, and the slope of the regressions tested against a null hypothesis of no difference between the observed slope and zero.

5.2.1 Experimental Methods

On the 13th and 14th of May, 1979, eighty patches were created on the pilings of the pier. Forty were rectangular blocks, constructed of 8 cm wide by 2 cm thick jarrah (*Eucalyptus marginata*) floorboard. Where necessary, sections were joined using the tongue and groove of the wood. The use of floorboards ensured a close-fitting seam on large panels. The panel dimensions are shown on Table 5.2. Seven patch sizes were used; 25 cm^2, 45, 90, 120, 180, 625 and 2500 cm^2. As detailed previously, a range of panel sizes was needed, but the exact areas of these panels were determined by previous work. The 45, 90, and 180 cm^2 panels were chosen to correspond to the recruitment panels used in Chapter 3. The other sizes correspond to the areas of cleared patches in previous experiments on the piling fauna (Kay 1980; Kay and Keough 1981). Replicate numbers are shown on Table 5.1. The low replicate numbers for the larger panel sizes were due to logistic limitations; large panels require correspondingly large time periods for censusing.

All patches were under the eastern quarter of the pier. Only piling columns 3 and 4 were used, and piling rows 3 to 11 (Figure 5.3). This ensured that all piling surfaces were shaded equally by the pier above. All patches were placed in a zone from 0.5 to 2.5 metres from the seafloor, and were on faces of the pilings which faced inwards from the centre of the pier. The pilings were numbered, and the two metre wide zone on each piling divided into four quadrats.

Random number tables were used to allocate patches to piling areas. Each patch on the piling to be cleared was marked at the corners with galvanised nails. A knife was used to cut an outline of the patch, and the sessile organisms were removed with a paint scraper, after which the area was scrubbed clean with a stiff brush. These were designated "non-isolated patches".

The isolated patches were positioned close to the non-isolated patches. The isolated patch was put 45 cm away from the non-isolated patch on one of four random directions; up, down, left, right. The distance of 45 cm ensured that the isolated patch would not affect the growth of organisms surrounding the non-isolated patch. Isolated patches were attached by 10 cm galvanised nails, with a 4 cm thick wooden block on the back of the panel to prevent colonies attached to the pilings from growing along the back of the panel and hence onto the surface of the panel.

The experiment was visited at approximately monthly intervals. For each visit until December 1979, the number of colonists was recorded for both isolated and non-isolated patches. Colonists could be identified to specific level, with the exception of the two bryozoans *Schizoporella shizostoma* and *Membranipora perfragilis*, both of which form small, circular orange colonies. For non-isolated patches, the percent cover for those species which had occupied the patch by vegetative extension of colonies was estimated by dividing the patch into smaller quadrats and estimating the cover in each quadrat.

At four times after commencement of the experiment, panels were photographed from a distance of 0.5 metres using the photographic technique detailed in Chapter 2. The camera quadrat completely enclosed all but the 625 and 2500 cm^2 patches. These were divided into smaller areas, which were photographed in the same way. When the slides were traced, a large composite tracing was made for the large patches. This

had the advantage of keeping sampling efficiency constant.

Slides were traced onto white paper, and percent covers determined by planimeter. The exception to this was the colonial tunicate *Podoclavella cylindrica*, which has a bushy, upright growth form with a small area of attachment. Area of attachment has been measured directly in the field to be 0.5 cm^2 per colony (Kay and Keough 1981).

Percent cover of tunicates, sponges, bryozoans, as well as species number, were analysed by analysis of variance. The experimental design was a two-way factorial with unequal but proportional subclass sizes. Some isolated patches were covered with a canopy of *Podoclavella* which obscured the fauna on the panels. Two isolated panels were overgrown by February 1980, so that up to six panels were missing. Maintenance of a balanced experimental design required removal of the corresponding non-isolated patch from the analysis. In view of previously reported between-patch variation on the pilings (Kay and Keough 1981), I decided that to do this would have reduced replicate numbers too much, and the resulting loss of power in the analyses would have been greater than if I considered all isolated and non-isolated patched as replicates, rather than paired patches. I then used a two-way ANOVA with unequal subclass sizes (Nie *et al.* 1975) to test for differences in species number and the abundances of sponges, tunicates and bryozoans. This analysis was done for each occasion when the patches were censussed photographically, i.e. at 105, 165, 289 and 394 days after the experiment was commenced.

Percent covers were transformed to angles (Sokal and Rohlf 1969, p. 386), and homogeneity of variances determined by the F-max test (Sokal and Rohlf 1969).

In some cases, least squares regressions of mean percent cover against patch size were calculated, and the slopes of the regressions tested against a variety of null hypotheses. These are detailed where relevant in the text. Standard notation is used throughout: the regression equation is

$y = a + bx$; s_b is the standard error of the regression coefficient, and t is the value of the t-statistic for the test of the null hypothesis $\beta = \beta^1$, where β is the true regression coefficient, of which b is the estimate, and β^1 is the hypothesized slope against which the observed slope is to be compared.

5.2.3 Accuracy of estimation of percent covers

In October 1979, patches were censussed both by eye, and also photographically, in order to assess the accuracy of the field estimations. Field-estimated percent covers were treated as the dependent variable, and least-squares regression used with planimeter-determined values as the independent variable. Model I regression (Sokal and Rohlf 1969) was done, since planimeter values are the standard against which other methods of estimating percent cover are usually compared. The fitted regression was

$$y \text{ (field est)} = 1.0015 \times \text{(planimeter)} - 0.9636$$

(Figure 5.4), $r^2 = 0.94$, $n = 43$.

The analysis of variance for the regression is shown on Table 5.3. The field-estimated covers could thus be used as reliable estimates for the true percent cover.

5.3 RESULTS

5.3.1 Species number (S)

Patch size significantly affected species number at all four times (Table 5.4). More species were present on large patches than small at all times (Figure 5.5). For isolated patches, there were more

species colonising large patches than small (Figures 5.6-5.9). In non-isolated patches, the higher S was also because the perimeter of a patch increased with its area, and so more species were adjacent to large patches.

Patch type accounted for a significant amount of variation in species number at 105 and 165 days. Isolated patches had fewer species than non-isolated patches at both of these times (Figures 5.6-5.9). By 289 days, species number was not heterogeneous between patch types. In isolated patches, species number was low initially, remained low during winter, and rose as more colonists became available during spring. It remained steady in most patches after February 1980 (Figures 5.6-5.9). This was because total cover was high in most patches. The occupants of each patch were able to resist further invasion (see Kay 1980). This equilibration of species number was thus due to a lowering of the immigration rate, rather than a balancing of immigration and extinction rates. Extinction rate was zero in many patches, since most occupants were bryozoans, which are frequently unable to overgrow each other (Chapter 4).

Species number had begun to fall off in all replicates of the two largest sizes of patch. This was the result of colonization by good competitors (*Crella, Botrylloides,* and *Didemnum* sp. A), which proceeded to overgrow many other species. The data presented here are sufficient to show only a decrease in S for large patches. Data were collected for a further six months, and will be presented elsewhere. They show that species number declined further on the large isolated patches. Species number also declined on two of the 180 cm^2 patches, and although it did not produce a significant result in the ANOVA after 394 days, the variance of species number is increased.

In non-isolated patches, species number was high initially as a variety of species invaded patches by vegetative extension of colonies

(see Kay and Keough 1981). No colonisation occurred in the four smallest patch sizes, but S was bolstered by colonization in the larger patches. As the patches became occupied, colonists were overgrown, as were any poor competitors, and in many patches, especially small ones, only a single species was left.

S thus rose steadily in isolated patches, and rose initially, but fell subsequently in non-isolated patches. If the large non-isolated patches do allow bryozoans to survive for longer than in small non-isolated patches, it would be expected that the point at which S for non-isolated patches fell below S for isolated patches would occur later with increasing patch size, since declines in S are mainly due to the exclusion of colonising bryozoans.

The crossover point (days from commencement) was calculated, for each patch size from curves of mean species number against time for a given patch size. Linear interpolation was used to estimate the crossover. With the exception of the 25 cm^2 panels, the time until crossover increased with patch size (Table 5.5).

5.3.2 Abundances of individual taxa

Hypothesis 1 Bryozoans should be more abundant on small isolated patches than large.

As mentioned earlier, an increased within-sub-group variance is also expected, and this is likely to obscure any trend in bryozoan abundance. I therefore calculated a regression of mean bryozoan abundance (percent cover) on patch size. The regression statistics are shown on Table 5.8. Regression coefficients were usually positive, but after 394 days, the regression coefficient decreased, although it was still positive. The experiment commenced at a time when recruitment rates for most species were very low. For an individual small patch, the probability of a bryozoan recruiting is so low that most patches

received no recruits. Large patches sample a greater volume of water, so that even with few larvae available, the large panels receive a few recruits, and these grow quickly, so that the abundance of bryozoans is initially higher on large panels.

Percent cover was low for at least 165 days, (Figure 5.24). Sponges and tunicates do not settle until September or October at Edithburgh (Chapter 3; Kay 1980), and they were not recorded on the panels until 165 days after commencement. Many colonists did not survive, and it was not until 289 days that colonies of sponges and tunicates reached five percent cover. At 390 days, there was a marked decline in bryozoan abundance. The further census showed that bryozoan cover declined rapidly in the large patches due to overgrowth by sponges and tunicates (Figures 5.13-5.16), although these latter dates will not be analysed in any further detail.

Hypothesis 2 Bryozoans will be more abundant on isolated patches than non-isolated.

Bryozoan cover did not differ significantly between the patch types, nor vary with patch size after 105 days (Table 5.6). This occurred because patches were created in winter, so that few larvae were in the water, and most patches received no immigrants. At the three censuses after that, there was a highly significant difference between patch types (Table 5.6); bryozoans were much more abundant on isolated patches (Figures 5.10-5.12).

There was a significant heterogeneity between patch sizes at 165 days, but there was no obvious pattern to these differences (Figure 5.10).

Hypothesis 3 Bryozoans will be more abundant on large non-isolated patches than small.

Bryozoan covers were generally low in non-isolated patches, and so it was possible that any effect due to patch size could be swamped by the differences between patch types. I therefore analysed only the data from non-isolated patches, using one-way ANOVA with unequal replication (Sokal and Rohlf 1969). Results are shown on Table 5.6. There was no heterogeneity between patch sizes after 105 days or 289 or 394 days. There was heterogeneity after 165 days, but the distribution of percent covers showed no clear trend.

Percent cover of bryozoans was consistently low in the 180 cm^2 non-isolated patches. This was due to "position effects" (Kay and Keough 1981), since two of these patches were surrounded by *Botrylloides leachii*, which quickly occupied these patches, preventing other animals from settling. The large patch also showed consistently low bryozoan abundance, possibly due to lack of replication.

Although at some times there are trends towards high abundance of bryozoans in larger non-isolated patches, the variation within a given patch size is such that the null hypothesis of no difference cannot be rejected.

Kay (1980) and Kay and Keough (1981) have suggested that bryozoans survive for longer with increasing size of patch in patches cleared on the pilings at Edithburgh. Here, too, between-patch variation was high, and no trend is evident (Kay and Keough 1981, Appendix 2).

Sponges

Hypothesis 1 Will be more abundant on non-isolated patches than isolated.

The results of the analysis of variance for each time period

are shown on Table 5.9. At all times, there was strong heterogeneity in sponge abundance between patch types ($p < 0.001$), but no effect due to patch size. Sponges were consistently more abundant in non-isolated patches (Figures 5.17, 5.18). In most treatments, mean abundance of sponges rose steadily until it reached ≈ 80 percent.

Hypothesis 2 Sponges will be more abundant on large isolated patches than small.

Only two isolated patches were colonised by sponges, and so no analysis could be performed. The two patches which were colonised were 625 cm^2 patches, however.

Hypothesis 3 There will be no strong trend with patch size for non-isolated patches.

The regression coefficients for the regressions of mean abundance on patch size did not differ significantly from zero at any time. Full regression statistics are shown on Table 5.14. The hypothesis is thus retained.

Tunicates

Hypothesis 1 Will be more abundant on non-isolated patches than isolated.

Only four isolated patches bore encrusting colonial tunicates after 394 days. There is thus little point in comparing between patch types, since these tunicates were common in non-isolated patches (Figure 5.26). The hypothesis is therefore retained.

Hypotheses 2 and 3 Tunicates should be more abundant in large isolated patches than small, but there should be no strong trend in non-isolated patches.

Percent cover of tunicates had very high variances even after arcsine transformation had been performed on the percent covers. The Kruskal-Wallis non-parametric analysis of variance was performed separately for each patch type. Tunicates were only abundant from February 1980 onwards (see Chapters 3, 4), and so these analyses were only performed on the data after 289 and 390 days. Results are shown on Table 5.10. The distribution of tunicate covers with patch size after 390 days is shown on Figure 5.19. Least squares regression was performed using untransformed percent covers as before, and the regression coefficients tested by a one-tailed t-test (H_o $\beta = 0$ vs H_1 $\beta > 0$). The isolated patches showed a significant increase with patch size ($b = 0.0099$, $t = 4.7082$, $p < 0.01$), while the non-isolated patches showed no trend ($b = -0.0035$, $t = 0.4069$, $p > 0.5$).

After a further 101 days, the trend was more marked in isolated patches. On the smaller patches, the tunicates quickly grew and occupied 100% of any patch in which they became established. The total amount of space which they could occupy in, for example, the 90 cm^2 patches, was limited by the number of patches colonised. This was generally fairly small, with the result that tunicate cover quickly became asymptotic in small patches. In later patches, cover continued to increase, since more patches of a given size were colonised. At 465 days, for example, the regression slope was 0.0215 ($t = 7.23$, $p < 0.001$).

The hypotheses are thus retained.

Some hypotheses could not be tested due to the rarity of the events concerned. An example is the pattern of sponge abundance on isolated patches. However, the model makes predictions about the abundances of groups of species which are good competitors, but poor

recruiters, and therefore a similar analysis was performed after pooling the abundances of sponges and tunicates. The following species were pooled: Sponges, *Mycale* sp., *Crella* sp., *Aplysilla rosea, A. sulphurea, Tendania* sp. A, SP 5, and SP 55, and *Callyspongia* sp.; Tunicates, *Botrylloides leachii, Didemnum* sp. A, and didemnid sp. B (T 18).

Pooled good competitors

Three hypotheses are erected as for sponges and tunicates.

Hypothesis 1 Will be more abundant on non-isolated than isolated patches.

Two-way ANOVA on arcsine transformed data showed strong differences between patch types, but no heterogeneity between patch sizes. This was true for all times (Table 5.11). The abundance of these species was always greater on non-isolated patches (Figures 5.20, 5.21). Hypothesis retained.

Hypotheses 2 and 3 Will be more abundant on large isolated patches than small but there will be no strong trend for non-isolated patches.

There was no significant increase in the abundance of these species with isolated patch size after 105 days, since none had colonised. There was no significant trend after 165 days ($b = 0.0011$, $t = 0.6147$, $p > 0.25$), but after 289 days, there was a significantly increased abundance of these species with increased patch size ($b = 0.0028$, $t = 7.496$, $p < 0.001$), and this trend became more pronounced after 390 days ($b = 0.0109$, $t = 3.321$, $p < 0.05$).

For non-isolated patches, the abundance of these groups decreased significantly with patch size at 289 days, but showed no trend at all other times. This is explained as follows. The same net amount of growth will produce a larger change in percent cover in smaller patches than large. The smaller patches are quickly occupied,

but the time taken for this is longer in large patches (Kay and Keough 1981). The cover in large patches thus increases with time, and so we expect the relation between mean cover and patch size to have a slope which is negative initially, but which approaches zero with time. Growth of many of these organisms is highest is summer, and the slope of the regressions was low and negative early, and fell very low in October (Figures 5.22, 5.23). It should be noted that if a one-tailed test of the regression slope is used, the slopes at 105 and 165 days also differ significantly from zero.

Hypotheses 2 and 3 are also retained.

5.3.3 Total occupancy of patches

Cleared patches were occupied more quickly than isolated patches (Table 5.11, Figure 5.24). Total cover was higher in non-isolated patches up until 289 days, at which time there was no difference between the two patch types. There was a difference between patch types at 390 days, but the reason for this is difficult to determine, since on inspection of the data, there appears to be little difference between the data at 289 days and that at 390 days, and there appears to be no clear trend in the data.

Small non-isolated patches were occupied more quickly than were large. Least squares regression of mean cover on patch size had a significant negative slope at 105 and 165 days ($b = -0.0136$, $t = 2.98$, $p < 0.05$; $b = -0.015$, $t = 5.0571$, $p < 0.01$, respectively). After this time, there was no significant trend with patch size (289 days; $b = -0.0048$, $t = 0.758$, $p > 0.4$; 390 days; $b = -0.0040$, $t = 1.2574$, $p > 0.10$). Vegetative growth of adjacent colonies into these patches is only possible from the edges, and a greater proportion of small patches is abutted by other colonies, and the net growth into a patch is a greater proportion of a small patch. A similar result has been reported for other work in Gulf St Vincent (Kay 1980; Kay and Keough

1981).

The isolated patches showed no pattern across patch sizes until 289 days, at which time mean cover increased with patch size ($b = 0.0148$, $t = 2.985$, $p < 0.05$). A similar pattern was evident after 390 days ($b = 0.0137$, $t = 3.487$, $p < 0.01$). The reasons for this are covered in the section dealing with bryozoans.

A summary of the relative contributions to the total fauna of each group can be seen on Figure 5.25.

As mentioned earlier, species composition was extremely variable, (Figure 5.26). This was especially true for sponges.

5.3.4 Habitat Selection

Jackson (1977b) and Buss (1979a) have mentioned the potential importance of habitat selection in maximising the chances of survival for a planktonic larva. In this case, where patterns of survival have been shown to differ with patch size and isolation, we might expect, for example, that there would be a selective advantage for bryozoan larvae which select small, isolated patches. Similarly, the better competitors would do better by selecting large substrata.

The major problem in demonstrating habitat selection with respect to size of patch lies in the generation of a null hypothesis against which observed settlement patterns may be tested. If we consider the curve of settlement rate (per unit time) against area, then a number of curves is possible, assuming no active habitat selection by the larvae (Figure 5.27).

Case 1

The probability of a larva encountering a patch is proportional to the area of the patch, for example a soup of larvae drifting along in a current, perpendicular to which is a number of patches. The result is a curve of the form $I = a + bA$, where I is the immigration

rate, and A the area of the patch.

Case 2

The flow of water against a patch creates an eddy, so that larvae remain in the proximity of the patch for longer. This "water backup" might only become effective at larger patch sizes, leading to a curve of the form $I = ae^{bA}$ or $I = a A^{b}$.

Case 3

Similar to case 2, except that the "water backup" asymototically approaches a constant value as patch size increases, producing a sigmoid curve.

These possibilities are not exhaustive, but serve as examples of possible null hypotheses. It is thus difficult to test the settlement patterns of any one group. The different patterns of species abundance on patches of different types allow us to make some tests, however. Bryozoans survive for longer in small patches, and so we might expect them to select substrata which are small. The good competitors, on the other hand, are limited by the size of the patch if they settle in small patches (Kay and Keough 1981; Appendix 2). Their reproductive output is thus lower than a larva which established itself on a large substratum.

There are thus two different settlement patterns predicted, and the presence of habitat selection can be investigated by comparing the recruitment densities of groups of species which are expected to show different settlement patterns, while recalling the relation between settlement and recruitment (Chapter 3). Tunicates and sponges recruited in low numbers, and recruitment was only sufficiently dense during one time period (September-October 1979) to be able to test the patterns of recruitment against those for bryozoans. Rare events are involved and so, for the reasons detailed previously, large and heterogeneous variances are expected. I therefore used the mean number of recruits per patch for each of the seven patch sizes, and divided each value by patch size

to give a density of recruitment for each patch size. The difficulty in generating null hypotheses means that we have *a priori* no preferred regression model, and so non-parametric methods were used. I used the settlement data for the period 22.ix.79 to 17.x.79, a period of 25 days, and recorded the number of established bryozoan colonies and *Didemnum* sp. A colonies. *Didemnum* sp. A settled only at this time. Mean number of colonists per 180 cm^2 was plotted against log of patch size (Figure 5.28). These curves were compared by the Kolmogorov-Smirnov two-sample test (Siegel 1956). They were significantly different ($\chi^2_2 = 6.77$, $p < 0.05$).

Habitat selection is occurring, but the difficulties with null hypotheses do not allow us to say which one(s) are actively selecting patches of particular sizes. It seems most likely that bryozoans at least are selecting actively, for the following reasons. Firstly and trivially, it is difficult to generate a null hypothesis which results in a curve of the form $\frac{df}{dx} = a + bx$; $b < 0$, and so the rule of parsimony suggests that bryozoans are most likely to be deviating from a null hypothesis curve or region (see Figures 5.27, 5.28). Secondly, the literature records many examples of sophisticated habitat selection by bryozoans (e.g. Wisely 1958; Ryland 1959; Gordon 1972, and see further examples in Meadows and Campbell 1972; Scheltema 1974). Few examples of such behaviour are known for tunicates, and these are mostly examples of photonegative behaviour at settlement (Goodbody 1963; Woodbridge 1926; see also Buss 1979a).

If the competitive abilities of the two groups are considered, there would appear to be a greater selective advantage for bryozoans which select habitats than for tunicates. A bryozoan which settles on a large patch will be eliminated quickly, whereas a tunicate which selects a less than optimal patch size will survive, but produce fewer larvae.

5.4 DISCUSSION

It is now possible to review the results of testing the series of hypotheses proposed in the introduction, and from this make some decision about the usefulness of the model. As predicted, bryozoans are more abundant on isolated patches than non-isolated. The prediction of decreased abundance with increased patch size could not be confirmed in the duration of this experiment, but there was a hint of decreased bryozoan cover in larger patches after 464 days.

Predictions about the abundance of bryozoans on non-isolated patches were not borne out. The growth rates of sessile organisms vary widely, so that patch occupation rates also varied. This obscured any trend. An example can be seen in the 45 cm^2 patches. By chance, two of these patches were cleared within a colony of the stony coral, *Culicia* sp. This species grows relatively slowly at Edithburgh, (Kay 1980) so that these patches were closed slowly. Bryozoans were able to persist for some time in these patches. Another patch of the same size was cleared in what appeared to be an area which had been recently cleared by natural disturbance, and so it too was surrounded by bryozoans.

Sponges settled on three patches only during the experiment, and so all that could be said of their abundance is that they were more abundant on non-isolated patches, and showed no trend in abundance with patch size in non-isolated patches.

Tunicates settled more frequently. They showed greater abundance on non-isolated patches than isolated, and their abundance increased with increasing size of isolated patches, but showed no trend for non-isolated patches.

When sponges and tunicates were pooled, the total abundance of good competitors was in accordance with the predictions made.

No attempt was made to investigate between-patch variation, since this experiment was conducted concurrently with others, and I was unable to use any more replicates than were used. The numbers were too small to give estimates of variances within patch sizes which were precise enough to make comparisons between patch sizes.

The model was thus successful in predicting broad patterns of abundance in this community. Several problems need discussion, however.

Firstly, replicate numbers were low for larger patch sizes. The reason for this was mainly logistic. It should be pointed out in defence that the total area of larger patches was greater than that for small patches. The flaw was that the area available as large patches was restricted to a few locations in space. This would be serious in the case of large scale (greater than 10 metres, say) patchiness in the distribution of larvae. The events on a large patch could be determined by an encounter with a plankton patch containing, for example, many bryozoan larvae, and consequently bryozoans would be more abundant than expected on this particular patch. With small replicate numbers, the results of the experiment could be more strongly influenced by this than by biological interactions between adult organisms within the patch. Other work (Kay 1980; Kay and Keough 1981) showed, however, that events within large patches cleared on the pilings are similar, at least on the level of broad taxonomic groups. After two years, all patches of a given size had high abundances of sponges and tunicates, and bryozoans were not very common.

I also had the problem in designing the experiment, of not knowing exactly what a "large" patch was. The graph of abundance of good competitors against patch size is sigmoid (Figure 5.2), but the actual point of inflection can only be determined empirically. I was thus forced to use small numbers of replicates of a range of panel sizes. This was also a design forced by the distribution of variances as

mentioned earlier: the desirable qualities for an analysis of variance design and a regression design differ, and this experiment was a compromise.

The duration of the experiment was only 394 days. This was suggested as the reason why some predictions were not supported. The model was only derived in 1979 and the experiment commenced almost immediately. I have continued to monitor this experiment, and a more comprehensive set of data will be presented at a later date.

Thirdly, only one series of experiments was conducted. The results were for patches created in one season of one year. Kay and Keough (1981) investigated the importance of time of creation of a patch on its subsequent reoccupation. These patches were non-isolated. After twelve months, the total percent cover did not differ between patches which were cleared in February, May, August and December. The shape of the curves of percent cover versus time varied, since most growth and recruitment occurs in late spring to late summer (October to February). Patches cleared in December were thus occupied most quickly, although the end result was the same as for patches cleared at other times.

We might hypothesize that bryozoans would be excluded more quickly from non-isolated patches created in late spring than early autumn. Similarly, large isolated patches would become dominated by good competitors more quickly than in late spring. In this experiment, the effect of clearing patches in winter was only manifested as a period of little growth in isolated patches. In ecological time, the season of creation is not likely to be very important. On an evolutionary time scale, the time of creation of patches is important. The likelihood of habitat selection by bryozoans will be influenced by the selective advantage for a larva which settles in a small patch. If a patch is created in autumn, a bryozoan will have an expected life span of, say,

t_1 days on a small isolated patch, ($t_1 \simeq 1000$) but may only survive for $t_2 \simeq 300$ days on a large isolated patch. If a patch were created in summer, these times would be reduced to, say, $t_1' = 900$ days, and $t_2' = 100$ days, so that the selective differential may be much greater in summer. The advantage of habitat selection behaviour would be much greater if most patches arose in summer than if they were created in winter. In the field, our subjective impression is that most patches are cleared in winter-early spring, when storms are most frequent, although patches are being created constantly by the senescence of old colonies.

There is considerable between-year variation in recruitment patterns (Chapter 3; Kay 1980). However, the hypotheses tested here operate at a level of higher taxa, so that the variations in the recruitment of individual species will be damped by lumping them together in to larger groups. There is no evidence that there are generally good or bad years for the recruitment of all species in general (Chapter 3); rather, for whole phyla, the relative abundances do not change greatly between years. The rates of these processes may change between years depending on which species recruited heavily in a given year, but the end point should be relatively unchanged. Again, the selective advantage of habitat selection would not be constant; if tunicates were settling in large numbers in a given year, the selective advantage for a bryozoan larva which settled on a small substratum would be increased considerably.

5.4.1 Permanency of refugia

Life expectancy of colonies of various species have been estimated at Edithburgh (Kay 1980), and it is of interest to know whether in time all small patches will be monopolised by good competitors, since after becoming established they may recolonise the

same patch as the original colony dies off. Alternatively, the colonisation rate may be so low relative to the colony life spans that there is a constant supply of small patches which are not occupied by good competitors. The distinction is important in considering whether small patches act as refuges in ecological or evolutionary time. If poor competitors are to persist in moderate to high abundances, the first of these alternatives requires a much higher rate of patch formation than the latter. The low recruitment rate of *Pinna* makes this distinction important, since this is likely to be the major source of new small isolated patches. The piling experiment was too short to allow any assessment of the probability of all small isolated patches being monopolised eventually, but since the most abundant small isolated substrata are *Pinna*, I will consider the combination of recruitment rate and longevity for their epifauna. As mentioned earlier, the tunicate *Didemnum patulum* may live for 5-7 years. This is the only good competitor for which good data exist on *Pinna*, but this is similar to the figures for piling species derived by Kay (1980). If we then consider colonisation rates for panels in the study grid and on uncaged *Pinna*, a probability of 0.01 $year^{-1}$ for the establishment of a tunicate colony seems reasonable. The actual settlement rate is of course much higher, but it is recruitment which is important. Then, in a given year, we expect about 1% of *Pinna* shells to gain tunicate colonies. This is about the observed figure. Further, the dying off of various tunicates during the experiment, together with the observation that even in a good year, the probability of establishment is probably less than 0.03, suggest that the proportion of shells occupied by tunicates never becomes very large. Thus, *Pinna* probably provides a permanent supply of spatial refuges at Edithburgh.

In order to extrapolate from the results of the piling experiment to *Pinna*, we need to compare recruitment rates onto piling patches of

various sizes with recruitment rates into panels of the same size in the study grid. These experiments allow comparisons to be made between the 45, 90 and 180 cm^2 panels for identical periods of time. I was only able to count recruitment onto the isolated jarrah patches for two months after commencement. After that, recruitment rates were higher, and I was unable to distinguish new recruits from old. As space became occupied, the area for settlement decreased, and the space occupied varied between patches, so that the actual amount of space available for larvae to settle varied between patches, and was certainly less than the area of the patch.

I compared recruitment between piling and grid patches by first transforming counts of recruits (x) to $\sqrt{(x + 0.5)}$, which Sokal and Rohlf (1969) suggest is appropriate to standardise the variances of counts. Two-way ANOVA was then performed using unequal subclass sizes, since again I could not afford to exclude replicates from the analysis. The two treatments were panel type: pilings or grid, and panel size: 180, 90 or 45 cm^2. Recruitment was much greater onto piling panels than onto those in the study grid (Tables 5.12, 5.13). Tunicates did not recruit sufficiently frequently to be analysed separately. Part of this was because I measured recruitment and many of the tunicate larvae were eaten before censussing. Nevertheless, recruitment was greater onto the piling panels. Serpulids did not differ between panel types.

The probability of colonisation by a good competitor would thus appear to be much lower for *Pinna* in the study grid than for isolated patches on the pilings. The reason for this is unclear. It may be a true distance effect, since some tunicates, for example, have short planktonic stages (e.g. *Botrylloides leachii*, (Brunetti 1976)). Alternatively, the pilings may be encountered by more larvae because of their size. These larvae may then search over a substratum seeking bare space. The increased recruitment could thus be an artifact of the

patches' being attached to the pilings. I was unable in the time available to investigate the reasons for these differences.

It is notable that *Pinna* beneath the pier also seem to have a higher incidence of tunicates and sponges than do *Pinna* in the study grid.

It is sufficient to say that the persistence of bryozoans and serpulids is likely to be even greater on *Pinna* than on the piling patches. The abundance of bryozoans on *Pinna* shells is thus more readily understood by viewing *Pinna* shells as one of a range of substrata at Edithburgh. The patch model which was developed makes reasonably correct predictions about the assemblages in various patches. It has the advantage of being stochastic, and acknowledging that predictions at the level of individual species cannot be made accurately. It is a model on one trophic level only (sessile filter feeders), and is thus limited.

We can modify the model to take account of changes in the overall rates of recruitment in a habitat, as follows.

The level of recruitment is likely to be of some importance. Consider a habitat in which the probability of a patch of a given size being colonised by the larva of a good competitor is much higher than at Edithburgh. Then, all patch sizes would have a higher frequency of occurrence of good competitors. On the large patches, we would expect large to moderate numbers of colonies, and the size that a given colony attains will probably be limited by the colonies that surround it. On a slightly smaller patch, a colony of the same species will be limited by the physical size of the patch, since with a smaller patch, the probability of colonisation by a good competitor is lower, and as patch size becomes small, patches are likely to have only one colony of a good competitor. This colony will be able to overgrow the poor competitors, and so will be the only colony left on the patch. We can then compare two colonies of the same size, one of which is surrounded by other species, the other occupies the whole patch.

The two colonies would have access to approximately the same amount of food, although it is possible that the colonies on the large patch would compete for food, as shown by Buss (1979b) for bryozoans. The comparison then is between two colonies, both with approximately the same energy intake, but one of the colonies must expend energy in combatting other species. The energy available for the production of larvae is thus likely to be greater for the colony on the smaller patch. Therefore, with increased recruitment rate, the optimal patch size for good competitors would be decreased, resulting in a curve as shown on Figure 5.2. The optimal patch size for poor competitors is determined primarily by the patterns of abundance of good competitors. In the above example, the fitness of poor competitors will be decreased across all patch sizes, as good competitors become more abundant. The shape of the curve of fitness against patch size is likely to be changed, also, because of the change in the shape of the curve for good competitors (see Figure 5.2).

In the following chapter, this model will be discussed in more general terms, and its potential applicability to other patchy systems considered.

TABLE 5.1 Recruitment and competitive abilities of the major higher taxa.

Taxon	Recruitment level	Competitive ability
Tunicates	Moderate-poor	Very Good
Sponges	Poor	Good
Bryozoans	Good	Poor
Serpulids	Very Good	Very Poor

TABLE 5.2 Panel sizes and replicate numbers.

Panel	Dimensions (cm)	Area	No. Replicates
1	5 x 5	25	10
2	7.5 x 6	45	9
3	11.5 x 8.0	92	6
4	12 x 10	120	6
5	15 x 12	180	6
6	25 x 25	625	2
7	50 x 50	2500	1

TABLE 5.3 ANOVA table for regression of eye-estimated % cover on planimeter determined covers.

Source	df	SS	MS	F	P
Explained	1	66165.56	66165.6	2902	***
Unexplained	42	957.6	22.8		
Total	43	67123.16			

$r^2 = 0.94$

TABLE 5.4 Analysis of variance table for species number.

Data are the number of species on isolated/non-isolated patches of seven sizes. ns, non-significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

(1) July 1979

Source of variation	df	SS	MS	F
Subgroups	7	143.30	20.47	29.55 ***
Patch type	1	60.88	60.88	87.87 ***
Patch size	6	82.11	13.69	19.75 ***
Interaction	6	35.73	5.96	8.59 ***
Residual; error	61	42.26	0.69	

F-max = 11.50, ns

(2) October 1979

Source of variation	df	SS	MS	F
Subgroups	7	223.80	31.97	12.61 ***
Patch type	1	12.22	12.22	4.82 *
Patch size	6	210.36	35.06	13.83 ***
Interaction	6	21.97	3.66	1.45 ns
Residual; error	59	149.56	2.54	

F-max = 5.97, ns

TABLE 5.4 continued.

(3) February 1980

Source of variation	df	SS	MS	F
Subgroups	7	178.65	25.52	8.82 ***
Patch type	1	5.56	5.56	1.92 ns
Patch size	6	172.48	28.75	9.93 ***
Interaction	6	26.55	4.43	1.53 ns
Residual; error	58	167.81	2.89	

F-max = 4.37, ns

(4) May 1980

Source of variation	df	SS	MS	F
Subgroups	7	209.43	29.92	11.39 ***
Patch type	1	0.93	0.93	0.35 ns
Patch size	6	207.52	34.59	13.18 ***
Interaction	6	33.74	5.62	2.14 ns
Residual; error	54	141.89	2.63	

F-max = 10.73, ns

TABLE 5.5 Time for species number on isolated panels to exceed that on cleared patches for different size patches.

Patch Size	Time (days)
25	170
45	90
96	100
120	130
180	180
625	390+
2500	390+

TABLE 5.6 Analysis of variances tables for bryozoan abundance. Data were percent covers of bryozoans on isolated/non-isolated patches of seven sizes. Percent covers were transformed by arcsine$\sqrt{p}$.
ns, non-significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

(1) July 1979

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	102.42	14.63	0.81 ns
Patch type	1	44.02	44.02	2.43 ns
Patch size	6	58.10	9.68	0.53 ns
Interaction	6	54.71	9.12	0.50 ns
Residual; error	61	1105.55	18.12	

F-max = 146.23*

(2) October 1979

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	2311.72	330.25	3.106 **
Patch type	1	758.74	758.74	7.147**
Patch size	6	1566.86	261.14	2.46 *
Interaction	6	1068.69	178.12	1.68 ns
Residual; error	60	6378.89	106.32	

F-max = 154.55 **

TABLE 5.6 continued.

(3) February 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	19698.95	2814.14	10.564 ***
Patch type	1	16710.01	16710.01	62.73 ***
Patch size	6	2810.76	468.46	1.76 ns
Interaction	6	1004.18	167.36	0.63 ns
Residual; error	57	15184.31	266.39	

F-max = 115.51 *

(4) May 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Sub groups	7	19056.41	2722.34	9.83 ***
Patch type	1	17287.88	17287.88	62.43 ***
Patch size	6	1516.26	252.71	0.91 ns
Interaction	6	1056.59	176.10	0.64 ns
Residual; error	54	44812.60	668.84	

F-max = 154.55**

Results of one-way ANOVAs (unequal replication) on bryozoan abundance in non-isolated patches at four different times. Only the value of F = MS (between patch sizes)/MS (error), the associated degrees of freedom, and the probability level are shown.

Time	F	df	P
July 1979	1.73	6,24	ns
October 1979	4.32	6,23	**
February 1980	0.79	6,22	ns
May 1980	2.13	6,20	ns

TABLE 5.7 Regression of bryozoan cover on patch size for non-isolated patches.

Non-isolated

$H_o : \beta = 0; H_1 \beta > 0$

Time	r^2	a	b	s_B	t	P
10/79	.2465	4.1076	-.0015	.0012	-1.2791	>0.9
2/80	.0102	4.538	.0002	.0010	.2266	>0.4
5/80	.03	7.716	-.0010	.0026	-.4057	>0.5

TABLE 5.8 Regressions of bryozoan cover on patch size for isolated patches.

$H_o : \beta = 0; H_1 \beta < 0$

Time	r^2	a	b	s_B	t	P
10/79	.0524	8.0071	.0018	.0034	.5257	>0.8
2/80	.5172	53.09	.0099	.0043	2.3142	>0.99
5/80	.39	55.68	.0070	.0040	1.7750	>0.80

TABLE 5.9 Analysis of variance tables for percent cover of sponges. Data were percent cover of sponges on isolated/non-isolated patches of seven sizes. Data were transformed to arcsine$\sqrt{p}$.

ns, non significant; *, $p < 0.05$, ** $p < 0.01$; *** $p < 0.001$.

(1) July 1979

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	14053.37	2007.62	5.209 ***
Patch type	1	12809.48	12809.48	33.171 ***
Patch size	6	1274.52	212.42	0.55 ns
Interaction	6	1274.52	212.42	0.55 ns
Residual; error	61	23555.72	386.16	

F-max = 74.97 *

(2) October 1979

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	12175.93	1739.42	4.504***
Patch type	1	10328.33	10328.33	26.75 ***
Patch size	6	1878.51	313.09	0.81 ns
Interaction	6	1878.51	313.09	0.81 ns
Residual; error	61	23555.72	386.16	

F-max = 163.25 ns

TABLE 5.9 continued.

(3) February 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	37559.36	5365.62	11.93 ***
Patch type	1	33854.96	33854.96	75.25 ***
Patch size	6	3291.78	548.63	1.22 ns
Interaction	6	3693.25	615.54	1.37 ns
Residual; error	58	26095.00	449.91	

F-max = 288.86 *

(4) May 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Subgroups	7	33711.59	4815.92	9.99 ***
Patch type	1	32231.84	32231.84	66.88 ***
Patch size	6	1567.84	261.31	0.54 ns
Interaction	6	2185.02	364.17	0.76 ns
Residual; error	59	28436.00	1303.13	

F-max = 2529.63 **

TABLE 5.10 Kruskal-Wallis analysis of variance on untransformed tunicate cover after 289 and 394 days.

Patch type	Time	H	Prob.
Isolated	2/80 (289 days)	4.824	>0.05
"	5/80	13.3617	<0.05
Non-isolated	2/80	4.45	>0.05
"	5/80	14.37	<0.05

TABLE 5.11 Analysis of variance for abundance of good competitors. Data were percent covers of sponges and tunicates on isolated/non-isolated patches of seven sides. Numbers were transformed to arcsine$\sqrt{p}$.

(1) July 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Patch type	1	16935.3	16935.3	45.727 ***
Patch size	6	1710.896	285.15	0.770 ns
Type and Size	6	1534.135	255.689	0.690 ns
Error	60	22221.5	370.358	
Total	73	59227.2		

F-max = 27.28 $p > 0.05$

(2) October 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Patch type	1	20614.5	20614.52	48.372 ***
Patch size	6	1191.428	198.57	0.466 ns
Type and Size	6	2842.6	473.768	1.112 ns
Error	58	24717.4	426.16	
Total	71	74500.7		

F-max = 217.9 **

TABLE 5.11 continued

(3) February 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Patch type	1	1154.7	1154.7	3.486 ns
Patch size	6	953.0	158.8	0.479 ns
Type and Size	6	4662.7	710.5	2.145 ns
Error	56	18551.8	331.3	
Total	69	294477.9		

F-max = 235.61 **

(4) May 1980

Source of Variation	df	Sum of Squares	Mean Square	F ratio
Patch type	1	1814.77	1814.8	7.334 **
Patch size	6	516.7	86.1	0.348 ns
Type and Size	6	2811.3	468.5	1.893 ns
Error	53	13115.5	247.5	
Total	66	22963.6		

F-max = 243 **

TABLE 5.12 Comparison of bryozoan and serpulid recruitment to grid panels and piling panels of different sizes.

Bryozoans

Source	df	MS	F
Main effects	3	27.325	91.75 ***
Patch position	1	79.160	265.795 ***
Patch size	2	6.278	21.08 ***
Interaction	2	6.587	22.16 ***
Residual	101	0.298	-

Serpulids

Source	df	MS	F
Main effects	3	10.425	7.679 ***
Patch position	1	2.767	2.039 ns
Patch size	2	12.693	9.349 ***
Interaction	2	1.373	1.011 ns
Residual	101	1.358	

TABLE 5.13 Recruitment of bryozoans, serpulids and tunicates to piling and grid panels at Edithburgh from 22.vii.79 to 22.ix.79. Mean recruits per panel ± S.D.

Patch size	Patch Position	Bryozoans	Serpulids	Tunicates
180 cm^2	grid	.03±.17	8.4±9.0	.46±.78
	pilings	19±14.2	3.40±2.88	.80±1.30
90 cm^2	grid	0.27±0.87	11.6±8.0	0.31±0.62
	pilings	9.67±5.54	6.67±3.78	0.17±0.41
45 cm^2	grid	0.12±0.43	1.88±2.6	0.11±0.33
	pilings	4.11±4.91	2±1.66	0.11±0.33

TABLE 5.14 Regressions of mean sponge cover on patch size for non-isolated patches.

Time	r^2	a	b	s_B	t	P
7/79	0.5143	37.89	-.0088	.0038	2.30	>0.05
10/79	0.3351	52.71	-.0088	.0055	1.59	>0.1
2/80	0.0782	57.65	-.0037	.0057	-0.6511	>0.5
5/80	0.0023	59.26	-.0007	.0069	0.1077	>0.9

Figure 5.1 Comparison of pier pilings (a) and Pinna bicolor shells (b). Bar diagrams show the mean percentage cover of the four major faunal groups. Sponges, solid bar; bryozoans, spotted bar; tunicates, open bar; serpulids, striped bar. Pier piling data was calculated from 20 randomly allocated 20 cm x 30 cm quadrats. P. bicolor data were calculated from 42 shells.

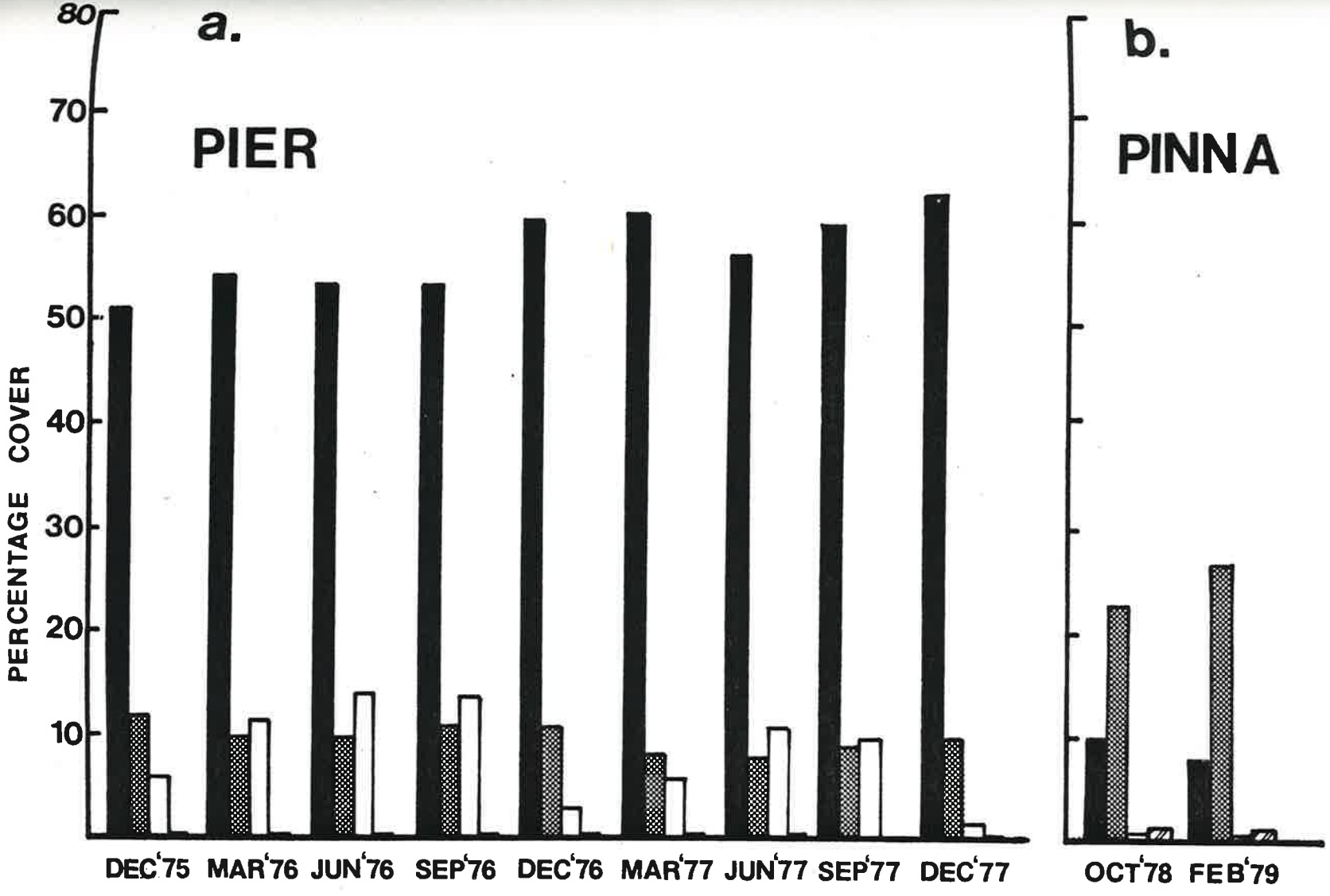

a.
PIER
b.
PINNA
PERCENTAGE COVER
80
70
60
50
40
30
20
10
DEC'75
MAR'76
JUN'76
SEP'76
DEC'76
MAR'77
JUN'77
SEP'77
DEC'77
OCT'78
FEB'79

Figure 5.2 Hypothetical fitness vs patch size relationships for larvae of species which are good or poor competitors, and at two different abundances of larvae of good competitors. F = mean fitness for all larvae of given species settling on given patch sizes; C = colonization rate (a measure of the probability of a patch of given size being colonized by a good competitor).

LRGC - Low recruitment, good competitors
HRGC - High " " "
LRPC - Low recruitment, poor competitors
HRPC - High " " "

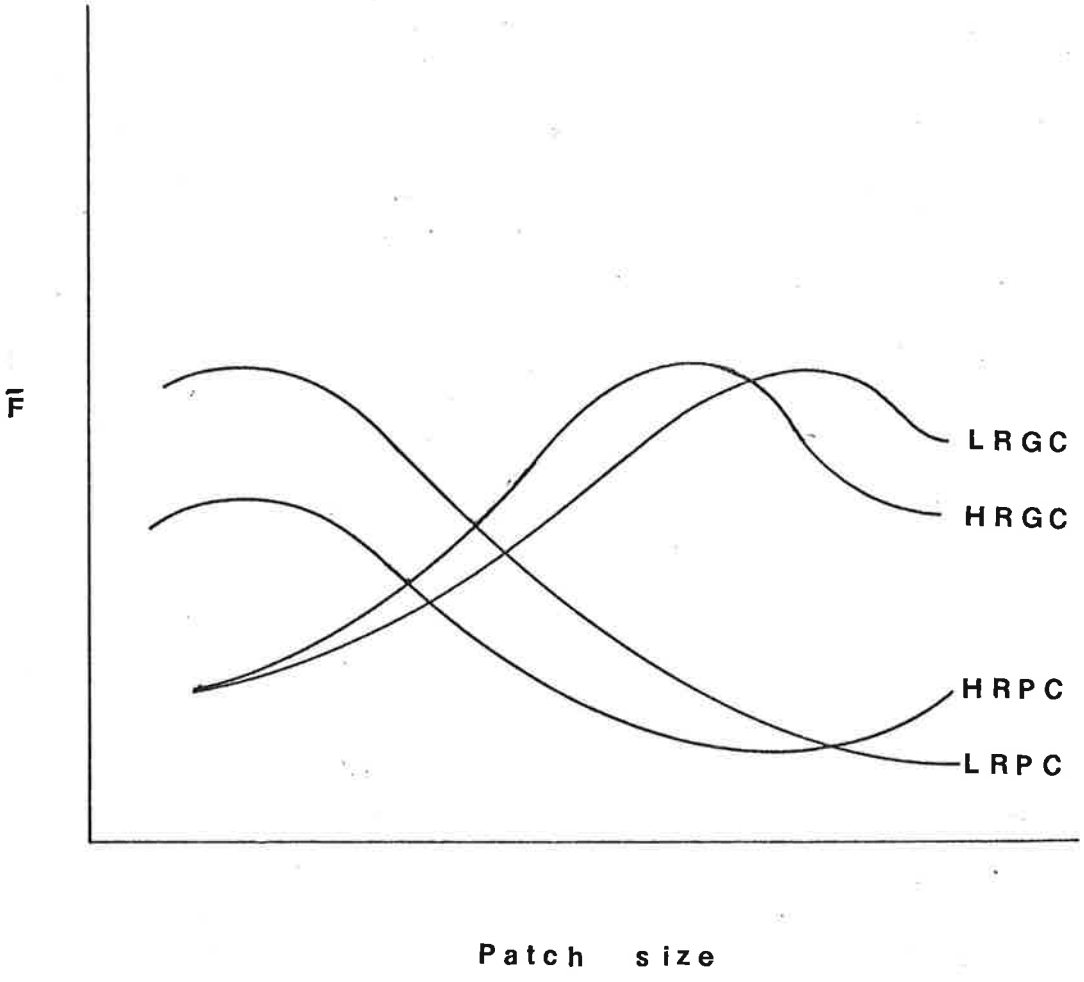

$\bar{F}$
LRGC
HRGC
HRPC
LRPC
Patch size

Figure 5.3 Map of the end of Edithburgh pier, showing the location of patches used in patch size experiment. Closed circles indicate pilings, and open triangles denote pairs of isolated and non-isolated panels.

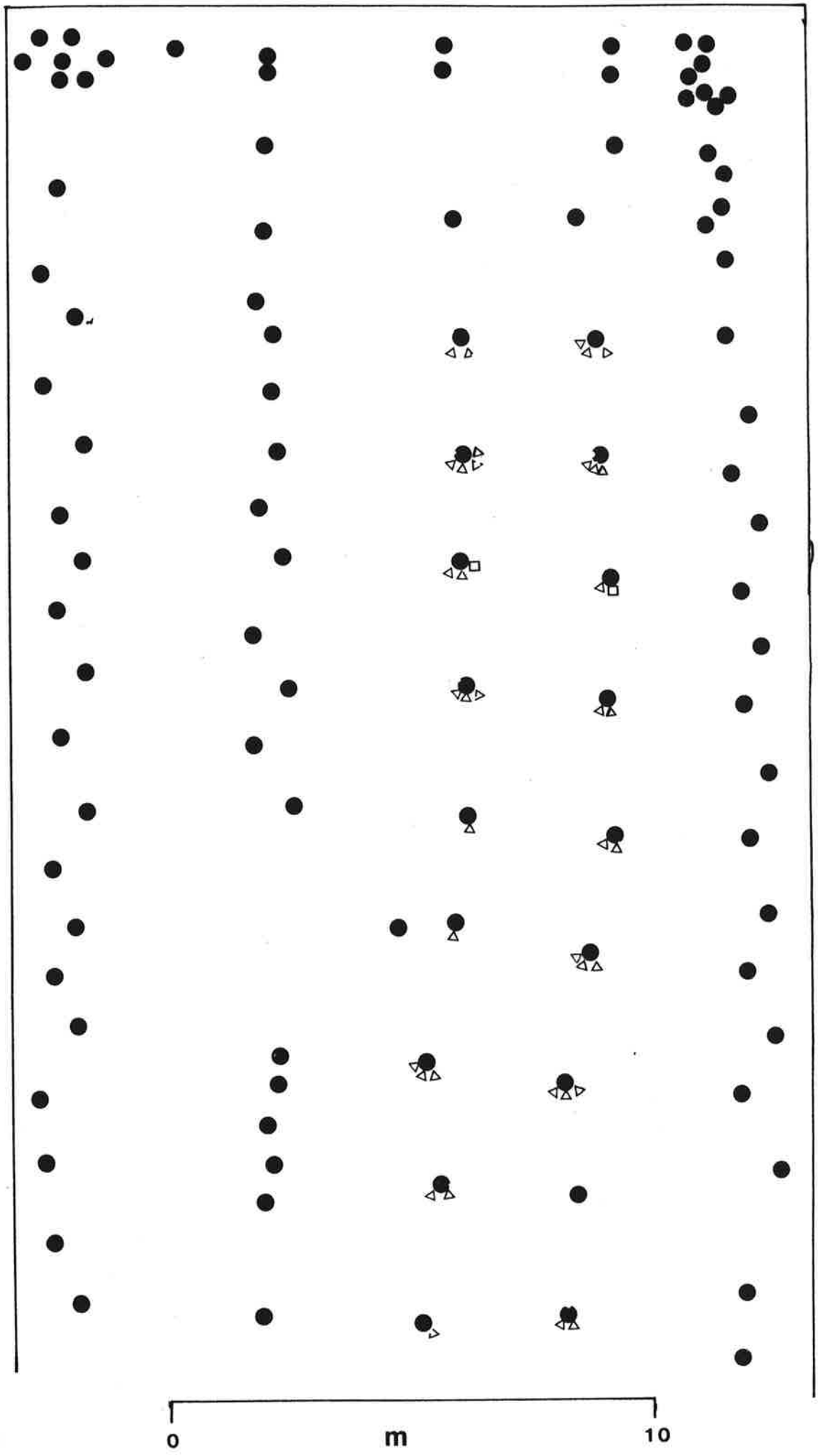

0
m
10

Figure 5.4 Relation between field estimates of percent cover ("Eyeball") and planimeter determined values. Note that ▼ indicates that there were eleven points at this value.

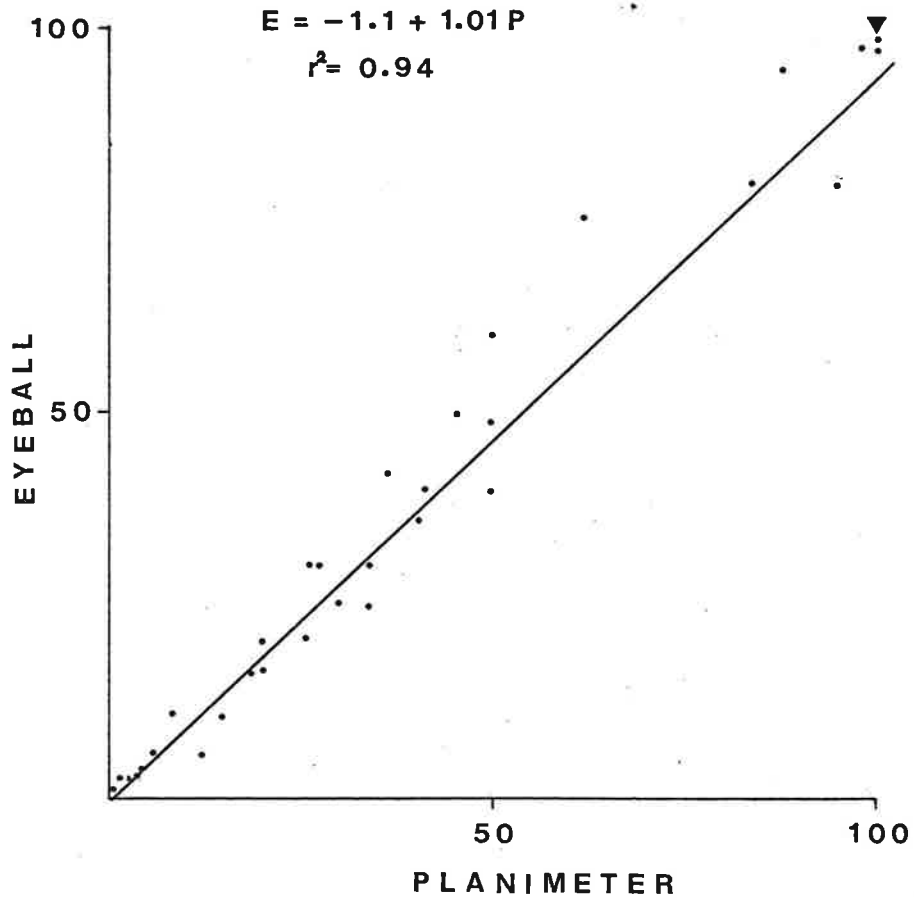

E = −1.1 + 1.01 P
r² = 0.94
100
50
EYEBALL
50
100
PLANIMETER

Figure 5.5 Distribution of species number against patch sizes at four different times on (a) non-isolated and (b) isolated patches.

□ May 1980

■ February 1980

○ October 1979

△ July 1979

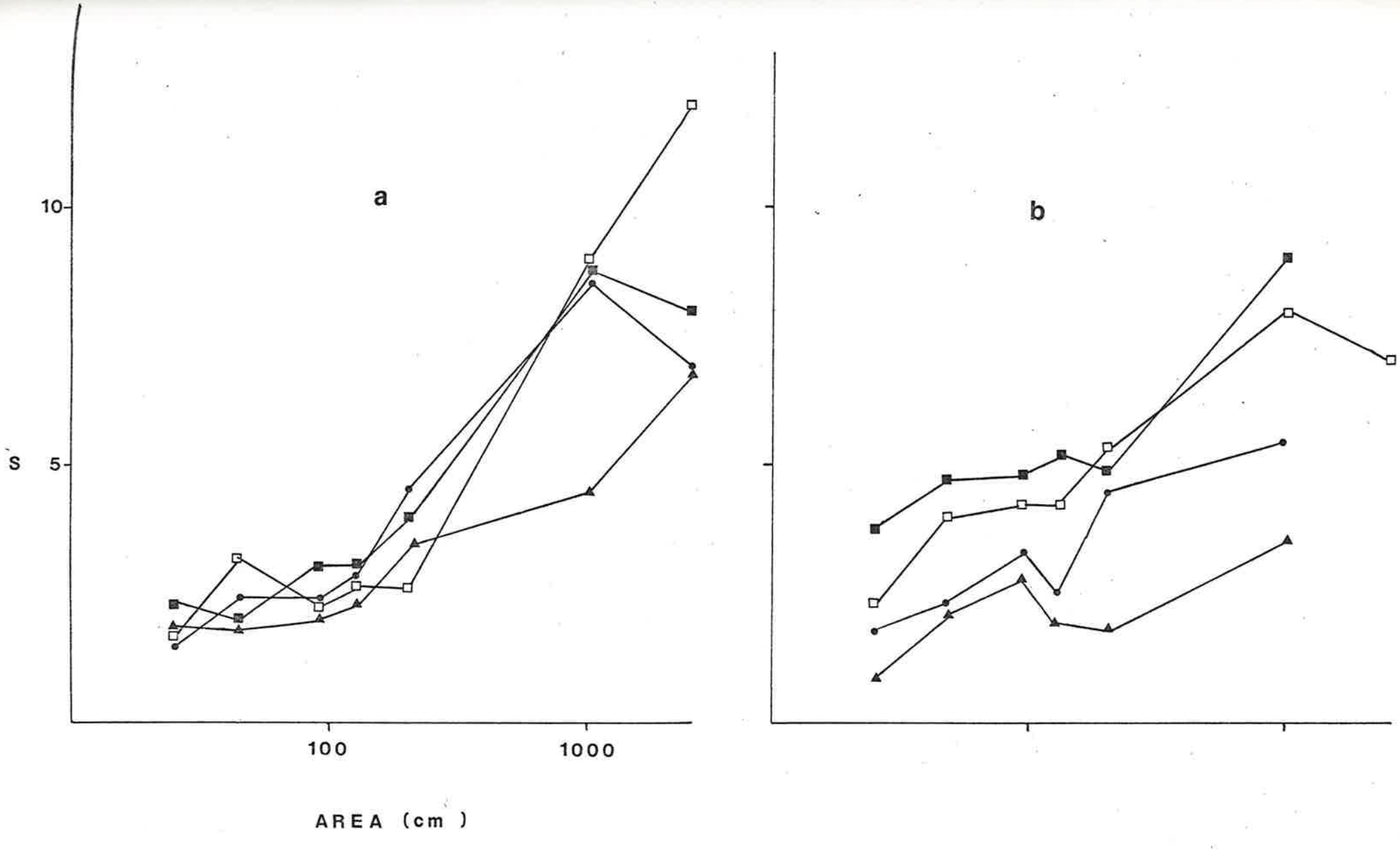

a
b
10
5
S
100
1000
AREA (cm)

Figure 5.6 Change in species number with time on 2500 cm^2 patches.

△ non-isolated

▲ isolated

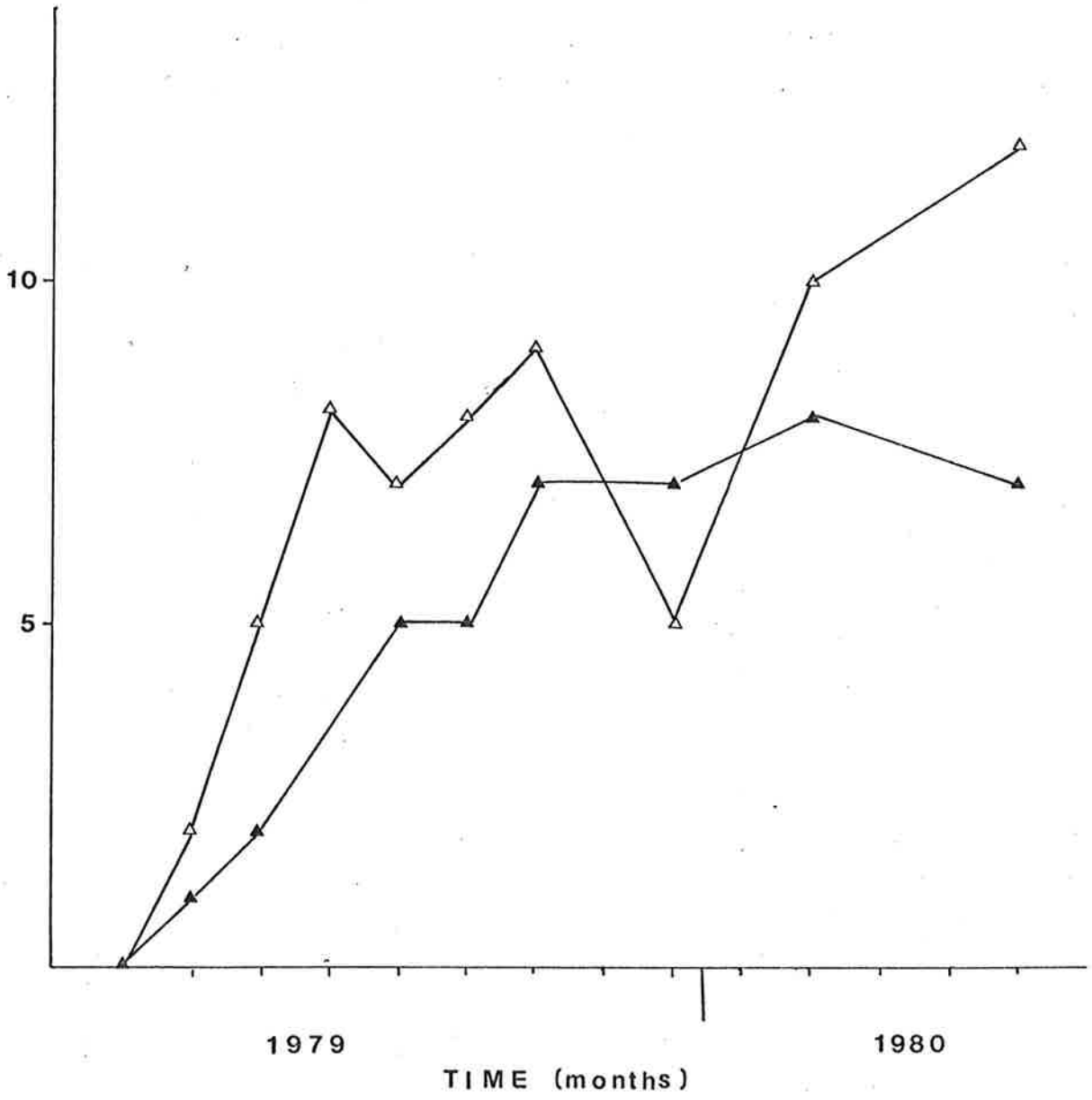

10
5
1979
1980
TIME (months)

Figure 5.7 Change in species number with time on (a) 625 cm^2 and (b) 180 cm^2 patches. Points are mean $\pm$ S.D. □ non-isolated and ■ isolated patches.

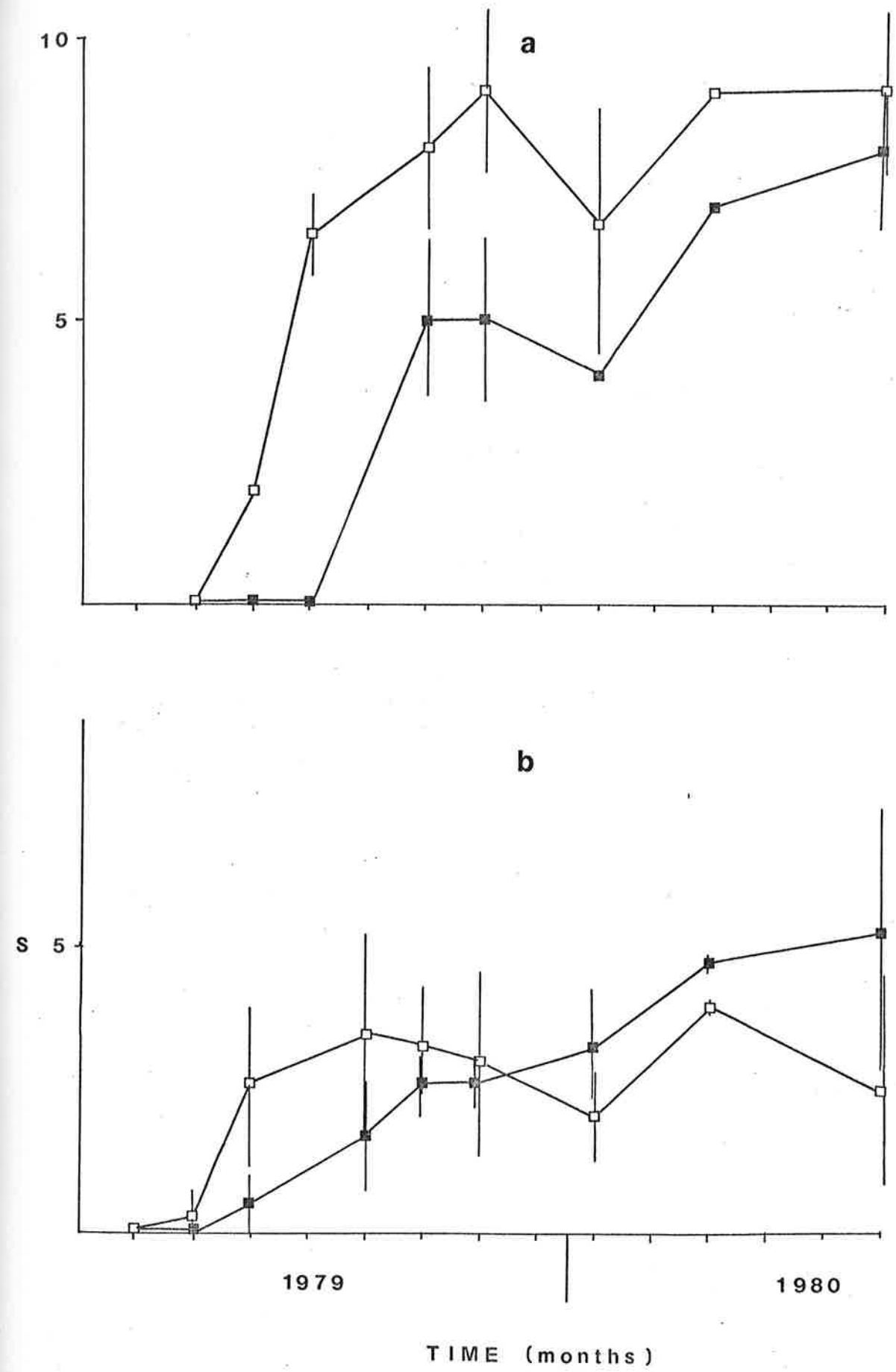

10
5
a
b
S
5
1979
1980
TIME (months)

Figure 5.8 Change in species number with time on (a) 120 cm^2 and (b) 90 cm^2 patches. Points are means $\pm$ S.D. □ non-isolated, ■ isolated patches.

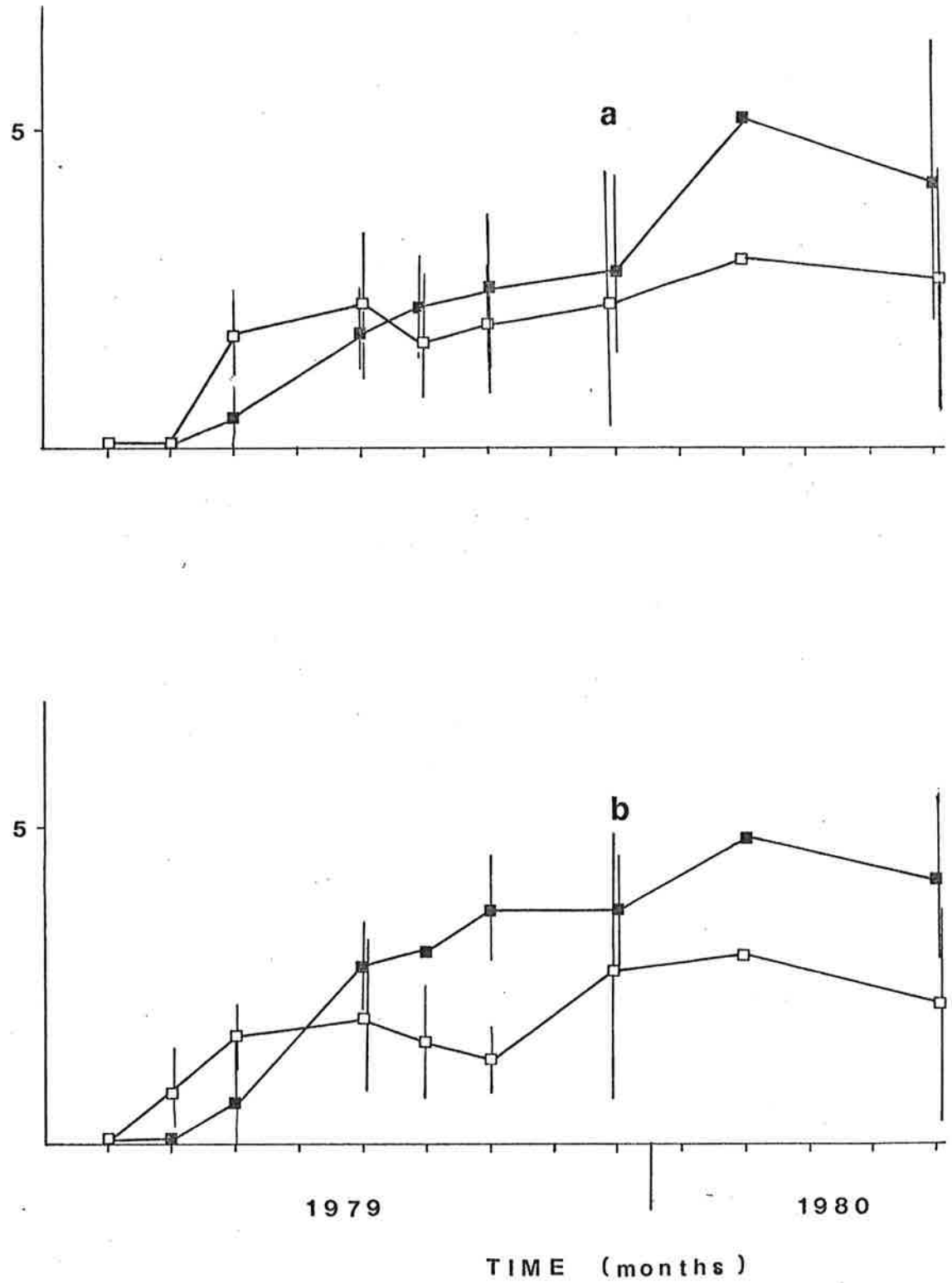

5
a
5
b
1979
1980
TIME (months)

Figure 5.9 Change in species number with time on (a) 45 cm^2 and (b) 25 cm^2 patches. Points are means ± S.D. □ non-isolated, ■ isolated.

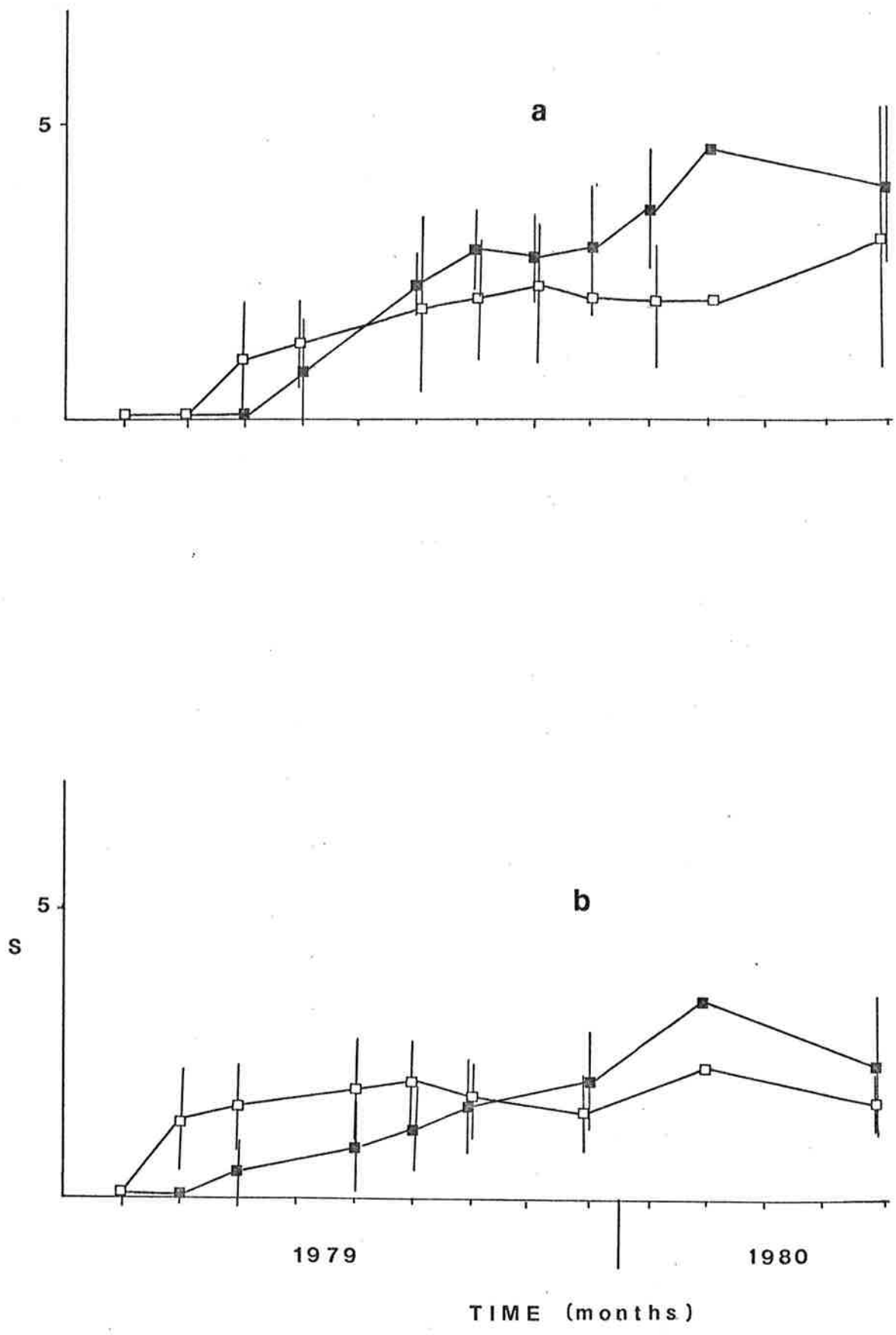

a
5
b
5
S
1979
1980
TIME (months)

Figure 5.10 Variation in bryozoan cover with patch size in October 1979. Points are means ± S.D. □ non-isolated, ■ isolated.

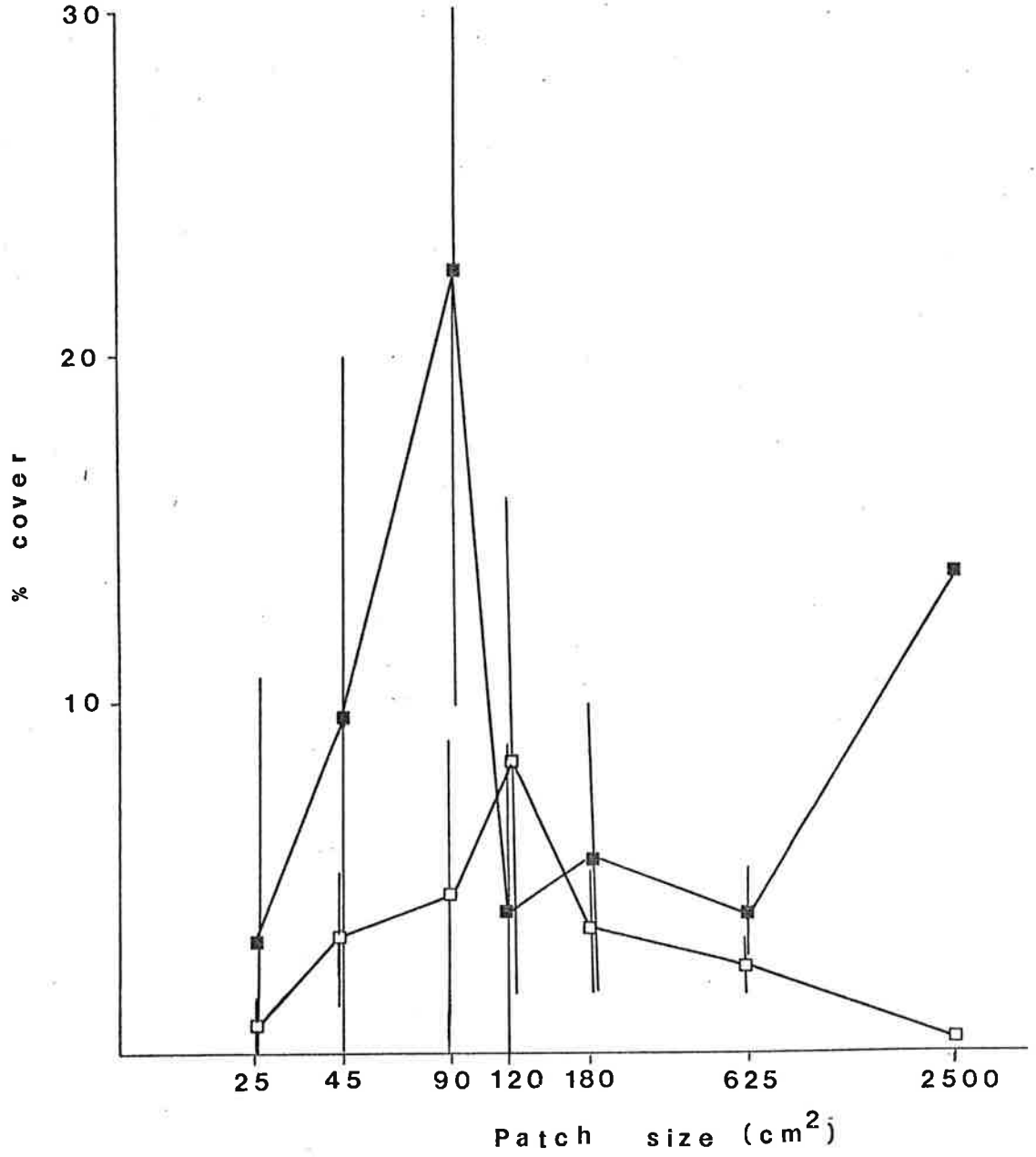

30
20
10
% cover
25
45
90
120
180
625
2500
Patch size (cm2)

Figure 5.11 Variation in bryozoan cover with patch size in February 1980. Points are means $\bar{+}$ S.D.

□ non-isolated patches

■ isolated patches

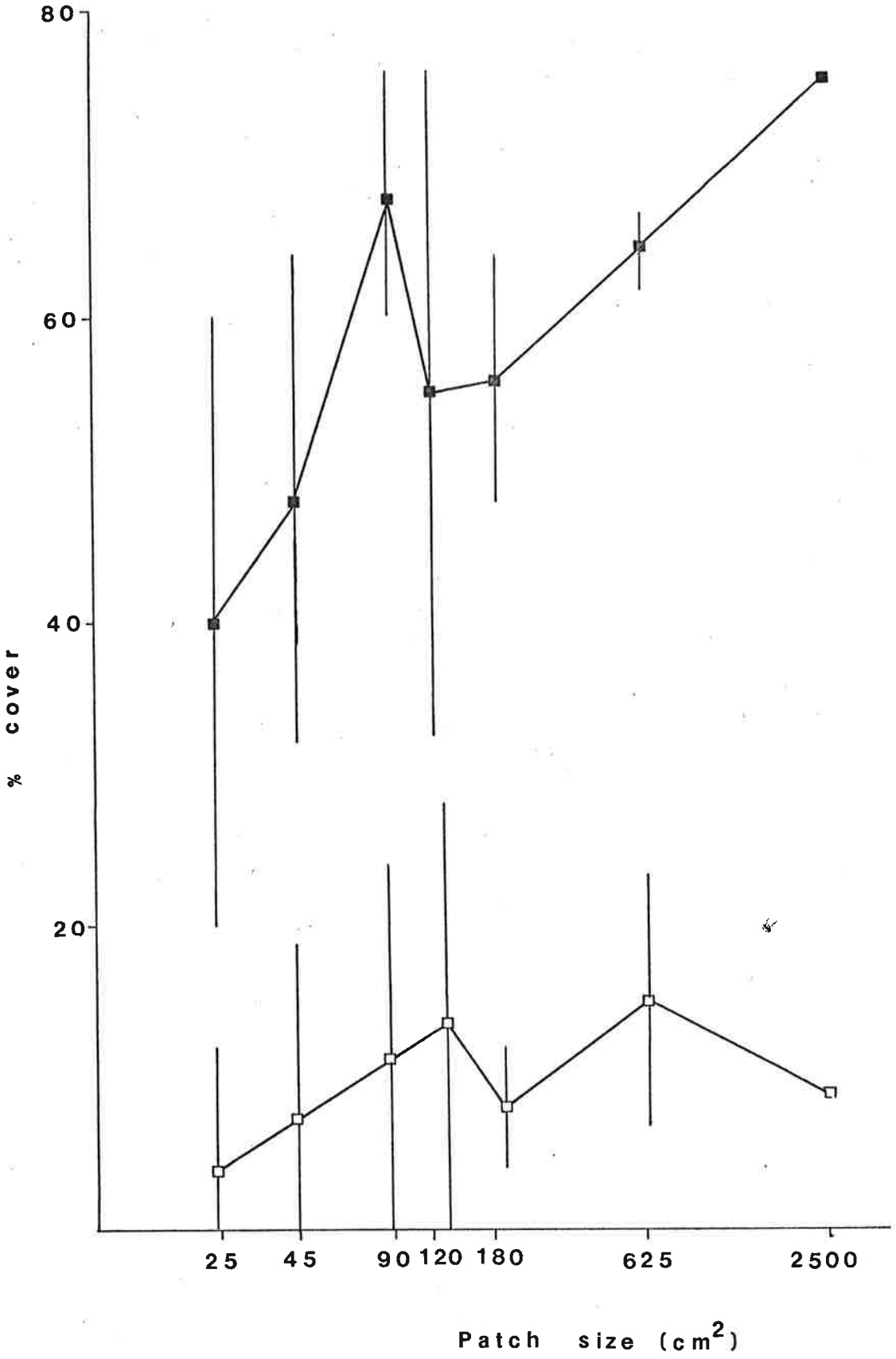

80
60
40
20
% cover
25
45
90
120
180
625
2500
Patch size (cm²)

Figure 5.12 Variation in bryozoan cover with patch size in May 1980. Points are means ± S.D.

□ non-isolated patches

■ isolated patches

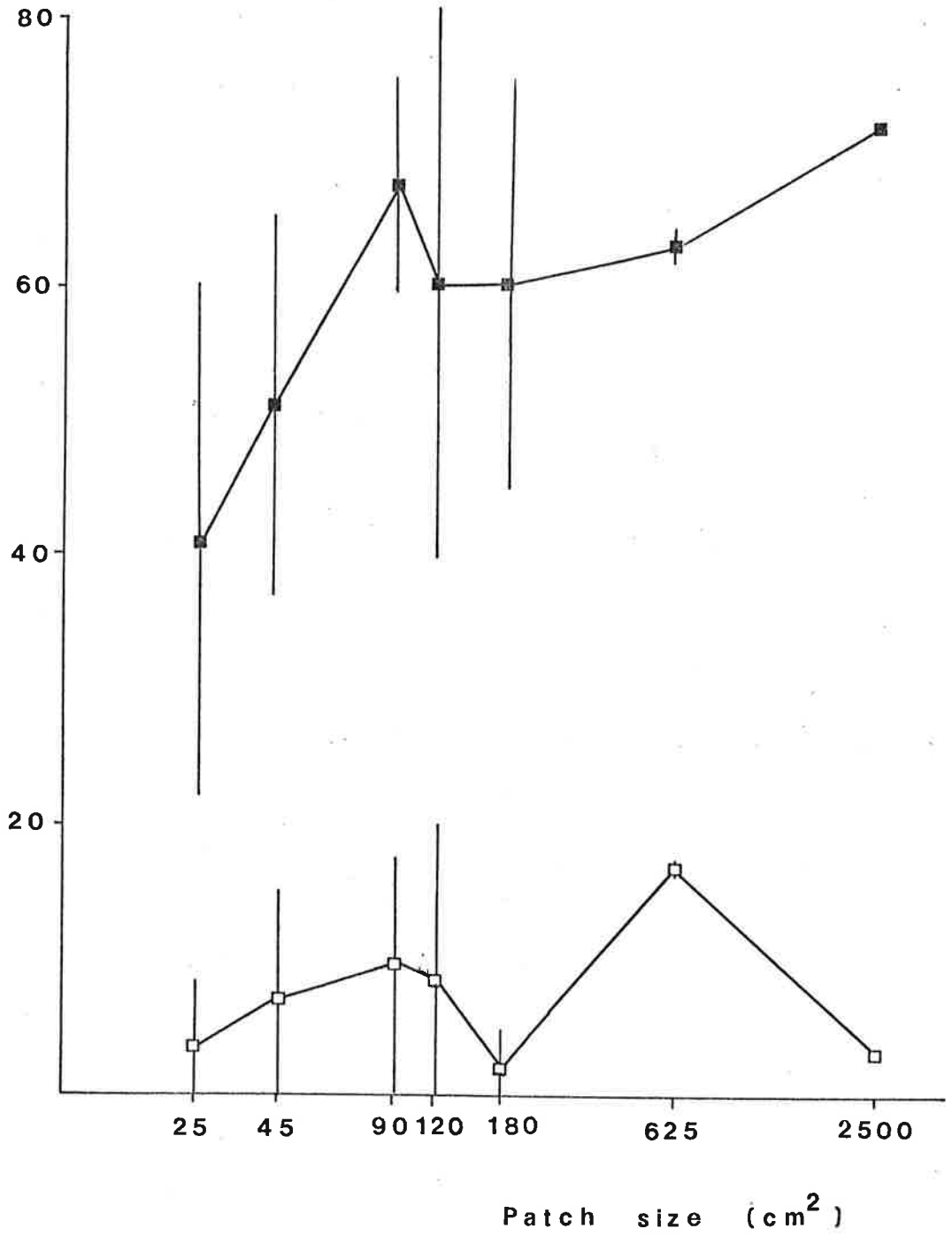

80
60
40
20
25
45
90
120
180
625
2500
Patch size (cm2)

Figure 5.13 Change in bryozoan cover with time on 2500 cm^2

□ non-isolated

■ isolated

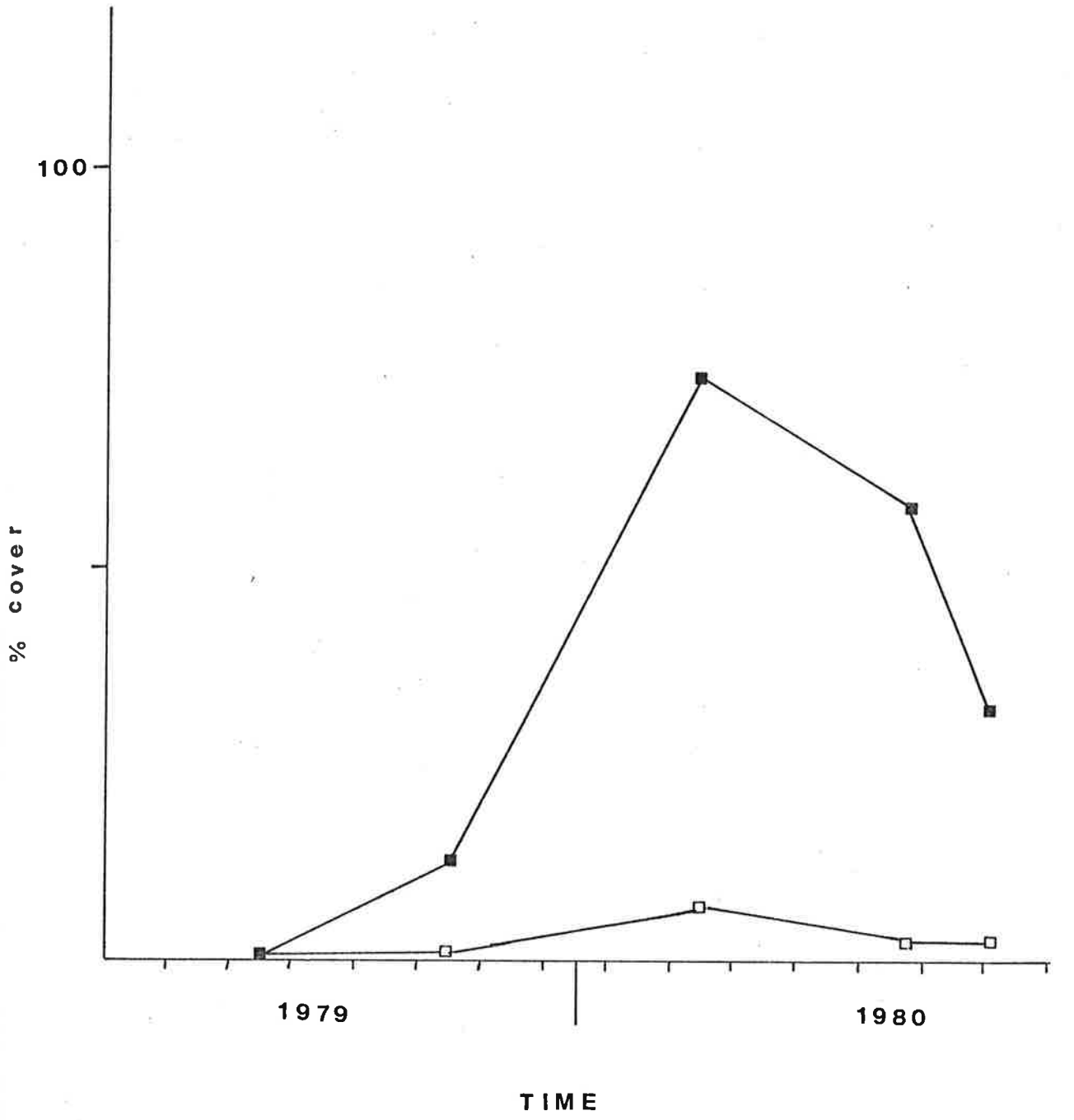
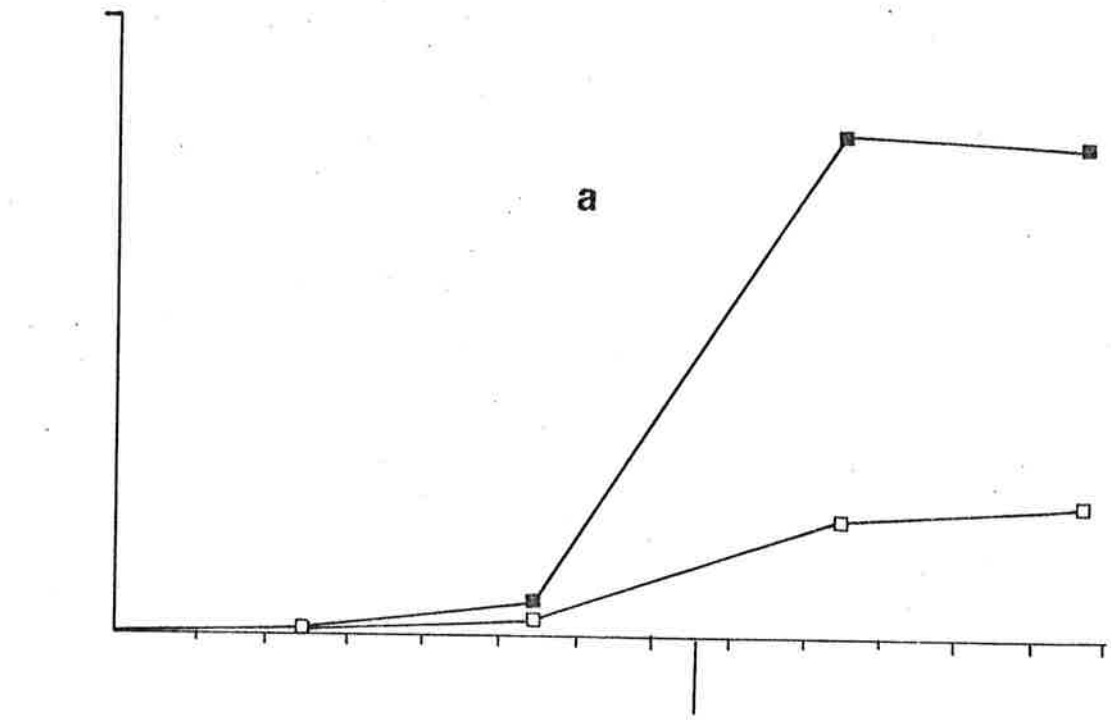

100
% cover
1979
1980
TIME

Figure 5.14 Change in bryozoan cover with time on (a) 625 cm^2 and (b) 180 cm^2 patches. Points are means

□ non-isolated

■ isolated


a

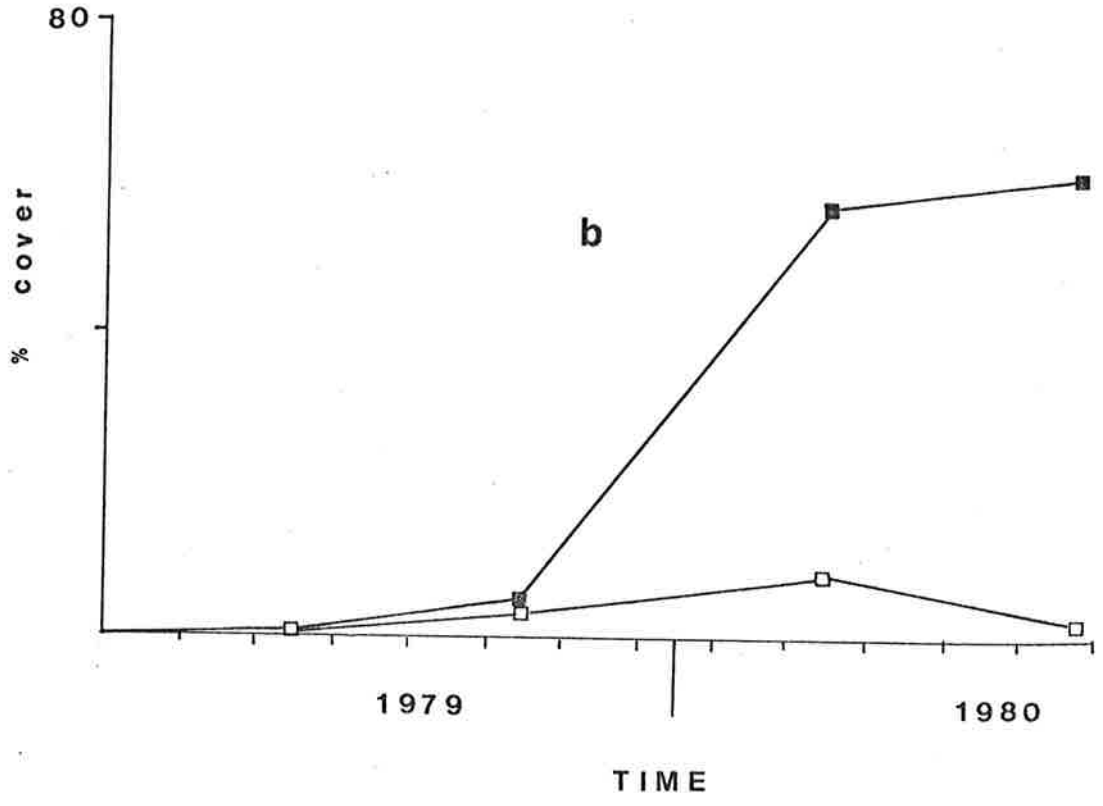

80
% cover
b
1979
1980
TIME

Figure 5.15 Change in bryozoan cover with time on (a) 120 cm^2 and (b) 90 cm^2 patches. Points are means

□ non-isolated

■ isolated

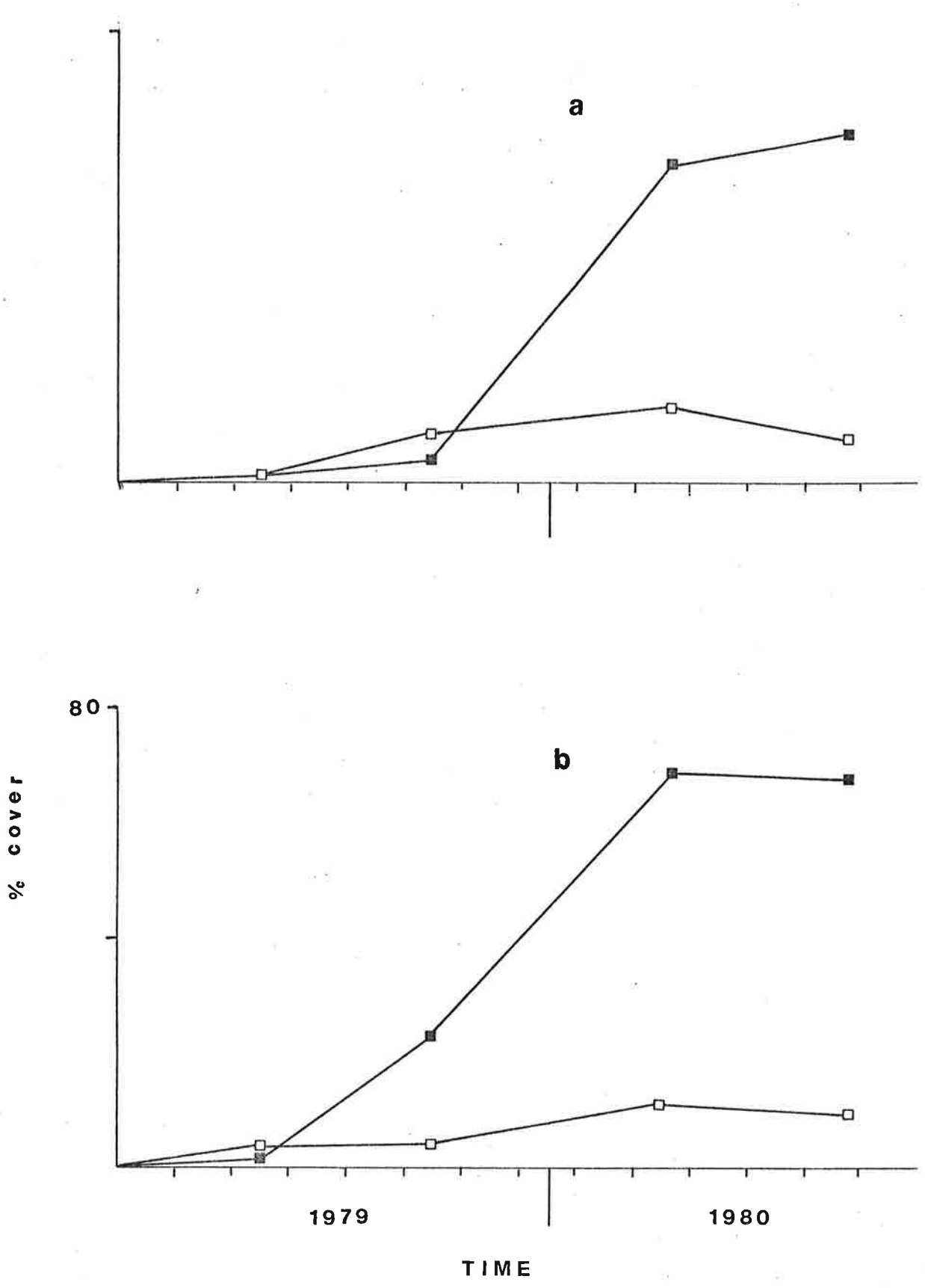

a
b
80
% cover
1979
1980
TIME

Figure 5.16 Change in bryozoan cover with time on (a) 45 cm^2 and (b) 25 cm^2 patches. Points are means

□ non-isolated

■ isolated

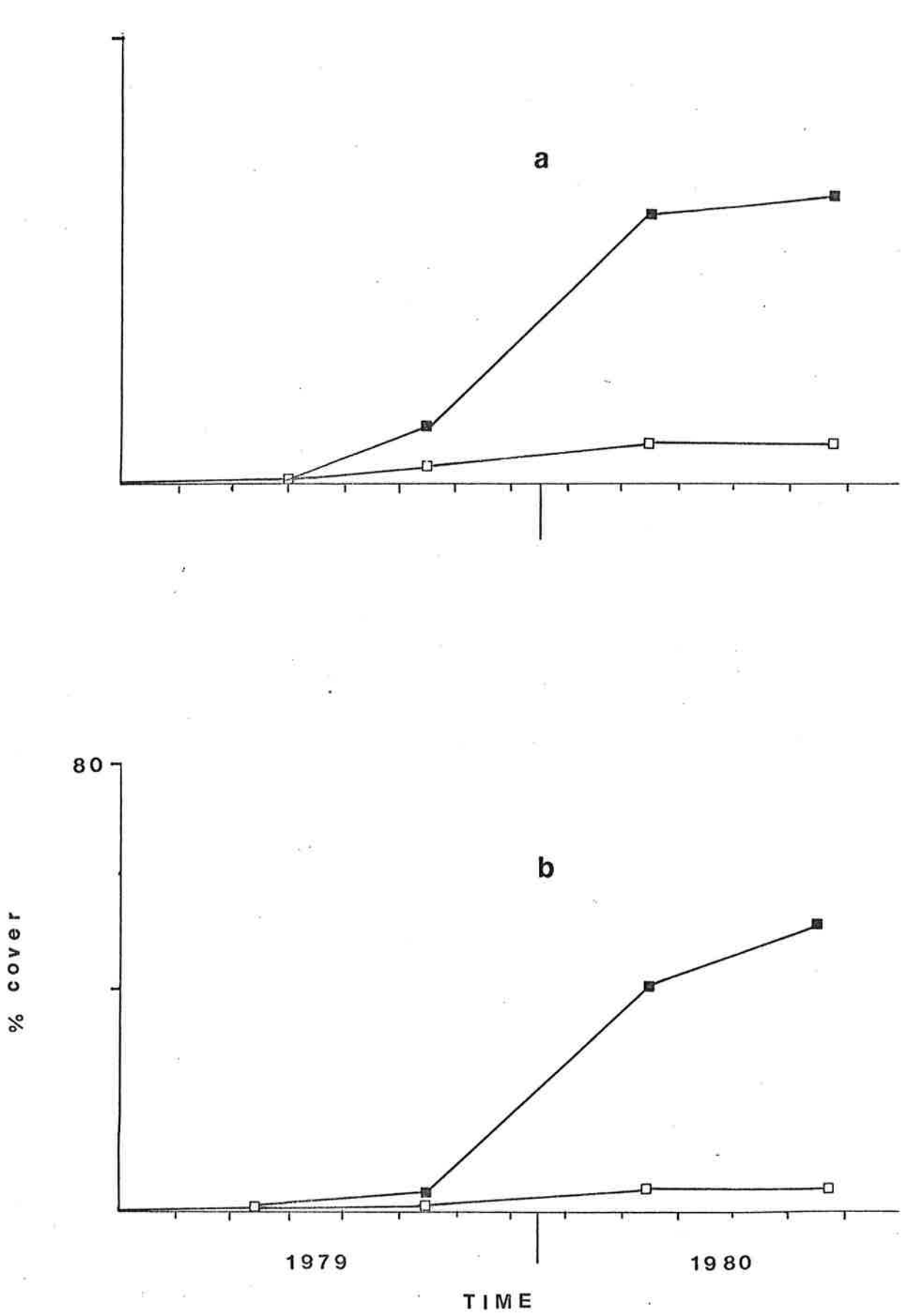

a
80
b
% cover
1979
1980
TIME

Figure 5.17 Change in sponge cover with time for (a) 2500 cm^2, (b) 625 cm^2, (c) 180 cm^2 and (d) 120 cm^2 patches. Points are means $\pm$ S.D.

△ non-isolated

▲ isolated

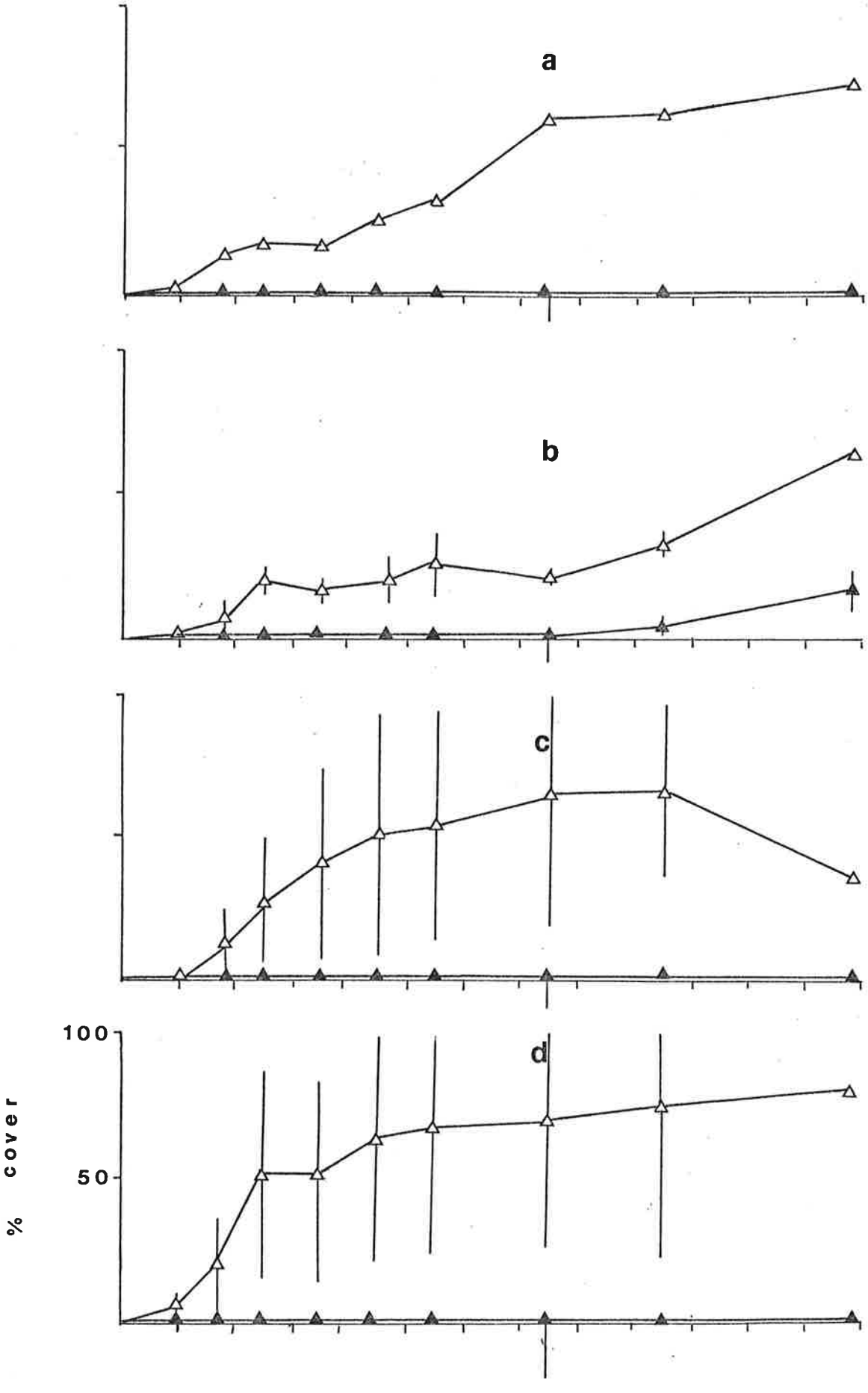

a
b
c
d
100
50
% cover
1979
1980
TIME

Figure 5.18 Change in sponge cover with time for (a) 90 cm^2, (b) 45 cm^2, and (c) 25 cm^2 patches. Points are means $\pm$ S.D.

△ non-isolated

▲ isolated

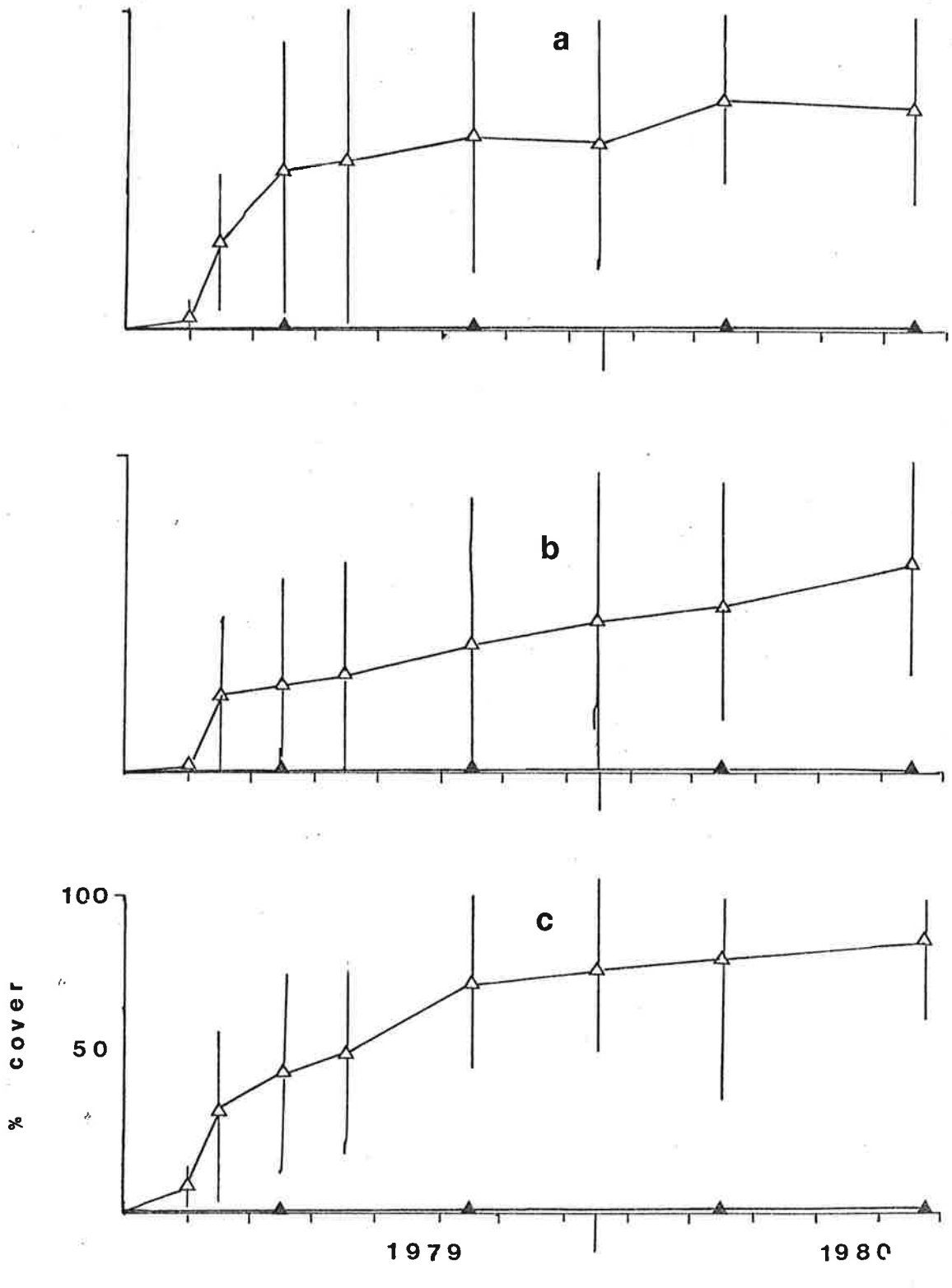

a
b
c
100
50
% cover
1979
1980
TIME

Figure 5.19 Variation in percent cover of colonial tunicates with patch size in May 1980. Points are means ± S.D.

△ non-isolated

▲ isolated

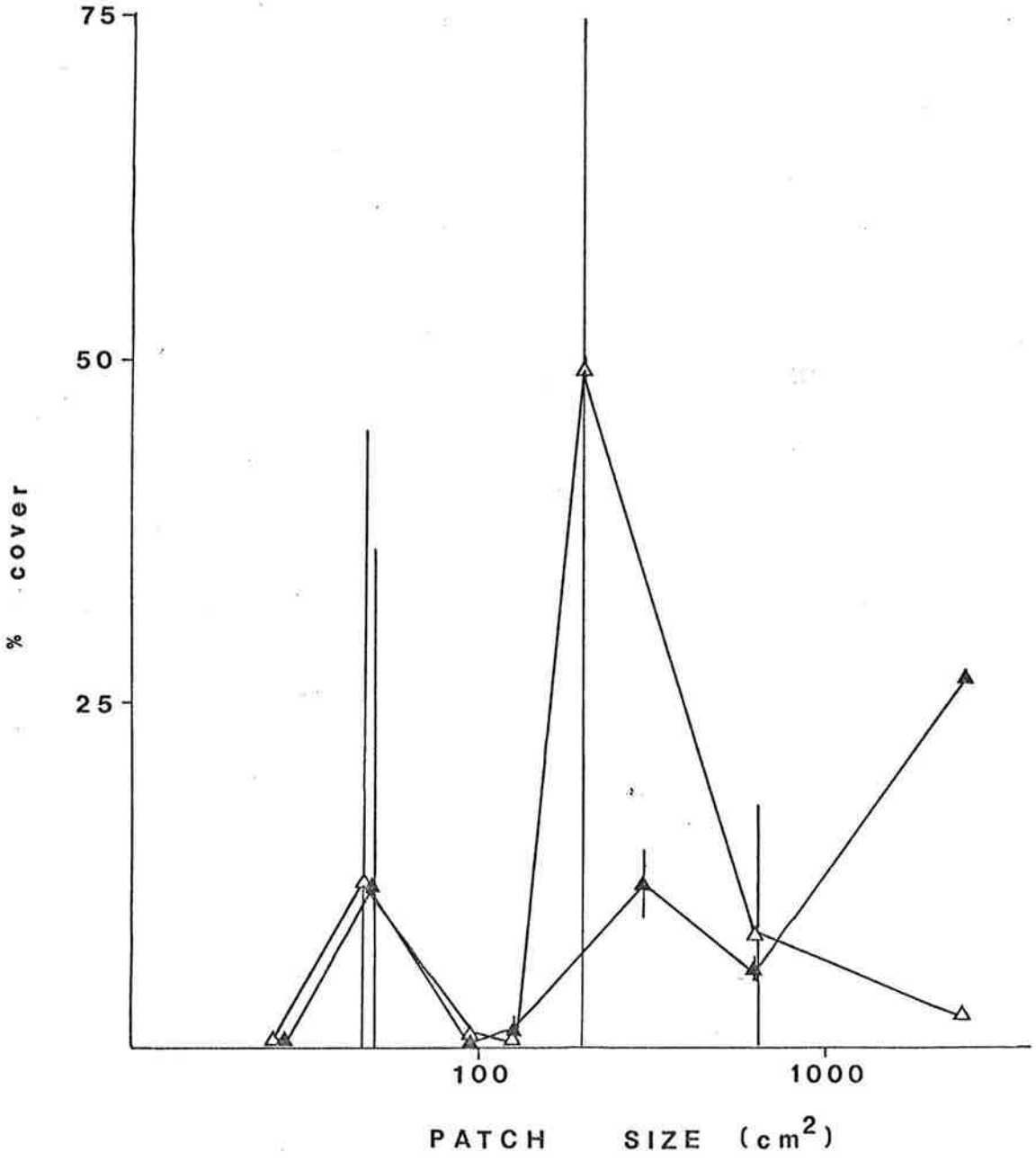

75
50
25
% cover
100
1000
PATCH SIZE (cm2)

Figure 5.20 Change in percent cover of all good competitors with time on (a) 2500 cm^2, (b) 625 cm^2, (c) 180 cm^2, and (d) 120 cm^2 patches. Points are means $\pm$ S.D.

△ non-isolated

▲ isolated

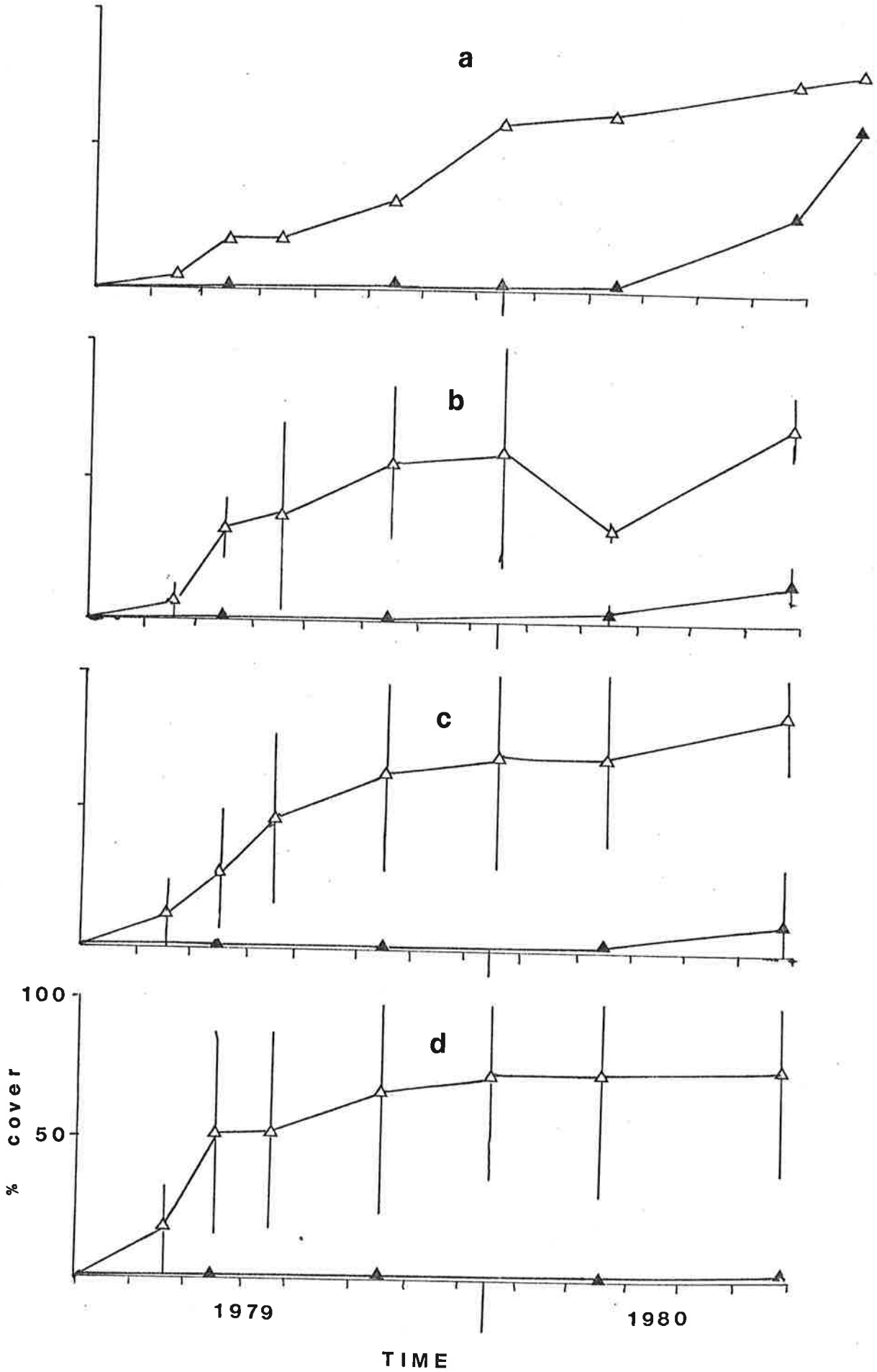

a
b
c
d
100
50
% cover
1979
1980
TIME

Figure 5.21 Change in percent cover of all good competitors with time on (a) 90 cm^2, (b) 45 cm^2, and (c) 25 cm^2 patches. Points are means $\pm$ S.D.

△ non-isolated

▲ isolated

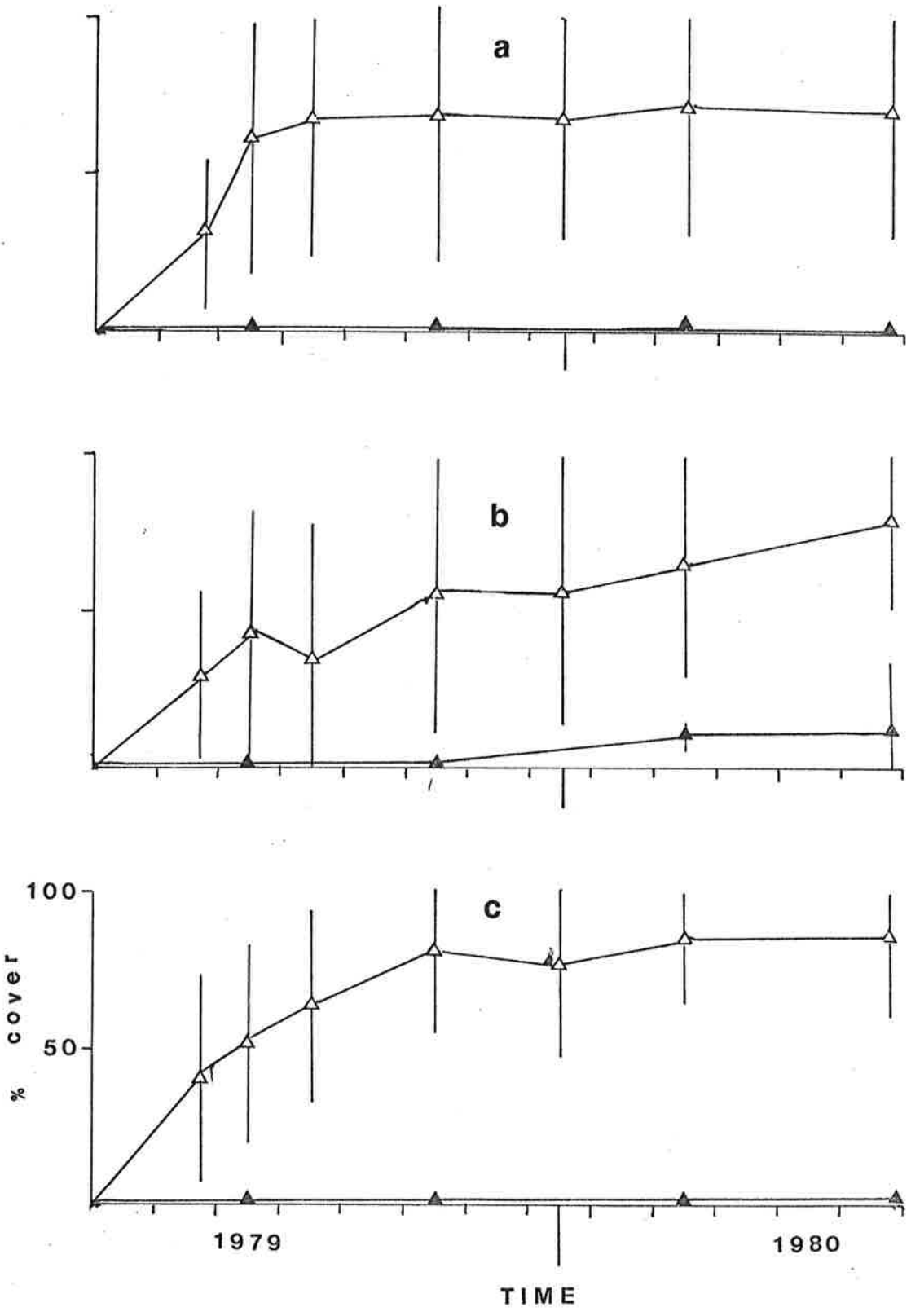

a
b
c
100
50
% cover
1979
1980
TIME

Figure 5.22 Variation in total percent cover of good competitors with patch size (a) July 1979, (b) October 1979. Points are means ± S.D.

△ non-isolated

▲ isolated

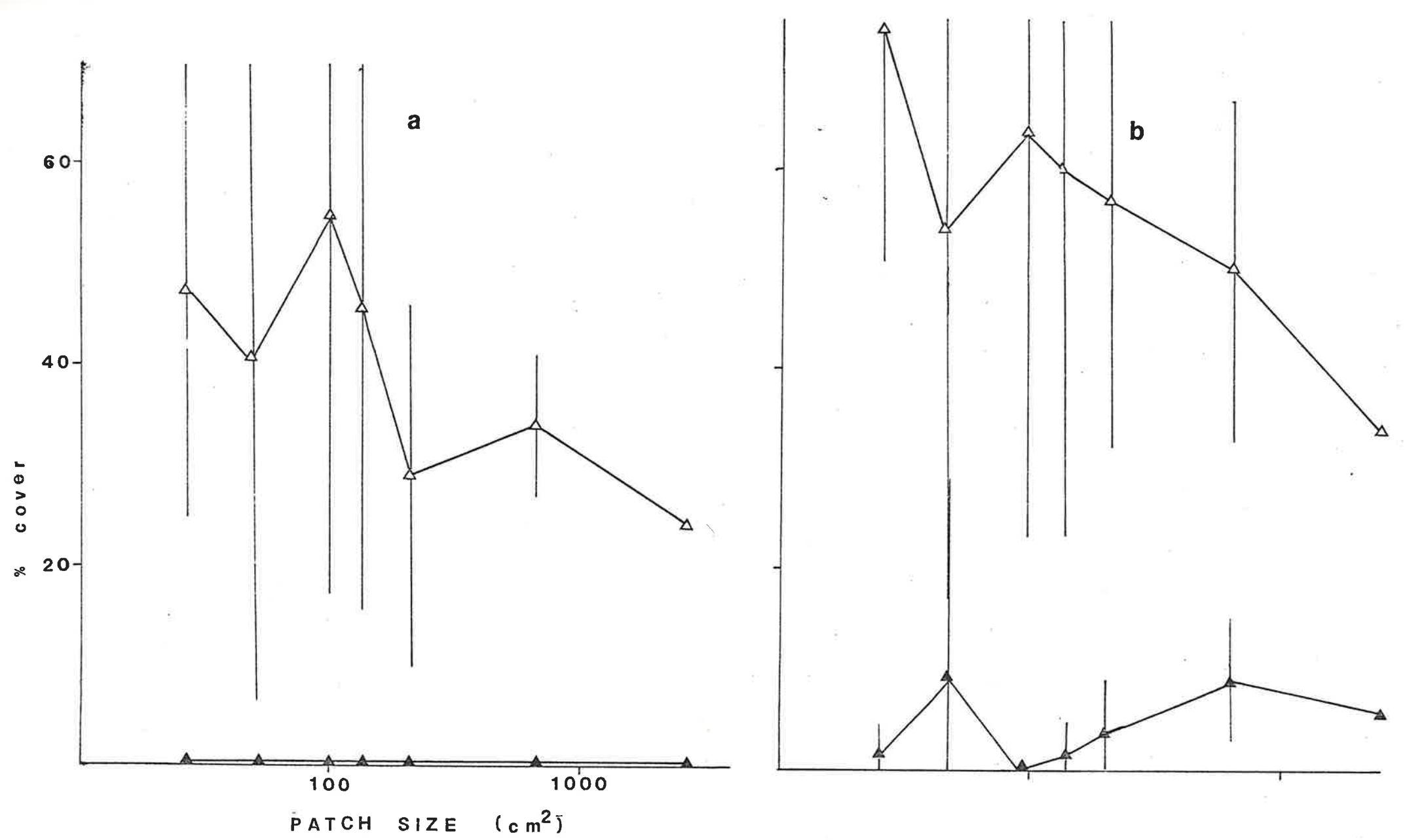

a
b
60
40
20
% cover
100
1000
PATCH SIZE (cm²)

Figure 5.23 Variation in total percent cover of good competitors with patch size; (a) February 1980, (b) May 1980. Points are means ± S.D.

△ non-isolated

▲ isolated

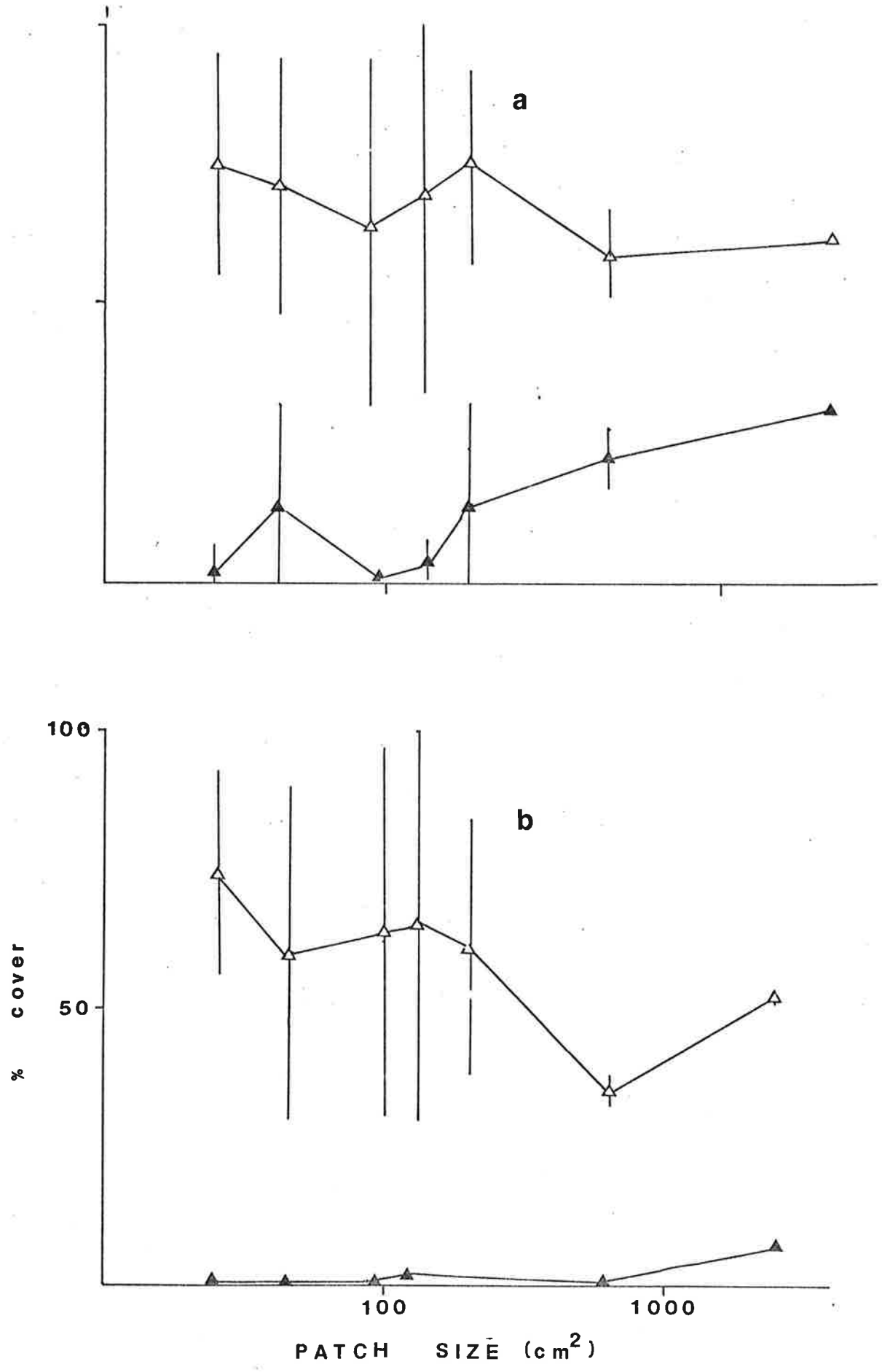

a
b
100
50
% cover
100
1000
PATCH SIZE (cm²)

Figure 5.24 Variation in total percent cover (all species pooled) with patch size at four times (a) July 1979, (b) October 1979, (c) February 1980, and (d) May 1980. Points are means $\pm$ S.D.

△ non-isolated patches

▲ isolated patches

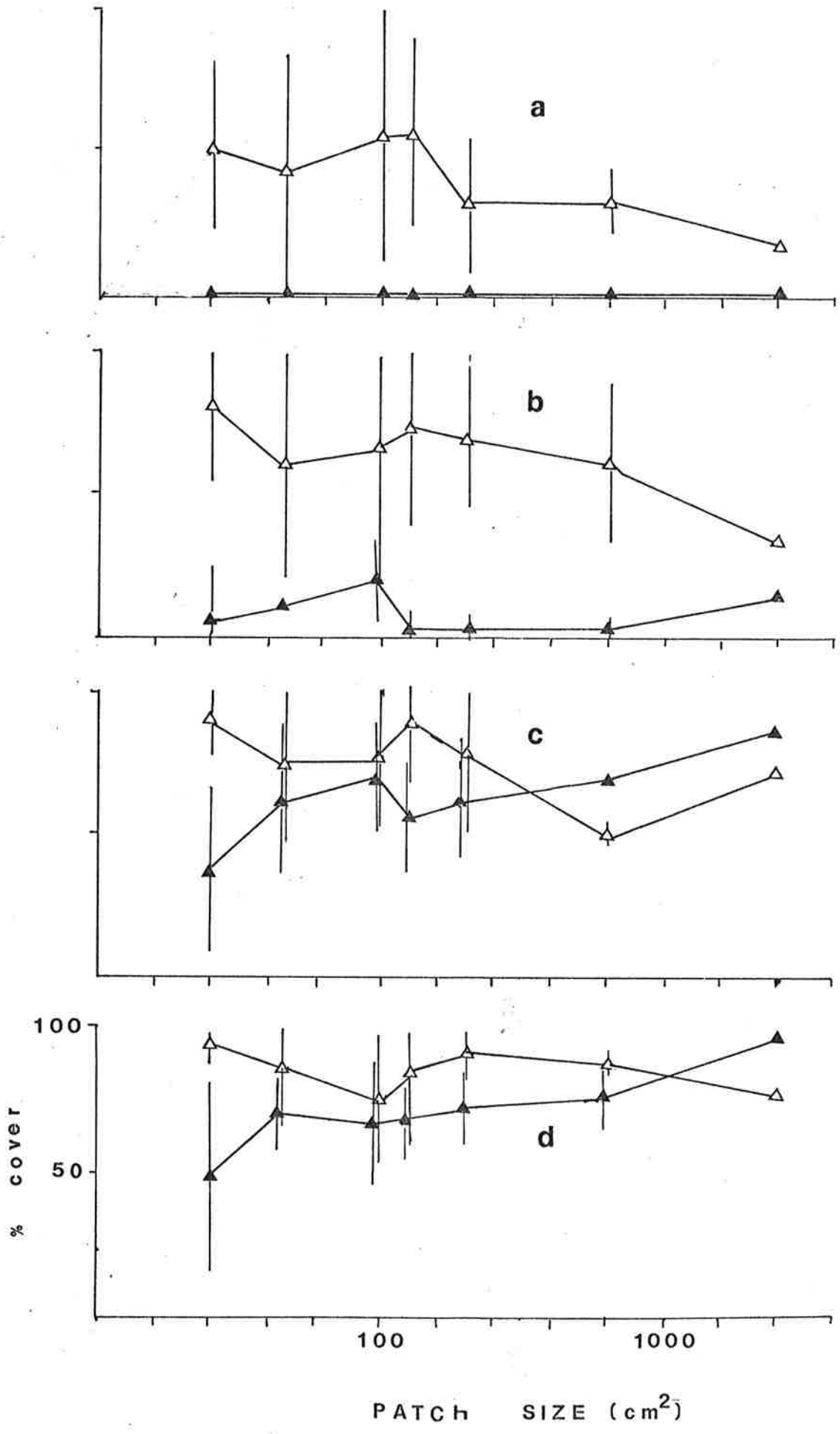

a
b
c
d
100
50
% cover
100
1000
PATCH SIZE (cm²)

Figure 5.25 Contribution to the total fauna of each patch size by each major taxon after 394 days.

nI - non-isolated patches

I - isolated patches

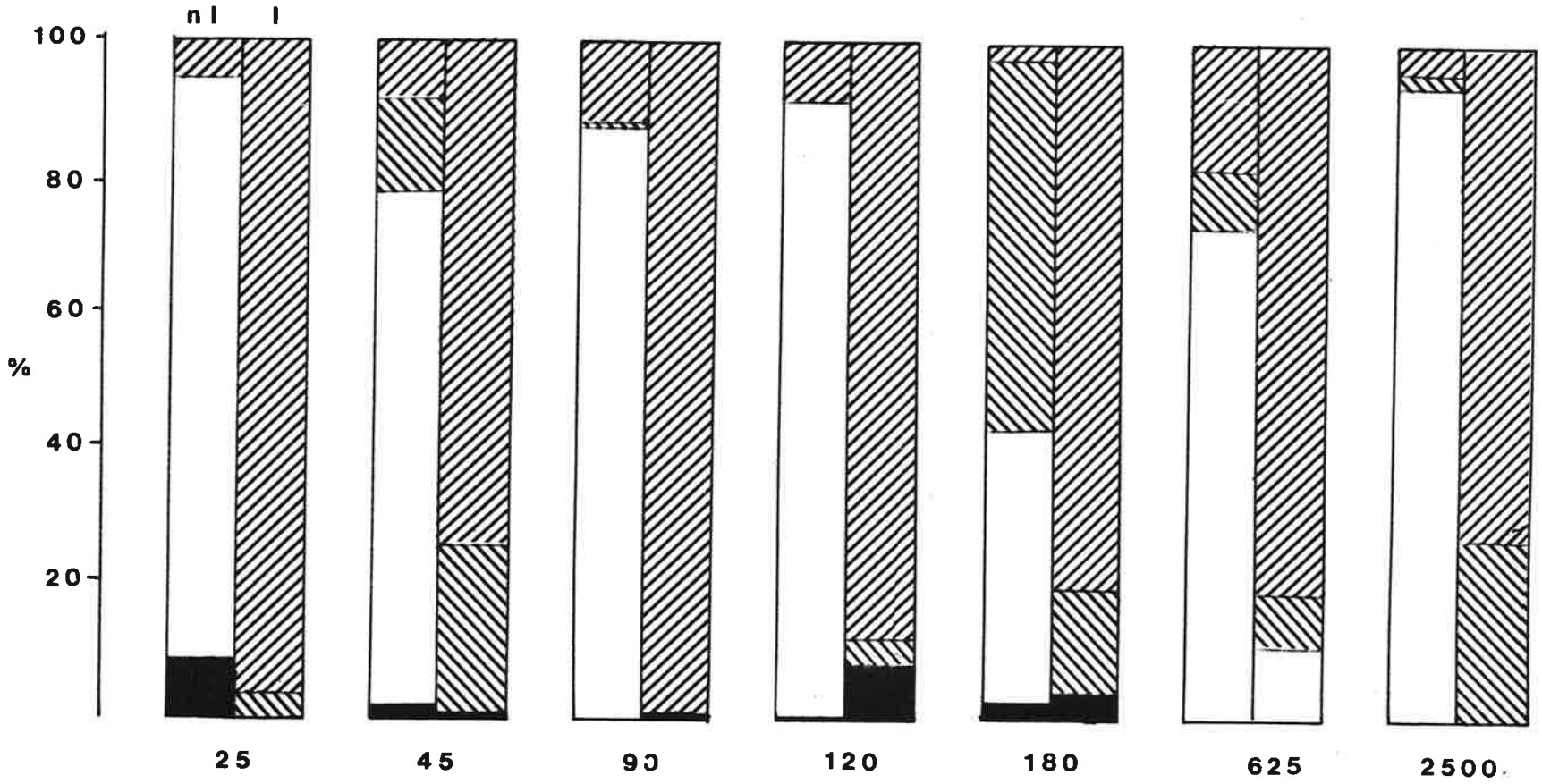

nl
l
100
80
60
%
40
20
25
45
90
120
180
625
2500

Figure 5.26 Species composition of individual patches. The row axis shows patch sizes and replicate numbers; the column axis shows species. A circle in a given cell indicates that the species in question was present in the patch concerned.

(●) present in isolated patch

(○) present in non-isolated patch

Se
Cu
Es
Mp
Cf
Cv
Pa
Cp
T5
T9
T11
T18
SP1
SP2
SP5
SP12
SP30
SP20
SP50
SP55
25
45
90
120
180
625
2500

Figure 5.27 Hypothetical curves of recruitment versus patch sizes. 1, 2 and 3 refer to examples given in the text on page 160 ff.

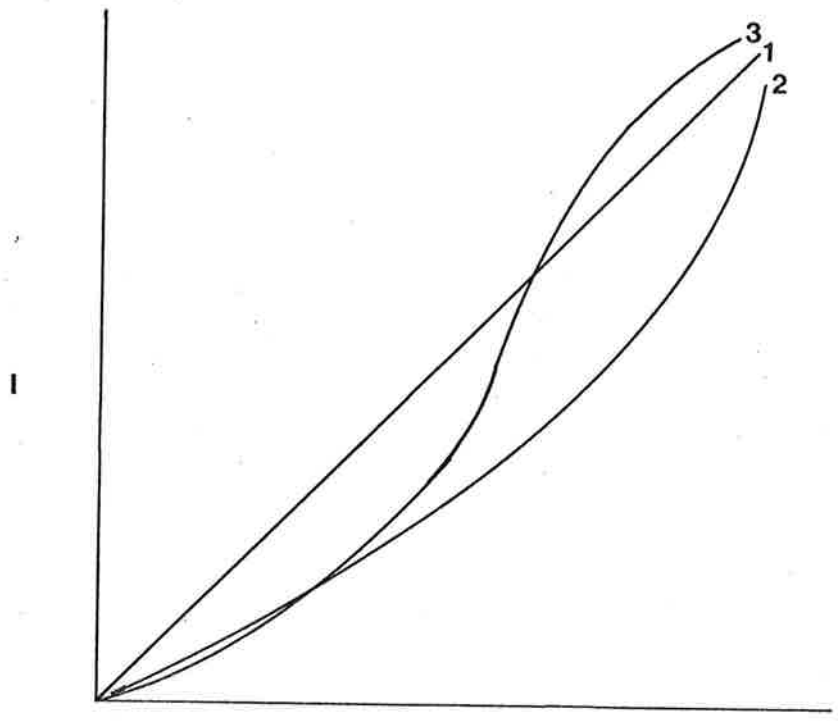
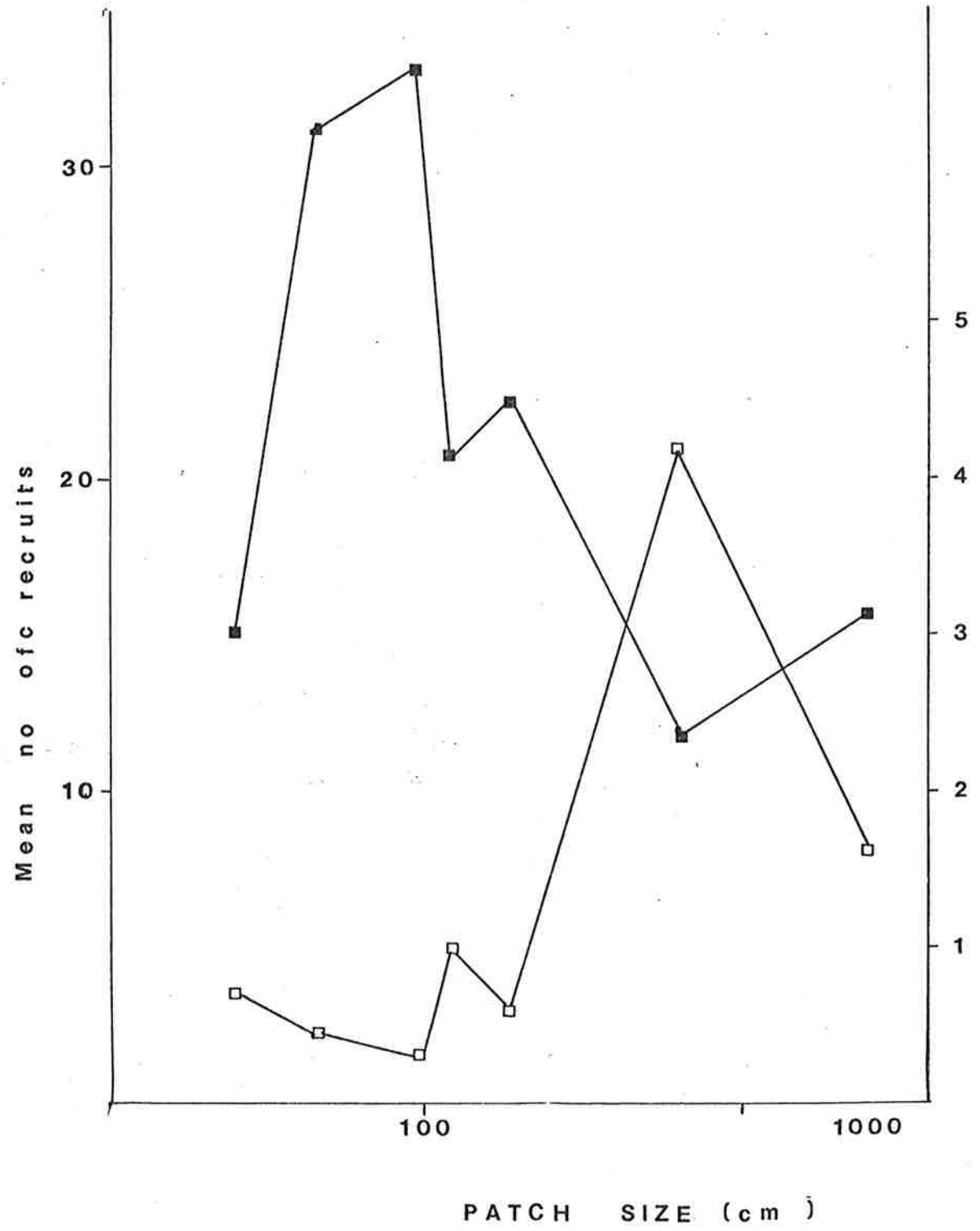

3
1
2
I
AREA

Figure 5.28 Recruitment patterns of bryozoans (■) and colonial tunicates (□). The graphs show the mean number of recruits per panel per 30 days, for seven panel sizes. The left-hand scale is for bryozoans, the right-hand for tunicates.


30
20
10
5
4
3
2
1
100
1000
Mean no ofc recruits
PATCH SIZE (cm)

6. DISCUSSION

It is now possible to review the results of testing the five hypotheses detailed in Chapter 1, and to draw conclusions about the usefulness of the equilibrium model in describing the dynamics of the epifauna of *Pinna* shells; from this, some comments can be made about the general usefulness of the MacArthur-Wilson model. Finally, the applicability of alternative models will be considered.

6.1 Hypotheses 1 to 5.

The tests of these hypotheses have been covered in Chapter 4, but some reiteration is probably useful.

Hypothesis 1 Most patches have fluctuations in S which are narrowly bounded, i.e. S values fall with 95% probability within the region $\bar{S} \pm w\bar{S}$, where $w = 0.20$.

This hypothesis can be rejected unequivocally. Less than 50% of patches are narrowly bounded. Indeed, if the envelope about $\bar{S}$ is to contain the fluctuations on 95% of the patches, we must relax the criterion of narrow boundedness so that w is approximately 0.5, i.e. the region is $\bar{S} \pm 0.5\ \bar{S}$. This is clearly unacceptable.

Hypothesis 2 The recruitment rates of individual species differ, but this variation in recruitment is smoothed out by considering all species together, and the numbers and abundances of species colonizing do not differ greatly between similar patches.

Recruitment rates of individual species were indeed highly variable, differing by as much as three orders of magnitude. Moreover, the recruitment rates of many individual species varied greatly with time. This variation occurred on both short (monthly) and longer (between years) time scales. The variation in recruitment was

accentuated by the behaviour of individual species, which ranged from spatially random recruitment to strongly aggregative settlement, and also by patchiness in the distribution of planktonic larvae.

The recruitment at the two sites differed consistently. West Lakes panels received consistently higher recruitment than Edithburgh. The number of species colonizing per unit time showed clear summer peaks in West Lakes, and relatively smooth declines as winter approached. In contrast, seasonal trends were much more difficult to identify at Edithburgh, because the number of recruits was usually less than ten per 180 cm^2 per 60 days, and these recruits were spread over a pool of approximately 20 species. There was thus great variation in the number of species colonizing individual panels.

These factors combined to make the variances high for most variables, such as the numbers of recruits of a given species per panel per 60 days, total recruits per panel, or species number. Indeed, standard deviations were often as large as the means. Thus, the colonization events were highly dissimilar, even when the distance between the panels was very small (0.1 m).

Hypothesis 2 must also be rejected.

Hypothesis 3 Chance fluctuations in recruitment are large, but the S values are influenced more by interactions between adult organisms so that the variation in recruitment becomes unimportant.

Interactions between adult organisms on *Pinna* shells are relatively uncommon, with the exception of interactions between colonial forms and serpulid polychaetes, especially *Spirorbis* spp. The next most common interactions are between bryozoan colonies. There is frequently more than one colony of a given species on a single *Pinna* shell, and so two species may interact more than once on a given shell.

These interactions involve overgrowth of one species by another, and, for many pairs of species, neither one can overgrow the other consistently. Interactions on a given *Pinna* shell will then not result in the exclusion of one species by another.

The interactions between colonial tunicates or sponges and other forms have predictable outcomes; the tunicate or sponge will overgrow and exclude the other form. These interactions occur infrequently however, and cannot be said to influence the species composition of many patches.

Thus, interactions between adult organisms, although they occur, appear not to be major influences on the species composition of individual patches, and the composition more strongly reflects those species which recruited successfully into the patches.

Hypothesis 3 is also rejected.

Hypothesis 4 The action of predators modifies the variation in S, and also the existence of a species equilibrium. This hypothesis should be considered together with Hypothesis 5.

Hypothesis 5 Species have differing competitive abilities, and the variation between patches is modified by the presence or absence of particular species.

As mentioned previously, colonial tunicates will overgrow bryozoans and serpulids, and data from pier pilings at Edithburgh (Kay and Keough 1981) suggest that they frequently overgrow sponges. Sponges, again by extrapolation from the pilings as well as by data from *Pinna* shells, generally overgrow bryozoans and always overgrow serpulids. Bryozoans always overgrow serpulids.

There are thus great differences in the competitive ability of individual species. Serpulids and bryozoans can clearly have little effect on the dynamics within a patch. This is hardly the case for sponges, and certainly not for colonial tunicates. Colonial tunicates,

when present, have drastic effects on the composition of a patch. Similarly, their removal (by death of a colony) allows S to increase quickly. The same effect is sometimes seen for sponges, but their growth rate is lower, and they frequently did not cover a shell completely, so that there was only a slight decline in S, spread over a long period of time. Their removal resulted in rapidly increased S, however.

Despite this competitive superiority, sponges and colonial tunicates are not very abundant on *Pinna* shells, especially when compared to their abundance on the pilings. The reason for this can be seen by examining Hypothesis 4.

Colonial tunicates are eaten by small monacanthid fish when the colonies are small. Thus, although reasonable numbers were recorded on settlement panels, no uncaged *Pinna* was colonized by a tunicate which survived to a size at which it could be detected photographically. When predators or, more particularly, monacanthid fish were excluded, there was no change in tunicate numbers for 16 months, presumably because 1978 was not a good year for settlement of these tunicates. There was a dramatic effect in the summer of 1979, when up to 27% of *Pinna* shells in a given caged treatment were colonized by colonial tunicates. Most of these new recruits were *Didemnum* sp. A, an annual species which settles in late spring-early summer and dies off at about the same time the following year (Kay and Keough 1981). In this case, a dramatic fall in S is likely, followed by a rise after the colony dies. The second main tunicate, *Didemnum patulum*, also settles in late spring-early summer, but is longer-lived, with a colony life span of at least 3 years. Thus, when this tunicate becomes established, S declines to 1 and remains low for a number of years. It should be remembered that the longevity of many species is of the order of months, so that a period of 3+ years represents a number of generations for most of the organisms studied. In order to discuss patchiness in a variety of

habitats, we need to make measurements on relative, rather than absolute scales, in this case, number of generations rather than absolute time. Any effect which persists for most species for a number of generations is clearly important.

Little could be said of sponges, since they recruited rarely, and little could be said of the impact of predators on them.

There are thus species which are capable of exerting a profound effect on the composition of a patch, but their effect is not often manifest. We must therefore reject hypothesis 5.

The reason for this lies in the action of predators. They in fact damp the fluctuations in S by removing those epifaunal species which are capable of exerting the greatest influence on S. In this case, whether or not a predator visits a particular patch may influence the subsequent dynamics of that patch, depending on whether tunicates are present. If not, the predators have little effect. In view of the annual life cycles of most of the tunicate recruits together with their low recruitments, it is unlikely that the abundance of tunicates would ever be high, even on caged *Pinna*, since the previous year's recruitment would die off by the following year, and so only a single years recruitment would be present at a given time. It is likely that only a minority of patches would be occupied by tunicates.

We therefore retain hypothesis 4, but note that predators are important on considerably less than half of the observed *Pinna*.

Individual species differ greatly in their properties, and the most dramatic changes are produced by a few tunicate and sponge species. It appears that the tunicates are only vulnerable for a few weeks, until the colony matrix becomes packed with calcareous spicules. I have not observed any fish species feeding on large didemnid ascidians. During the vulnerable stage, the tunicates are preyed upon heavily by two species of mobile predators, which are themselves abundant for only a

short period each year. This is sufficient to keep the abundance of tunicates low. The most important interactions on *Pinna* shells thus involve only a few species, and the synchrony of various aspects of their life histories for a few weeks of each year.

Although predators are important, and diminish the fluctuations in S, it should be emphasized that the fluctuations in S are still far from being narrowly bounded.

The conclusion then is that the equilibrium model of MacArthur and Wilson is not very useful in explaining the dynamics of the epifauna of *Pinna bicolor* at Edithburgh. There are several reasons for this, and while it may be possible to classify some causes as more important, it would be pointless to erect one of these artificially as the cause.

Recruitment is clearly variable and, when colonization occurs in low numbers (i.e., with low probabilities on a particular shell) for most species, we would expect chance to be important, and to result in widely disparate colonization events on similar patches. Recruitment can be shown to be more similar when patches are closer together.

Plankton patchiness and the behaviour of larvae may have predictable effects, but the existence of patches, and their position, is difficult to predict *a priori*, and may in practice need to be regarded as random variables. Similarly, the distribution of recruits of a given species whose larvae are gregarious may be predictable when the distribution of adults is known, but the latter may be impossible to predict accurately, and may need to be regarded as a random variable. The variation in colonization events is further enhanced by the behaviour of individual species, which varies widely.

After colonization, interactions between adult organisms are not common. Nevertheless, their competitive abilities vary, and range from species which are unable to influence patch composition to those

which can exert a profound influence.

The assumption that differences in the behaviour of individual species are insignificant is thus unjustified, and contributes to the failure of the equilibrium model, in this case mainly by variation in recruitment. This finding may seem trivial, but it was nevertheless possible that the differences in behaviour of individual species could "average out", and S, with its flaws, still prove to be a useful descriptor. This does not appear to be the case.

6.2 The Generality of these Results.

Some mention has been made in earlier chapters of the difficulty in obtaining sufficient replicates to measure the levels of chance variation. Similarly, the method of testing for equilibrium or narrow boundedness requires a number of censuses of the biota of a patch, and such sample sizes appear rare in the literature. Thus, the question of whether the concept of a species equilibrium is useful can not be answered for most patchy habitats.

It is, however, possible to consider the reasons for the failure of the model for the epifauna of *Pinna*, and hypothesize about their generality.

Variation in recruitment is likely to be highest when probabilities of colonization for individual species are low, and species pools are high. The question of whether immigrations onto islands are rare or common is unresolved (see Abbott 1979 for a review), but there is at least a body of evidence and opinion to suggest that for birds in some kinds of patchy habitats, immigrations are rare. In most other cases the species pools are much larger than that at Edithburgh, and since the variation in recruitment is a statistical phenomenon rather than a biological property of the component organisms, we would expect that a high level of between-patch variation in recruitment events would

be rather common in other patchy habitats.

In a similar way, individual species are acknowledged to differ greatly in their biology, and there are many examples in which one or a few species may exert a major influence on patch composition. It is difficult to remove or introduce such species in many habitats, and so their effect are difficult to document. It again seems likely that such species will be not uncommon. We should expect that the variables influencing patch composition in this study will not have the same relative degrees of importance in other habitats. For example, species which are good competitors may be more important than chance when probabilities of immigration are higher. Therefore, in some habitats, the actions of one or a few species may be enough to make the equilibrium model not useful.

The above of course does not remove the need to test the model in other habitats, but does suggest that the equilibrium model is not generally useful. This is reinforced when the communities in which disturbances are frequent (i.e. "non-equilibrium" situations) are taken into account.

With the knowledge that the equilibrium model does not help our understanding of the epifauna of *Pinna*, and that S is not a useful variable to describe the community due to differences in the behaviour of individual species, it is now appropriate to review the dynamics of *Pinna* epifauna, and to consider alternative approaches.

6.3 *Pinna* epifauna at Edithburgh

Recruitment is extremely variable, and occurs at very low levels. As a result of this total percent covers are low, and are less than 50% for most shells.

The epifauna of most shells is dominated by bryozoans, and

serpulids are numerous, even though they only occupy 1-2% of space on shells. The actual set of species which occur on each shell varies, but *Spirorbis* spp. occur on more than 98% of shells, and bryozoans on 97% of shells. *Schizoporella* and *Parasmittina* are usually present, with *Celleporaria fusca*, B7, and *Triphyllozoon monolifera* the most common of the rest.

Solitary forms occur not uncommonly, and the most common are the vermetid gastropod M48 and the solitary tunicate *Polycarpa pedunculata*.

Occasional shells bear colonial tunicates or sponges, and these species do very well when present, and are capable of excluding most other species. Tunicates in particular are limited only by the size of the patch in which they occur.

We can thus categorize the composition of most patches as being determined primarily by recruitment events, with adult-adult interactions being unimportant. In a minority of patches, interactions between mobile predators and juvenile ascidians are important, and competition between colonies is only important in those patches on which (a) there has been settlement of tunicates and sponges, and (b) these have not been eaten while small.

All of these processes are variable, and high standard deviations relative to means are general, and indicative of a high level of between-patch variation.

Physical disturbances appear rare. Apart from the time when the caging experiment was destroyed, I have no records of strong wave action, and certainly wave action was never sufficiently strong to overturn rocks or tear colonies off shells. Sand scour presumably can occur, but it is likely to be a continual stress, rather than the kind of disturbance which prevents "equilibria" being reached.

A number of interesting questions can be raised about the

abundance of various taxa such as tunicates and sponges, which are surprisingly rare considering their competitive ability.

As has been shown, tunicates are limited to a large degree by predation upon newly-settled juveniles. No such explanation could be postulated for sponges, however. They did not recruit heavily during the study, and Kay and Keough (1981) showed that they recruited less frequently than any other major taxon. Indeed their abundance on the pilings was due to the vegetative growth of established colonies, rather than the frequent settlement of dispersive larvae. On *Pinna*, the colonies can not grow beyond the edge of the shell, and major increases in the abundance of a given taxon must be made by the recruitment of larvae. Sponges are clearly unable to do this, and so I suggest that sponges have low abundance due simply to their low recruitment rates.

The low total percent covers are also puzzling. Total covers are low relative both to pilings on the pier, and to *Pinna* shells elsewhere. This study did not permit any investigation of the reasons for this, but a number of possible alternatives exists. One of the models for the circulation of water in Gulf St Vincent (Bye 1976) postulates that the main source of water for Edithburgh is that which comes up through Investigator Strait from the Southern Ocean. It is possible that the source area contains low densities of the species which live on *Pinna*, and only those with extremely long-lived planktonic larvae will be transported. Other larvae may be recently released in the area, but since total cover is low, we might expect that the number of such larvae is low. Total cover is high on the pilings (Kay 1980; Kay and Keough 1981), but the total area of the pilings is not large, and the number of larvae produced by species on the pilings may be low when dispersed over a moderately large area.

It is possible that the density of larvae is not low initially, but that food levels are low for the planktonic larvae or predators may

limit their numbers, so that few survive. Alternatively, the adult organisms may not receive much food, and their reproductive output and growth may be lowered.

Feeding by *Pinna* may reduce the number of settling larvae, but this does not explain the difference between *Pinna* at Edithburgh and elsewhere.

This question is clearly one that would warrant at least one additional thesis.

6.4 Alternative Approaches

The degree of chance variation makes it unlikely that any model can be used to make accurate quantitative predictions about individual species. The model developed and tested in Chapter 5 assumes that the actual identities of species are unpredictable, but that patches of a particular size and type will tend to be occupied by species which have a particular set of life-history characteristics. The model generated a series of predictions about the abundance of tunicates, sponges and bryozoans in patches of various sizes and degrees of isolation from each other. These predictions were for the most part fulfilled, and in no case was a hypothesis rejected.

Disturbances are rare at Edithburgh, and so the model did not include this. Although interactions between adult organisms are rare on *Pinna*, the model predicted that patch composition should become more heavily influenced by adult-adult interactions with increased patch size and with decreasing isolation of patches. It is thus intermediate between a neutral model which assumes no biological interactions, and hypotheses such as those of Diamond (1975), which postulate interspecific competition as the important factor.

Most other approaches assume either explicitly or implicitly, that the occupants of a patch will be a more of less random subset of the

available species pool. This model differs in this respect also, since although colonization is viewed as a random process the species which are most likely to occupy patches of a given type have a number of life-history attributes in common. The occupants of a patch are thus not a random subset of the available species pool.

As mentioned in Chapter 5, the model is simplified, involving a single guild, and excluding predators and physical disturbances. Before attempting to develop it further, we can get an initial idea of whether the model has any chance of proving to be of general use. Non-random subsets of species pools have been reported by Jackson (1977b) for sessile invertebrates beneath coral heads, although he did not demonstrate that the importance of biological interactions varied with patch size.

Similarly, Diamond (1974, 1975) found that certain bird species in New Guinea occur predominantly on small islands, while others are found only on larger islands. He labelled the small island specialists "supertramps", and alleged that they are excluded by other species on larger islands. They are notable for being good colonizers and poor competitors. These attributes seem rather similar to those of bryozoans or serpulids at Edithburgh, but the coining of "supertramps", together with "A-, B-, C-, and D- tramps", and "high-S species" to describe birds found mainly on various other patch types, seems a needless proliferation of jargon, since these are essentially arbitrary categories.

It is clearly premature to claim any generality for this approach, if indeed such generality is possible, but it seems hopeful that this approach may prove useful in other habitats.

We can expand the model somewhat, as follows. Consider the basic curves of abundance vs patch size for two types of species; good competitors, poor colonizers; poor competitors, good colonizers (Figure 6.1). These are merely examples which correspond to the major taxa at

Edithburgh, and other combinations of life-history attributes are possible, and to be expected. It is tempting to view the two examples as "K-" and "r-" species, but it should be remembered that the colonial tunicates are generally very short-lived, and thus do not fit this classification.

There is a number of factors which may affect these curves of abundance versus patch size, and I propose to explore them individually, considering their effect on the two basic curves. Factors may be combined to produce curves which apply to situations where a number of these factors operate. Again, relatively extreme cases will be used as examples, but interpolation is possible to generate expectations for intermediate situations.

Recruitment rate

This has already been covered in Chapter 5 (see Figure 5.2) but, briefly, increase in the recruitment rate causes a shift in location for the poor competitor good colonizer (PCGR) species, while the good competitor poor colonizer (GCPR) species show a change in location and shape of the curve. At high recruitment rates, GCPR species should be present on a wide range of patch sizes, and their optimal patch size should be reduced. They would do less well on large patches than when recruitment is low. PCGR species, on the other hand, would have their chances of survival lowered on all patch sizes, and their optimal patch size may be altered (see Figure 5.2).

Disturbance

Physical disturbances are likely to affect all patches, although the largest patches may not be as heavily damaged. Examples of this are fire, which would burn out a small patch of bushland completely, but would be stopped before a large patch was destroyed totally, or a piece of wave borne debris which might only damage part of a large patch, while obliterating a small one. Nevertheless, GCPR species would be destroyed in some patches and would be forced to reinvade by dispersive propagules.

This would be a slow process, and would result in a general lowering in abundance. This would be expected to occur across all patch sizes. PCGR species would then be able to invade a wider range of patch sizes, and could be expected to increase in abundance in larger patches. Their abundance should stay at a similar level in small patches. The resultant curves are shown on Figure 6.2.

Predators

The effect of predators will vary depending on their feeding behaviour. If a predator is generalized, and reduces the abundance of all species equally, the principal effect would be a lowering of the abundance of most species across all patch sizes. PCGR species, however, may become relatively more abundant in large patches, as space becomes available for colonization (Figure 6.3).

If the predator preys preferentially on GCPR species, we expect a downward shift in the GCPR curve, and again, since competitive exclusions are decreased in large patches, a change in the shape of the PCGR curve is expected (Figure 6.4).

Biological Interactions within patches

We can also generate some expected distributions for the importance of adult-adult interactions as a function of patch size for each of the above situations.

High recruitment

These interactions become more important in small patches, and remain important in larger patches (Figure 6.5).

Disturbance

Interactions remain unimportant on small patches, and become less important in larger patches.

Predation

(a) non-specific: Biological interactions become less important in all patch sizes.

(b) specific: Interactions remain unimportant in small patches, and decrease in importance in large patches.

The model can thus be expanded to generate patterns of abundance when disturbance or predation occur. These are relative patterns, however, and some knowledge of the habitat under study is necessary before the model can be used. It also requires considerably more detailed knowledge about the biology of the component species, and makes no specific quantitative predictions. While these are obstacles to quick and easy use, the results obtained by using this model are helpful for understanding the epifaunal communities at Edithburgh.

There is clearly a large number of predictions made by the above expansion, and considerable scope for testing them in the future.

Figure 6.1 Relation between abundance and patch size for species which are good competitors, poor recruiters (GCPR), and poor competitors, but good recruiters (PCGR). Graphs are for low levels of recruitment.

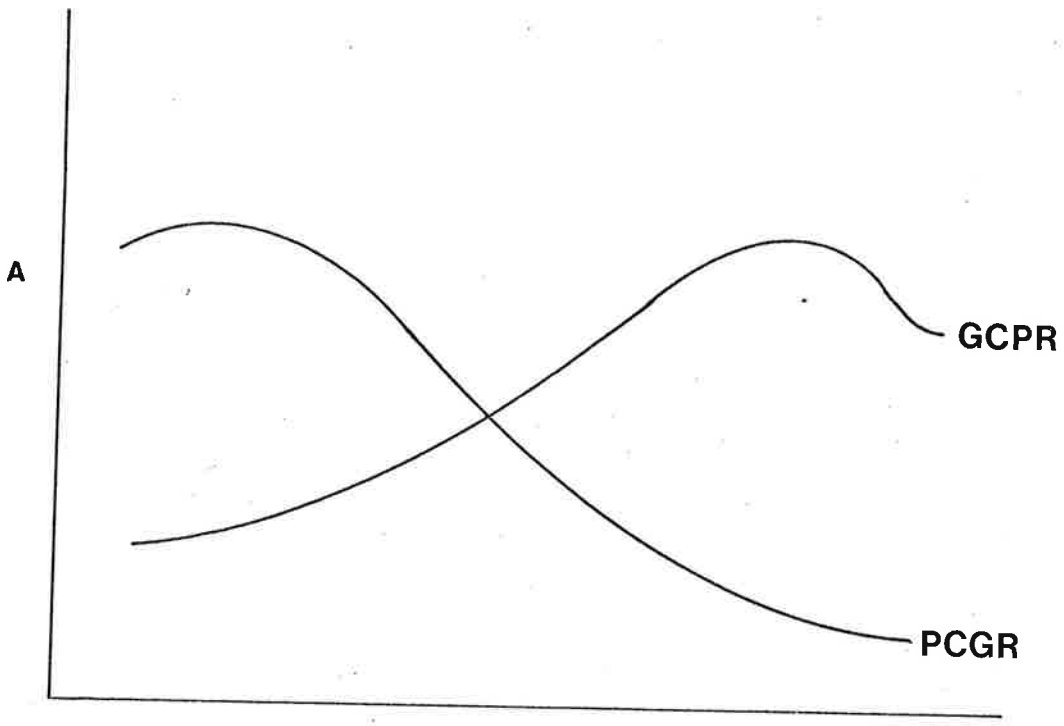
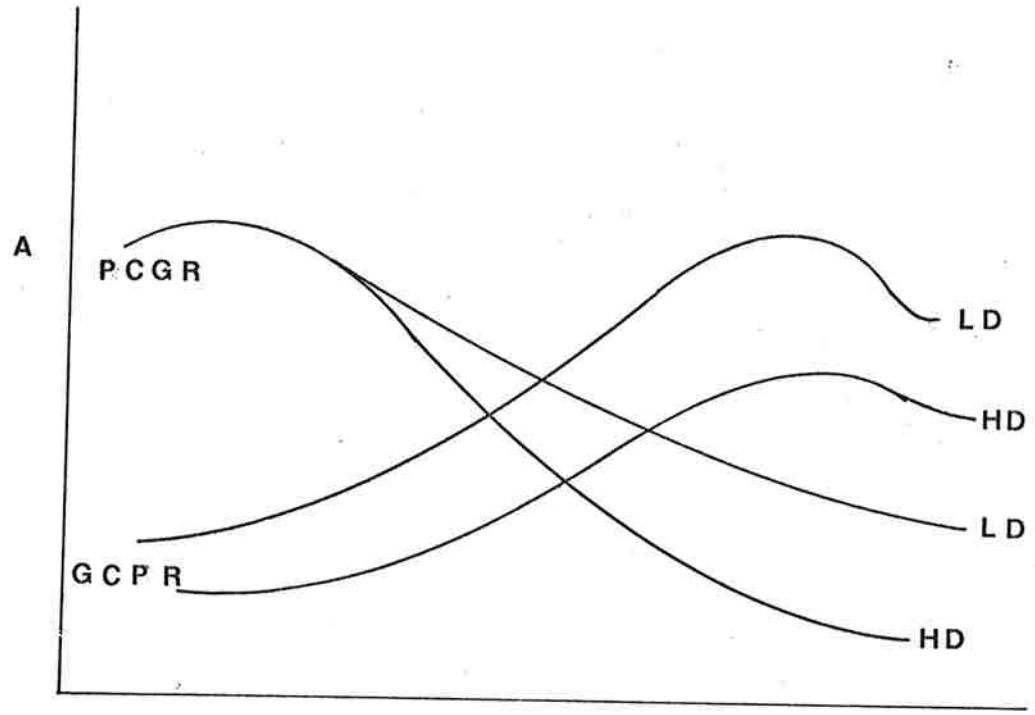
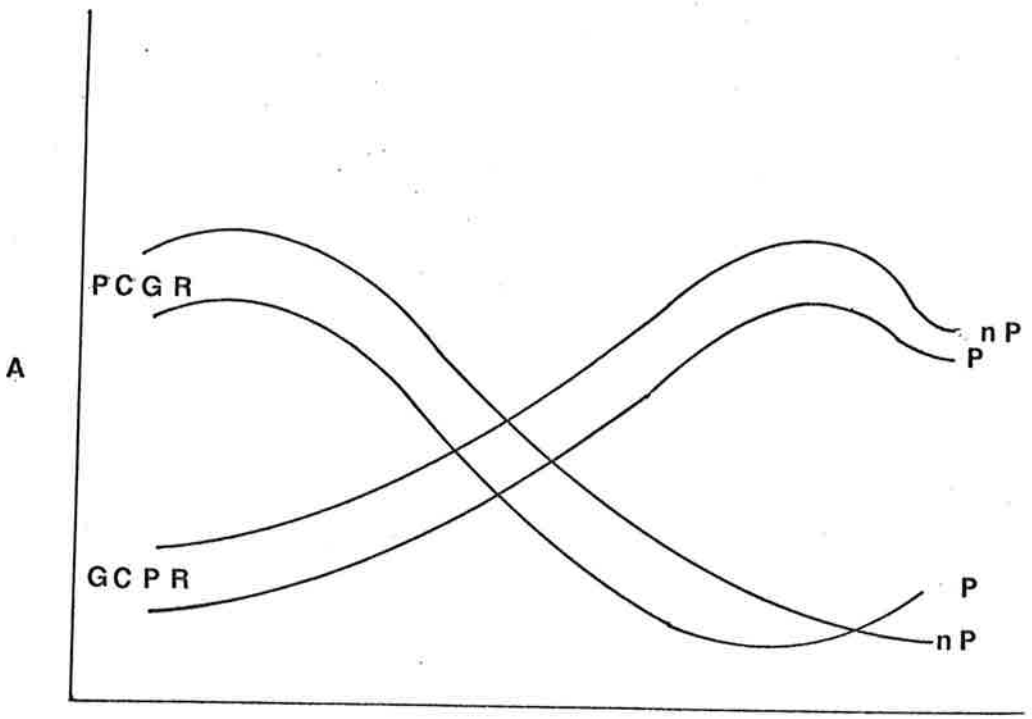

A
GCPR
PCGR
PATCH SIZE

Figure 6.2 Relation between abundance and patch size for species which are good competitors, poor recruiters (GCPR), and poor competitors, poor recruiters (PCGR), with either high(HD), or low (LD) disturbance levels.

Figure 6.3 Relation between abundance and patch size for species which are good competitors, poor recruiters (GCPR), or poor competitors, poor recruiters (PCGR), with a generalist predator either present (P), or absent (nP).





PATCH SIZE

Figure 6.4 Relation between abundance and patch size for species which are good competitors, poor recruiters (GCPR), and poor competitors, good recruiters (PCGR), when a predator which preys upon GCPR species is present (P), or absent (nP)

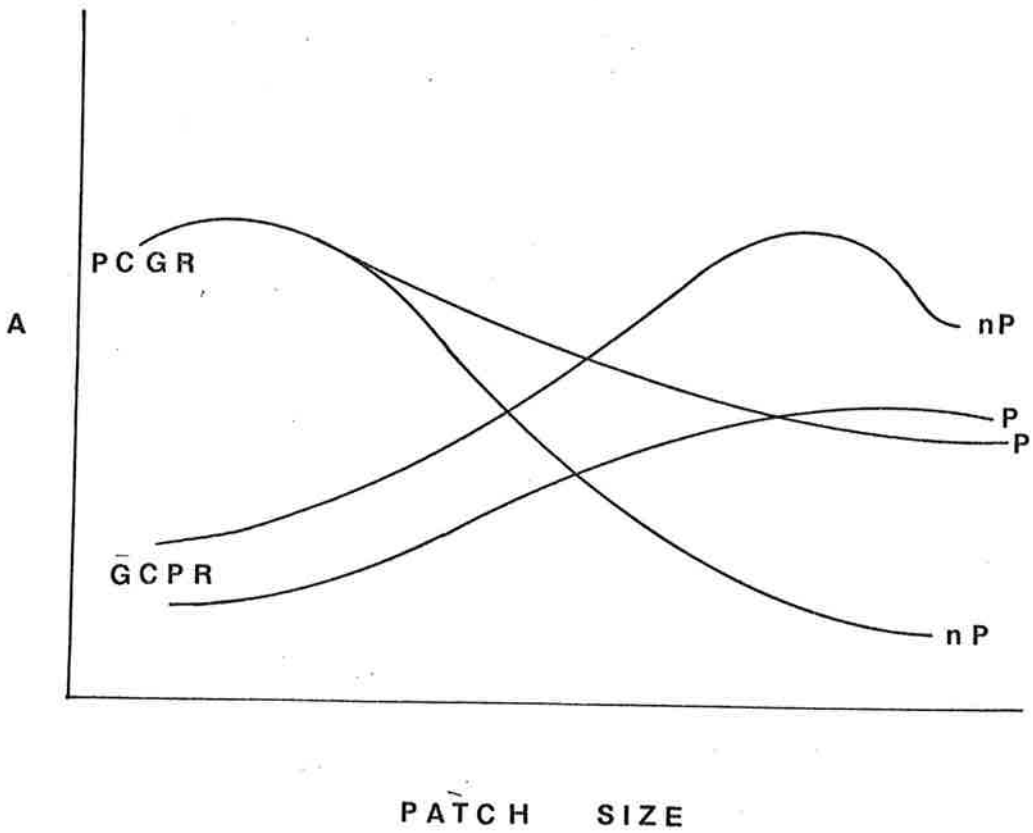
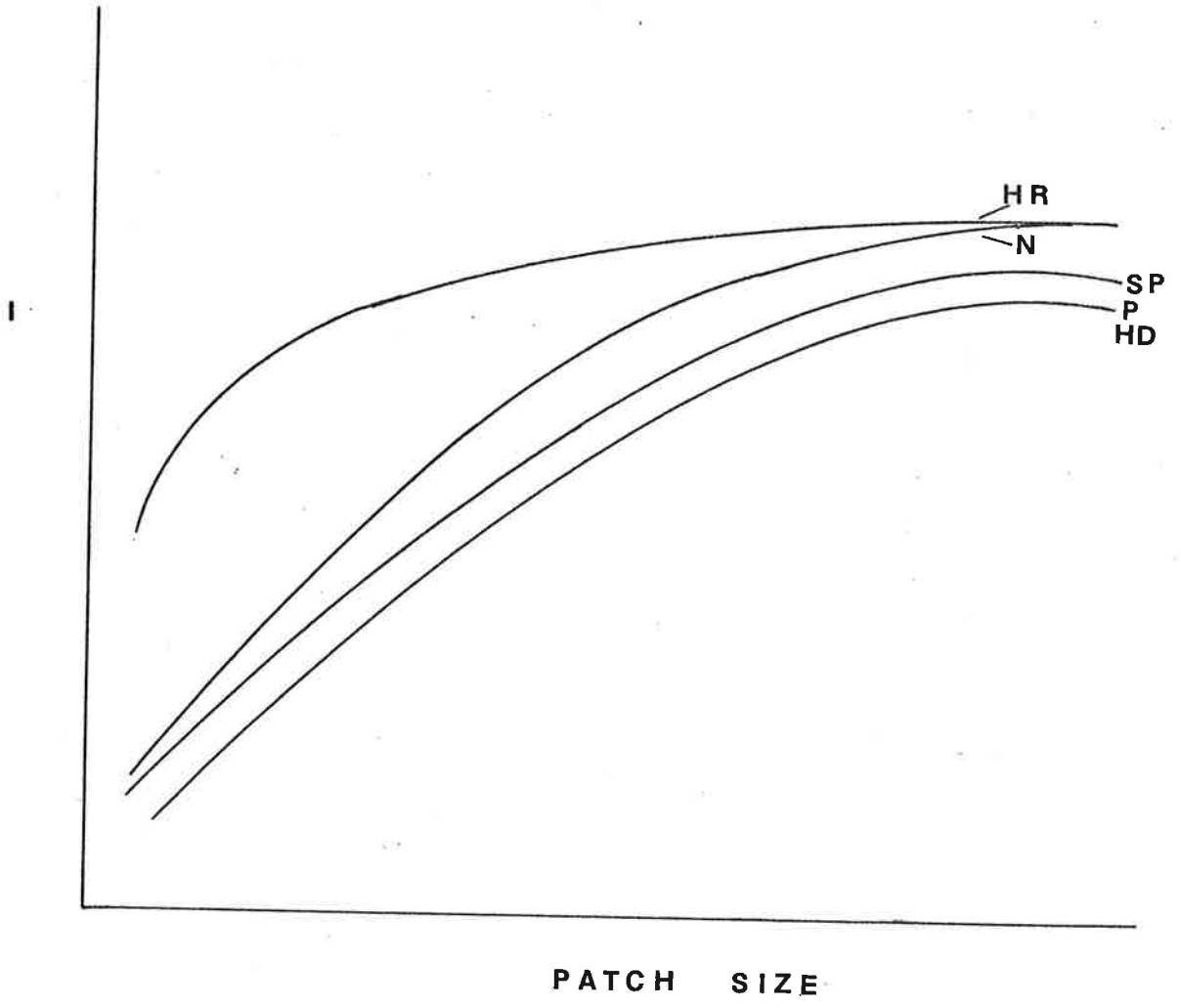

A
PCGR
GCPR
nP
P
P
nP
PATCH SIZE

Figure 6.5 Change in the importance of interactions between adult occupants of a patch in infuencing the composition of a patch, as a function of patch size. 'N' - normal, i.e low recruitment, low disturbance, no important predators. 'HR' - high recruitment levels for GCPR species. 'SP' - predator specific to GCPR species present. 'P' - generalist predator present. 'HD' - high levels of disturbance.


HR
N
SP
P
HD
I
PATCH SIZE

APPENDIX 1.1 : Species recorded from West Lakes.

PORIFERA

Aplysilla rosea Schulze

Aplysilla sulphurea Schulze

SP5

SP7

SP12

SP28

CNIDARIA

Anthothoe albocincta (Hutton)

Cnidopus verater

Tubularia larynx Ellis and Solander

ANNELIDA - SERPULIDAE

Galeolaria hystrix Morch

Hydroides norvegica (Gunnerus)

Pomatoceras terrae-novae

Spirorbis convexis Wisely

Spirorbis pagenstecheri (Quoy and Gaimard)

CRUSTACEA

Balanus amphitrite Darwin

Carcinus maenas Linnaeus

Elminius modestus Darwin

Halicarcinus ovatus (Stimpson)

Portunus pelagicus (Linnaeus)

MOLLUSCA

Aglaja taronga Allan	Aglajidae
Austreolis ornata (Angas)	Eolidae
Bedeva hanleyi Angas	Muricidae
Chlamys bifrons (Lam.)	Pectinidae
Cominella eburnea (Reeve)	Buccinidae
Dendrodoris nigra (Stimpson)	Doridae
Dorid sp.	Doridae
Electroma georgiana Quoy and Gaimard	Pterildae
Elysia sp. (?)	Elysiidae
Lepsiella vinosa Lamarck	Muricidae
Limatula strangei Sowerby	Limidae
Modiolus pulex Lamarck	Mytilidae
Monia ione Gray	Anomiidae
Mytilus planulatus Lamarck	Mytilidae
Nassarius pyrrhus Menke	Nassariidae
Ostrea angasi Sowerby	Ostreidae
Phasianella australis Gmelin	Turbinidae
Thais orbita Gmelin	Muricidae
M31	
M32	

BRYOZOA

Bugula stolonifera Ryland

Bugula neritina (Linné)

Cryptosula pallasiana (Moll)

Schizoporella schizostoma

Scrupocellaria sp.

ECHINODERMATA

Amblypneustes pachistus H.L. Clark

Amphipholis squamata (D. Chiaje)

Coscinasterias calamaria (Gray)

Heliocidaris erythrogramma (Valenciennes)

Patiriella brevispina H.L. Clark

Uniophora granifera Lamarck

ASCIDEACEA

Ascidia aspersa

Atapazoa fantasiana (Kott)

Botrylloides leachii (Savigny)

Botryllus schlosseri (Pallas)

Ciona intestinalis (Linnaeus)

Halocynthia hispida (Herdman)

Polycarpa papillata (Sluiter)

Polycarpa pedunculata Heller

Didemnidae sp. T18

TELEOSTII

Acanthopagrus butcheri Munro	Sparidae
Ammotretis rostratus Guenther (?)	Pleuronectidae
Arripis georgianus (Cuvier and Valenciennes)	Arripidae
Australuzza novaehollandiae (Guenther)	Sphyraenidae
Gobius bifrenatus Kner (?)	Gobiidae
Gymnapistes marmoratus (Cuvier and Valenciennes)	Scorpaenidae

APPENDIX 1.2 : List of species recorded from Edithburgh study grid.

PORIFERA

Aplysilla rosea Schulze

A. sulphurea Schulze

Callyspongia sp.

Dysidea fragilis Montagu

SP 35

SP 36

CNIDARIA

Carybdea rastonii Haacke

Cerianthus sp.

Culicia sp.

Plesiastrea urvillei Milne-Edwards and Haime

Scolymia australis (Milne-Edwards)

ANNELIDA - SERPULIDAE

Filograna implexa Berkeley

Galeolaria caepitosa Savigny

G. hystrix Morch

Hydroides norvegica (Gunnerus)

Spirorbis convexis Wisely

S. pagenstecheri Quoy and Gaimard

Spirorbis sp. C

Spirorbis sp. D

CRUSTACEA

Cryptodromia octodentata (Haswell)

Epopella simplex (Darwin)

Leander sp.

Leptomithrax australiensis (Miers)

Naxia sp.

Nectocarcinus integrifrons (Laetrille)

Scalpellum peronii

MOLLUSCA

	Family
Asteracmaea crebristriata Verco	Acmaeidae
Atrina tasmanica Tennison Woods	Pinnidae
Cardium sp.	Cardiidae
Ceratosoma brevicaudatum Abraham	Doridae
Chlamys asperrimus (Lamarck)	Pectinidae
C. bifrons (Lamarck)	Pectinidae
Chromodoris epicurea Burn	Doridae
Cypraea friendii thersites Gaskoin	Cypraeidae
C. comptoni Gray	Cypraeidae
Dendrodoris nigra (Stimpson)	Doridae
Eupyrmna stenodactyla Grant	Sepiolidae
Fusinus australis Quoy and Gaimard	Fasciolariidae
Haliotis cyclobates Peron	Haliotidae
H. laevigata Doravan	Haliotidae
Hapalochlaena maculosa Hoyle	Octopodidae
Lyria mitraeformis Lamarck	Volutidae
Notovola alba Tate	Pectinidae
Oliva australis Duclos	Olividae
Phasianella australis Gmelin	Turbinidae

	Family
Pinna bicolor Gmelin	Pinnidae
Pleurobranchus hilli Hedley	Pleurobranchidae
Pleuroploca australasia Perry	Fasciolariidae
Polinices conicum (Lamarck)	Naticidae
Pterynotis triformis Reeve	Muricidae
Octopus australis Hoyle	Octopodidae
Scutus antipodes Montfort	Fissurellidae
Sepia mestus Gray	Sepiidae
Sepioloidea lineolata Quoy and Gaimard	Sepioloideidae
Sepioteuthis australis Quoy and Gaimard	Lologinidae

BRYOZOA

Biflustra (*Membranipora*) *perfragilis* MacGillivray

Bugula sp.

Celleporaria fusca (Busk)

C. pigmentaria (Waters)

Celleporaria sp.

Cryptosula pallasiana (Moll)

Schizoporella schizostoma

Scrupocellaria sp.

Parasmittina raigii (Audouin)

Triphyllozoon monolifera (MacGillivray)

B7

ASCIDIACEA

Atapazoa fantasiana (Kott)

Botrylloides leachii (Savigny)

Botryllus schlosseri (Pallas)

Cnemidocarpa etheridgii (Herdman)

Cystodytes dellechiajei (Della Valle)

Didemnum patulum (Herdman)

Didemnum sp. A (T9)

Halocynthia hispida (Herdman)

Phallusia depressiuscula (Heller)

Podoclavella cylindrica (Quoy and Gaimard)

Polycarpa pendunculata (Heller)

Pycnoclavella diminuta (Kott)

Pyura irregularis (Herdman)

Sycozoa tenuicaulis (Herdman)

Didemnidae sp. T18

TELEOSTII and ELASMOBRANCHII

	Family
Aracana ornata (Gray)	Ostraciotidae
Aspasmogaster tasmaniensis (Guenther)	Gobiesocidae
Australuzza novaehollandiae (Guenther)	Sphyraenidae
Brachaluteres jacksonianus (Quoy and Gaimard)	Monacanthidae
Chelmonops truncatus (Kner)	Chaetodontidae
Cheilodactylus nigripes Richardson	Cheilodactylidae
Dactylophora nigricans (Richardson)	Cheilodactylidae
Diodon nichtemerus (Cuvier)	Tetraodontidae
Echinophryne crassispina McCulloch and Waite	Antenariidae
Enoplosus armatus (White)	Enoplosidae
Eubalichthys mosaicus (Ramsay and Ogilby)	Monacanthidae
Girella zebra (Richardson)	Kyphosidae
Glyptauchen panduratus deruptus Whitley	Syngnathidae
Gymnapistes marmoratus (Cuvier and Valenciennes)	Scorpaenidae
Gobius lateralis Macleay	Gobiidae
Hippocampus breviceps Peters	Syngnathidae

	Family
Histophryne scortea McCulloch and Waite	Anterariidae
Hypnus monopterygium (Shaw and Nodder)	Torpedinidae
Hyporhampus melanochir (Cuvier and Valenciennes)	Hemiramphidae
Neoodax sp.	Odacidae
Kathetostoma laeve (Bloch and Schneider)	Uranoscopidae
Parapercis haeckel (Steindachner)	Mugiloididae
Parequula melbournensis (Castelnau)	Gerridae
Pempheris klunzingeri McCulloch	Pempheridae
Phycodurus eques eques (Guenther)	Syngnathidae
Platycephalus bassensis Cuvier and Valenciennes	Platycephalidae
P. fuscus Cuvier and Valenciennes	Platycephalidae
Scorpis aequippinis Richardson	Scorpididae
Sillaginoides punctatus (Cuvier and Valenciennes)	Sillaginidae
Sphaeroides armilla (McCulloch and Waite)	Tetraodontidae
Sphyraena novaehollandiae (Gunther)	Sphyraenidae
Stipecampus cristatus (McCulloch and Waite)	Syngnathidae
Torquigener pleurogramma (Regan)	Tetraodontidae
Trachichthys australis Shaw and Nodder	Trachichthyidae
Upeneichthys porosus (Cuvier and Valenciennes)	Mullidae
Urolopus testaceus (Mueller and Henle)	Urolophidae
Vincentiana conspersus (Klunzinger)	Apogonidae
Labridae sp.	Labridae

Appendix 1.3

THE MARINE BENTHIC FAUNA OF EDITHBURGH.

I. THE ECHINODERMS.

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SUMMARY

Forty-nine echinoderm species are reported from a variety of habitats around the Coobowie Marine Research Station near Edithburgh. Notes on the abundance and microhabitat of each species are provided, together with a summary of the species associations found in each main habitat type.

There is a lack in South Australia of detailed faunistic studies of a single marine area. No survey comparable to those of Port Philip and Westernport Bays in Victoria or to that of Cockburn Sound in Western Australia exists. The result of this is that the marine collections in museums contain no account of the associations of animals that are to be found within a small geographic area. In addition, much of the collection of the South Australian Museum dates from the first half of this century, and specimens bear locality details which are not very useful.

The area around the Coobowie Marine Research Station of the University of Adelaide (Figure 1), including the pier at nearby Edithburgh, has recently become the focus of a number of ecological studies (Butler 1979; Butler & Brewster 1979; Kay & Keough 1980a, b; Keough 1979; McKillup & Butler 1979). Other works have made use of material collected from this area (e.g. Ey & Jenkin in press; Keough *et al.* in press; Schluter *et al.* in press). There is clearly a need for a detailed knowledge of the fauna of the area, and also the distributions and habitats of the various species. This paper is the first of a series each dealing with a particular faunal group.

Most of the collections being discussed here come from the area delimited by Marion Reef, Sultana Point, Coobowie, and Troubridge Island (Figure 1). The shoreline is generally of low wave energy, and both limestone reefs and sandy shores may be found. The shores vary in slope from tidal flats 100 - 1000 metres in extent to platform reefs. Subtidally, large beds of seagrass, *Posidonia australis* var. *angusta* Hook, are found close to shore in shallow water (0 to 5 metres in depth). Offshore, the seafloor varies from broken limestone rubble to broken limestone reefs to sandy bottoms. Aggregations of the bivalve *Pinna*

bicolor Gmelin occupy a large proportion of offshore localities. Beds of Posidonia australis Hook, along with lesser concentrations of the other seagrasses Halophila ovalis Hook and Amphibolis antarctica (Labill.) similarly occupy large areas of the sandy bottom, while many scattered rocks are covered with the alga Scaberia aghardii. The offshore Pinna bicolor habitat is more fully described by Butler and Brewster (1979). McKillup (1979)[1] and McKillup and Butler (1979; see their Fig. 1) similarly cover some of the intertidal localities, and Kay and Keough (in press), Butler (1979) and Kay (1980)[2] describe the environment around Edithburgh pier.

All specimens were taken by divers using SCUBA, with the exception of intertidal specimens. The study area was not sampled with uniform intensity. Figure 1 gives some idea of the frequency of sampling. Classification of specimens follows the schemes of Shepherd (1968), asteroidea; Baker (1981a), Ophiuroidea; Baker (1981b), Echinoidea; Rowe (1981), Holothurioidea; and Clark (1966), Crinoidea. Keys to the relevant group may be found in each of these publications. Species are listed in taxonomic order following each of the above sources. It should be noted that the method of collection must underestimate the abundance and/or presence of echinoids of the orders Clypeasteroida (sand dollars), Cassiduloida, and Spatangoida (heart urchins). Burrowing or very small holothurians will be similarly underrepresented in this account.

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[1] McKillup, S.C. (1979) Behavioural differences between populations of Nassarius pauperatus (Mollusca:Prosobranchia). Ph.D. thesis, Department of Zoology, University of Adelaide.

[2] Kay, A.M. (1980) The organization of sessile guilds on pier pilings. Ph.D. Thesis, Department of Zoology, University of Adelaide.

PHYLUM ECHINODERMATA

Subclass Asteroidea

Order Platyasterida

Luidia australiae Döderlein. The sole record of this species in the general area is a single specimen in the South Australian Museum taken "between Troubridge Island and Kangaroo Island", bearing no date or collector's name. Clark (1928) cited the collector as Dr Verco, but gave no further details. This large blue and yellow species is common on sandy bottoms in other parts of St. Vincent Gulf, so its presence would not be surprising. For the present, it must remain doubtful.

Order Phanerozonia

Astropecten vappa Müller & Troschel. This species burrows in sand, and is not often seen exposed. It has been recorded from the area mid-way between Edithburgh and Troubridge Island.

Pentagonaster duebeni Gray. This bright orange or yellow sea star occurs wherever rocky reefs are found within the area, for example the rocks abutting the pier at Edithburgh and the reefs between Troubridge Island and Marion Reef. It does not occur on the sandy bottoms of the area.

Tosia australis Gray. Almost all habitats contain some of this species, and it is the most common asteroid beneath the pier at Edithburgh. Also occurs on intertidal limestone reefs to the North of Edithburgh, and is widespread among Pinna beds. Further details of this species are given by Keough and Butler (1979). Shepherd (1968) also recorded the species as being common at Edithburgh.

Anthaster valvulatus (Müller & Troschel) is uncommon, and is occasionally recorded from sandy bottoms in the bay at depths of 5 to 8 metres.

Petricia vernicina (Lamarck). A large population of this species occurs under the pier at Edithburgh, feeding on the fauna of the pilings and also debris on the seafloor which bears encrustations similar to those on the pilings (Keough 1976)[3].

Austrofromia polypora (H.L. Clark) appears to be restricted to the only area of moderate surge, the rocky reefs between Troubridge Island and Marion Reef.

Order Spinulosa

Asterina atyphoida H.L. Clark. This little seastar lives under rocks. It is widespread, but never present in great numbers. The colour of living specimens taken from depths between 2 and 10 metres differs from the colour of specimens from deeper than 13 metres taken by Shepherd (1968). Specimens from the Edithburgh area are pink-red aborally, with green tips to the arms. Oral surfaces are cream.

Patiriella brevispina H.L. Clark is the most abundant species of the area. It may be found in large numbers in Posidonia beds close inshore, from one to five metres in depth, and is common under the pier. Frequent sightings of this species are made on the Pinna beds offshore. Keough and Butler (1979) record the diet of this species as being colonial ascidians and many moribund items.

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[3]Keough, M.J. 1976 The role of asteroid predators in determining the structure of jetty pile communities. B.Sc. (Hons.) Thesis, Department of Zoology, University of Adelaide.

Patiriella exigua (Lamarck) is the only seastar which is restricted to the intertidal zone, and it is extremely abundant on the tidal flats between Sultana Point and Coobowie. It is usually less than 20mm in diameter, and is green aborally, and blue-green orally. The seastars may live exposed on the sand or under small limestone rocks.

Patiriella gunnii (Gray). This variably coloured, cryptic species is occasionally found under rocks at a variety of depths, but is common only on the reefs between Troubridge Island and Marion Reef.

Nepanthia troughtoni (Livingstone). Shepherd (1968) cites this species as being indicative of relatively exposed environments, and it is confined to the area South of Troubridge Island, where it is common. It reaches R = 100mm, and is pinkish white in colour.

Echinaster arcystatus H.L. Clark. An uncommon species which appears confined to the same area as Nepanthia troughtoni.

Order Forcipulatida

Coscinasterias calamaria (Gray). This many-rayed species is the largest seastar in South Australia, and individuals up to 60cm in diameter have been recorded in the bay. Smaller specimens are common in shallower water (intertidal to 3m depth), and larger specimans are found in progressively deeper water. Juveniles are found living under rocks, while the adults move about in the open. Large individuals (R > 15cm) feed on Pinna bicolor and its epifauna, and also on a variety of species on and around pier pilings such as crabs, molluscs and ascidians, as well as scavenging. (Keough & Butler 1979).

Uniophora granifera Lamarck, Abundant around the pier, and common subtidally from Coobowie to Sultana Point. Commonly seen feeding on the epibiota of Pinna bicolor. Juveniles (R < 2cm) are found in the same general area as adults, but are cryptic. Maximum size of the adults is R = 70mm.

Allostichaster polyplax (Müller & Troschel). A small (R up to 3cm), cryptic seastar which is widespread throughout the area. It occurs under rocks and other debris from the intertidal down to at least 10 metres, where it is reported to feed on molluscs and encrusting organisms (Shepherd 1968).

Smilasterias irregularis H.L. Clark is an uncommon, cryptic seastar, only a couple of specimens of which have been taken, both near the pier. The species autotomizes readily when removed from the water.

SUBCLASS OPHIUROIDEA

Order Phrynophiurida

Ophiomyxa australis Lütken. A large, variably coloured species, it is found under rocks and debris at all depths within the area. Very common, and moves about ton the pond at night. Its arms are not very flexible, and these ophiuroids are relatively sluggish.

Astroboa ernae Döderlein. Only a single specimen of this species has been taken. It was found on a Pinna shell at the pier in only four metres. The branched arms and pink colour make this a very easily recognisable species.

Order Ophiurida

Amphiura constricta Lyman. This species rarely grows larger than a disc diameter of 7mm (Baker 1981a), although most specimens are only a few mm in disc diameter. It is abundant amongst the sessile fauna on pier pilings, rocks and Pinna shells. It occurs throughout the area.

Ophiocentrus pilosus (Lyman). A moderately common species which lives in the sand between Pinna shells. The whole animal is not often seen, but its presence is denoted by the distal third of each arm protruding vertically above the sand. The whole animal can then be scooped up from just below the surface of the sand. The arms are most often seen where there is a noticeable current.

Amphioplus ochroleuca (Brock). This is another species which is found buried in the sand. It is not very common, with only three specimens having been taken, both at the bases of Pinna shells. The species was not sufficiently common to be included in the key of Baker (1981a), and a short note is warranted. Disc diameter is about 7mm, but the arms are very fragile, so that estimation of their length is difficult. Arm length appears to be 15 to 20mm. Morphologically, the species is similar to Amphipholis squamata, having two central oral papillae, flanked by two distal oral papillae. It can be distinguished from A. squamata by the widths of these two distal papillae. A. squamata has the outermost two to three times the width of the inner (Baker 1981a), while Amphioplus ochroleuca bears two papillae of similar sizes.

Amphipholis squamata Delle Chiaje. A small species which is common among the sponges and tunicates on the pilings of the pier.

Ophiactis resiliens Lyman. Another species not listed by Baker (1981a), this small species is occasionally taken under rocks in the intertidal between Edithburgh and Coobowie. It is not as common here as it appears to be in the intertidal of more exposed shores. I have observed it subtidally in other parts of southern Australia, although no specimens have been taken from this area subtidally. It may be distinguished from the congener O. tricolor H.L. Clark by the

number of distal oral papillae; O. tricolor has one large fanshaped papilla, while O. resiliens has two squarish papillae (Clark 1966).

Ophiothrix caespitosa Lyman. This small species is very common wherever sponges, tunicates, and bryozoans occur. It lives in the crevices between these species.

Ophiothrix (Placophiothrix) spongicola Stimpson. This large species is not uncommon, and occurs under rocks and debris subtidally throughout the area. It is very active when disturbed.

Ophionereis schayeri Müller & Troschel. This is one of the commonest large brittle-stars, reaching an arm length of at least 150mm (Baker 1981a). It is found under rocks throughout the area from the intertidal down to 10 metres.

Clarkcoma canaliculata (Lutken). Together with Ophionereis schayeri, this is the commonest large ophiuroid. It is particularly abundant under rocks and debris beneath the pier, but occurs all over the area, again from the intertidal down. It appears to be more active at night.

Ophionereis semoni (Doderlein). This is possibly the most attractive of the ophiuroids seen commonly in South Australia. Baker (1981a) does not describe this species, and again some description is warranted. The disc diameter reaches 9mm, and the disc is covered with skin which obscures the scales. Colour of the disc is black, with white patterning . The arms are up to 70mm long, and slender. Little is known of this species, and few specimens exist in the South Australian Museum. It appears that this is due to lack of collecting, rather than to rarity. It has been taken out in the bay at the base of Pinna shells and is common around the pier among debris on the seafloor. The arms

are black-grey and cream, and can often be seen protruding through the debris. I have found it to be common at a number of sites further to the north (Wool Bay and Port Giles piers), and it is probably common over a larger area than this survey covers.

Ophiocomina australis H.L. Clark is only known from Gulf St Vincent, whence it was described by H.L. Clark (1928). It can be found at the base of Pinna shells, buried in the sand. It is not uncommon out in the bay.

Ophiurodon opacum H.L. Clark. This uncommon little species has only been recorded once, buried in sand at the base of a Pinna shell between Sultana Point and Troubridge Island. It is readily distinguishable from other species by the presence of hyaline edges to the teeth, which are wide and blunt (A.M. Clark 1966).

Ophiopeza arenosa (Lyman). This species is common around the pier. It lives under rocks and other debris, but often moves about on the sand at night.

Ophiopeza assimilis Bell. Larger than the previous species, it is also found under the pier, although it is less abundant than O. arenosa.

Ophiarachnella ramsayi (Bell). This is another fairly large species. The same comment as for the preceeding two species apply.

Ophiocrossota multispina (Ljungman). Only a single record exists for this species, from sandy bottom between Sultana Point and Troubridge Island.

CLASS ECHINOIDEA

Order Cidaroida

Goniocidaris tubaria Koehler. This small (test diameter up to 75mm) urchin is easily recognisable by its thick, thorny spines. It is widespread

over Pinna beds, although it is more common in the northern sections of both Gulfs in South Australia.

Phyllacanthus irregularis Mortensen. The "slate-pencil" urchin is rare within the area. The only place where numbers occur is the rocky reefs between Troubridge Island and Marion Reef, where individuals occur under ledges.

Order Centrechinoida

Amblypneustes pachistus H.L. Clark. This little urchin is very common in Posidonia beds throughout the area, where it grazes on the epiphytes of the seagrass.

Heliocidaris erythrogramma (Valenciennes). This is the most abundant echinoid of the area. It is seen occasionally around the pier, and is common on reefs in shallow water. Juveniles are found under rocks from the intertidal down to a few metres.

Microcyphus composus. Lives throughout the area, from the intertidal area downwards. It also appears to graze on epiphytes, although it is not seen as frequently as Amblypneustes pachistus.

CLASS HOLOTHURIOIDEA

Order Aspidochirotida

Stichopus ludwigi Erwe. A large species, it is quite common among Pinna shells on all sandy bottoms within the area.

Stichopus mollis (Hutton). This is the most abundant holothurian in the area. It is common over the whole area. It is uniformly brown.

Holothuria hartmeyeri Erwe. This is another large species, which occurs on sandy bottoms with Stichopus mollis and S. ludwigi. It is moderately common. It is sometimes difficult to distinguish between S. ludwigi and H. hartmeyeri in the field, since they may

be of similar size and colouration. H. hartmeyeri often has pieces of seagrass or other debris adhering to it.

Order Apodida

Leptosynapta dolabrifera (Stimpson). This small, white species is fairly common. It is occasionally taken under rocks from the intertidal down to ten metres, and is an active burrower in sand.

Trochodota shepherdi Rowe. This small black species is common in a mixed bed of Posidonia and Pinna off the end of the Edithburgh pier. It is most conspicuous when entwined in the meshes of experimental cages in the area, but is very active and often seen moving on the sand. It appears to be more abundant in winter and early spring.

Order Dendrochirotida

Lipotrapezia vestiens (Joshua). Only a single specimen has been recorded from under rocks in the intertidal region. It frequently has rubble and plant material adhering to it (Hickman 1962; pers.obs.).

Thyone nigra Joshua & Creed. This species rarely exceeds 5cm, and lives wedged between rocks in sand, with only the tentacles exposed. The tentacles are frequently seen exposed during day or night. It is common through most of the area.

CLASS GINOIDEA

Order Articulata

Comanthus trichoptera (Müller). This large orange or brown species is common through most rocky reefs in the area. It is found under rocks and in crevices.

Antedon spp. These small, brownish feather stars are occasionally found under rocks. They appear to be distributed throughout the study area, wherever rocks are found.

The fauna is thus composed of a small number of common species, with a large number of rare or uncommon species. Examination of the faunas for different habitat types (Table 1) shows that they bear assemblages of species which overlap broadly. Intertidal sand and shallow-water seagrass beds support the fewest species, while rocky reefs in deeper water contain the largest number of common species. Other habitats have intermediate numbers of species.

The total echinoderm fauna is surprisingly large. It is at least forty nine species, but is composed of many rare species which have been recorded once or twice per 150-200 hours underwater; a brief survey of the area would produce no more than thirty species even after sampling a broad area, and would thus underestimate the echinoderm fauna of the area by about one third.

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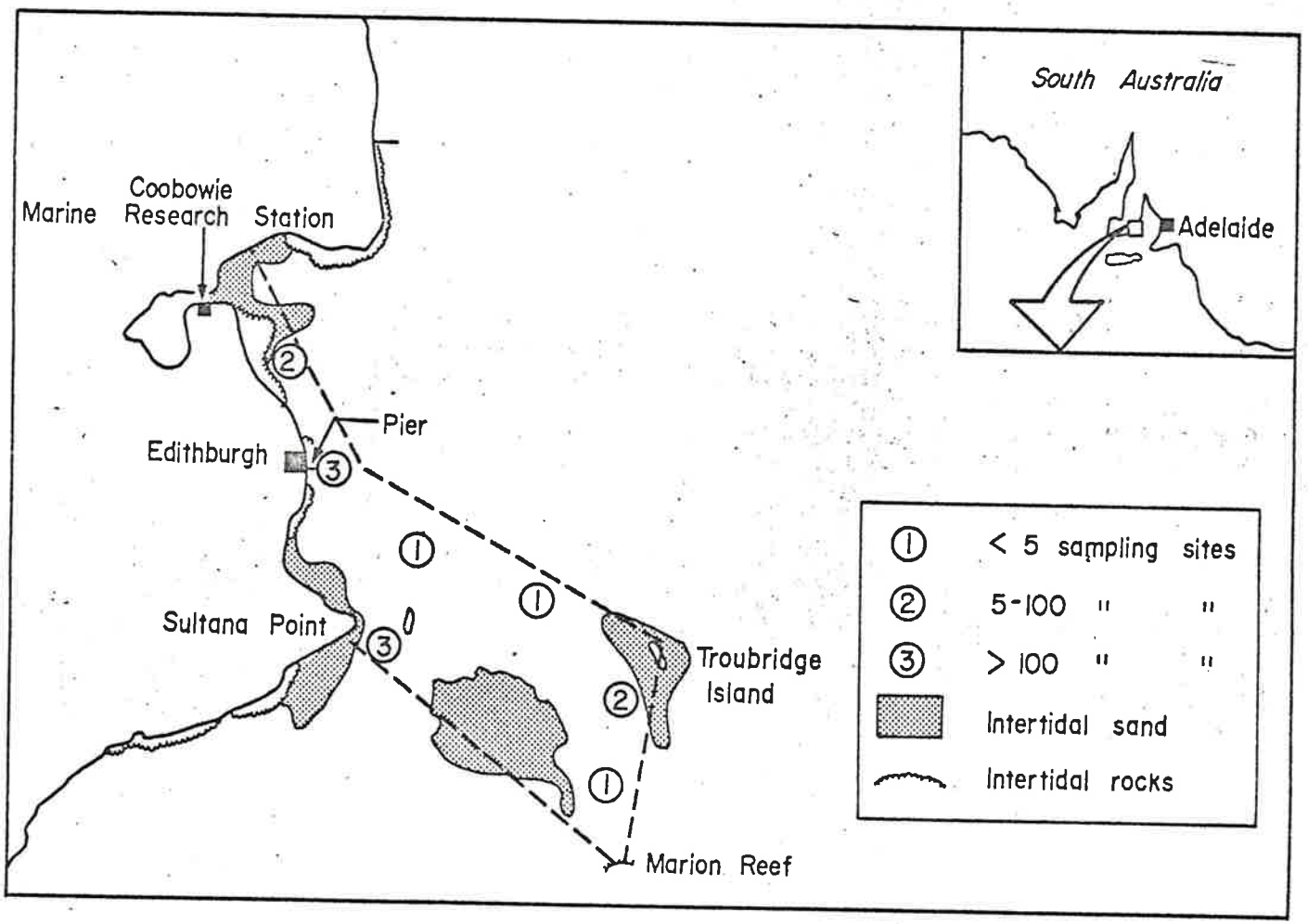
Table 1. Distribution by habitat type of common echinoderms. Blank denotes absence, X occasional presence, C common and VC very common.

	Intertidal		Shallow (0-3m)		Deeper (3m+)		
	Sand	Rock	Seagrass	Rocky	Rocky reef	rubble	sand/Pinna
Pentagonaster				C	C		
Tosia		C		C	C	C	C
Petricia				C	C		
Austrofromia					X		
Asterina		X		X	X	X	X
P. brevispina			VC	X	X	X	C
P. exigua	C	C					
P. gunnii					X		
Nepanthia					X		
Coscinasterias		C	X	X	C	C	C
Uniophora	X	X	C	C	C	C	C
Allostichaster		C		C	C	X	
Ophiomyxa		C		C	C		
Ophiocentrus							C
Amphiura		X		VC	VC	X	X
O. caespitosa				C	C		
O. spongicola				X	X	C	
Ophionereis schayeri		X		C	C	VC	C
Ophiopeza spp.				X	C	X	
Goniocidaris					X		C
Phyllacanthus					X		
Heliocidaris		X		VC	C		
Amblypneustes			C				X
Microcyphus			X				X
Stichopus ludwigi				X	X	C	C
S. mollis				X	X	VC	VC
Holothuria				X	X	X	C
Leptosynapta		X				X	
Trochodota							X(C)
Thyone				X	X	C	

CAPTIONS

Figure 1. Map of study area, showing intensity of sampling.


South Australia
Adelaide
Marine
Coobowie
Research
Station
Pier
Edithburgh
Sultana Point
Troubridge
Island
Marion Reef
① < 5 sampling sites
② 5-100 " "
③ > 100 " "
Intertidal sand
Intertidal rocks

OCCUPATION OF PATCHES IN THE EPIFAUNAL COMMUNITIES ON PIER PILINGS AND THE BIVALVE PINNA BICOLOR AT EDITHBURGH, SOUTH AUSTRALIA

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SUMMARY

The reoccupation of artificially cleared patches in a subtidal epifaunal community was investigated in two field experiments on the pilings of Edithburgh pier, South Australia. In most cases, the greatest proportion of the patch was reoccupied by the vegetative extension of established sponge and tunicate colonies adjacent to it. Larval recruitment by sponges, bryozoans, tunicates and serpulids contributed to the reoccupation but resulted in only a small proportion of the mean percentage cover. The relative abundances of individual species established in any patch were shown to be a function of the (1) position in space, (2) age, (3) time of creation, (4) initial size of the patch.

There was a large amount of between patch variation in all cases. Overgrowth interactions occurred frequently within patches, and for many pairs of species, neither species consistently overgrew the other. Overgrowth interactions were tested statistically, and a large number of pairs of species were found to be competitively equivalent. This represents a possible situation additional to the alternatives recognized in the literature, namely competitive hierarchies or networks. Interactions between species should be regarded as stochastic, with a wide range of possible outcomes. The situation at Edithburgh is likely to produce greater between-patch variability than either a network or a hierarchy.

Despite this large variation, super-specific taxa differ fairly consistently in capacity for overgrowth. Tunicates overgrow sponges, which overgrow bryozoans, which overgrow serpulids. The occupation of most patches was directional in the sense that bryozoans and serpulids invaded first, but tunicates and sponges excluded them and came to dominate the patch. These relationships are used to predict patterns

of abundance for substrata which are small and isolated, and these predictions are compared with the epifauna of the bivalve Pinna bicolor, which provides such substrata adjacent to the pier.

INTRODUCTION

In recent years several research workers (e.g. Grant 1977; Karlson 1978; Levin and Paine 1974; Osman 1977; Sutherland 1974;) have proposed that it is appropriate to view communities of sessile biota in marine environments as being composed of a mosaic of small patches with differing species compositions and developmental histories.

In some communities these patches first occur as holes or breaks in the sessile flora and fauna covering a two-dimensional surface (Dayton 1971, 1975; Grant 1977; Karlson 1978; Paine 1977). Alternatively, the patches may occur as isolated pieces of substratum surrounded by areas unsuitable for occupation (Jackson 1977a; Osman 1977, 1978;). The latter are also known as habitat islands (Schoener 1974). In both cases investigations designed to determine the factors affecting the formation of patches and the initial identities and abundances of species which invade and occupy these patches have been used to formulate explanations for overall community structure.

Much of the work in rocky intertidal systems has focussed on the processes responsible for creation of patches and thus provision of free space. Physical disturbances by wave-borne objects and wave action itself, or biological disturbances such as foraging by predators create holes in the sessile communities covering the substratum (Dayton 1971, 1975; Grant 1977; Paine 1966, 1971). Knowledge of events within patches is also necessary in order to understand patterns of species abundances via patch theory. In rocky intertidal systems, reoccupation of patches usually ends when one or more species exclude the early occupants of a patch through various methods of interference competition (Paine 1977).

Events within patches are less well understood for communities on hard substrata in subtidal habitats. Patches are reoccupied both

by colonisation by planktonic larvae and by the vegetative extension of adjacent colonies. These two sources have been shown to differ in importance between various subtidal communities (Jackson 1977b; Kay 1980; Sutherland and Karlson 1977). Irrespective of the source of inhabitants, interactions between the occupants are an important part of the reoccupation process. These interactions mostly take the form of overgrowth, where one occupant grows over the surface of the other. "Contact matrices" have been constructed which show the result of pairwise interactions between species. It has been suggested in some cases that the patterns of overgrowth shown in such matrices are linear, i.e. for a three species case, A beats B, B beats C, and thus A beats C (Connell 1978; Osman 1977). In others they have been suggested to form a network - A beats B, B beats C, but C beats A (Buss and Jackson 1979; Jackson 1979a). Much discussion has centred on these patterns, since they have different effects on the dynamics of the community. (Review: Buss and Jackson 1979.)

At Edithburgh pier in South Australia, we have observed that the outcome of interactions between a given pair of species is not constant, and each species wins some encounters. The same result has been reported from other areas (Jackson 1979a; Osman 1977; Russ 1980). Other studies of patterns of overgrowth have been from censuses at a single point in time (Buss and Jackson 1979; Jackson 1979a). At Edithburgh, we have records of interactions over extended time periods, in which one colony initially overgrows the other, but then the process is halted, and the initially overgrown species eventually wins. Censuses taken at a single point in time would thus include some misleading classifications of overgrowth interactions. Jackson (1979a) has shown that the outcome of interactions between some bryozoan species is influenced by the angle at which the colonies

encounter each other. Russ (personal communication) and Day (1977) have suggested that the outcome of the interaction changes with the relative sizes of the two colonies. Most authors have acknowledged this variability, but few have taken acount of it in their treatment of contact matrices. Contact matrices have been interpreted essentially deterministically. The information in each cell has been treated in terms of its most common outcome, not the frequency distribution of the several possible outcomes, and for each cell it has been assumed that there are only two possible "average" conditions; A wins or B wins. In reality, of course, it is common that neither species wins consistently, and we believe that a third possibility should be considered in the abstract interpretation of contact matrices; pairs of species in which neither species wins significantly more often than the other. These species should be designated "competitively equivalent". Further, the interactions between each pair of species should be tested statistically before being classified. We suggest using the Binomial test (Siegel 1956), and details are given in the methods section. The third possibility may be of some importance. A hierarchical pattern overgrowths results in lower variety of outcomes than either a network or a situation where equivalences are present. Consider a series of patches where three species are present. If their overgrowth pattern is hierarchical, all patches of this composition are likely to finish up with the same species composition If the arrangement is a network, each species will win in some patches. The outcome is influenced by growth rates and juxtapositions of species (Buss and Jackson 1979). Once growth rates and positions of species within a patch are known, the outcome becomes predictable. The abundance of the three species and the amount of between-patch variation is then influenced by the variations in growth rates and by

the frequency distribution of species juxtapositions. If equivalences are common, then even if the growth rates of species and the spatial arrangement of species within a patch are known, neither the dynamics within the patch nor the final outcome are predictable. The between-patch variation is thus high and independent of juxtapositions of species.

If this method is applied to published contact matrices, many of the cells do not have sufficient observations to categorise the interaction at all; in other cells the outcomes must be classified as competitive equivalence. Thus, the data are often inadequate to distinguish between the hierarchy and network ideas. Many of the outcomes fall into a category not included in many discussions of competitive interactions. Thus, we conclude that the occurrence of networks and/or hierarchies has not been well demonstrated in the literature. Jackson (1977, 1979b) and Buss (1979), however, provide convincing circumstantial evidence for the existence of networks among the inhabitants of cryptic coral reef environments. They suggest that there exists a great diversity of growth forms and directions, allelochemicals and growth rates, making it unlikely for any one species to consistently win against all other species.

The patterns of overgrowth are thus likely to be of importance in the reoccupation of patches. A number of other influences can be identified; the size of a patch of substratum should be important in determining the pattern of its reoccupation, as should its position in space (whether it is isolated, or what species border it). In addition, for example, Jackson (1977a) has suggested that different species may settle preferentially on substrata of different sizes. Thus, within-patch events on a large piece of substratum may not be well simulated on substrata that are small and isolated, such as

fouling plates. This paper details two field experiments on the reoccupation of cleared patches in the epifaunal community on pier pilings of Edithburgh pier in South Australia.

The first series of experiments was designed to test the hypothesis that the reoccupation of a patch is influenced strongly by the time at which the patch was created, since larval abundances vary seasonally. Alternatively, later composition of a patch may be more strongly influenced by the growth of organisms surrounding a patch. Rate of reoccupation may be affected in a similar way by size of patch and by its position (i.e. the identity of the species surrounding it). A small patch surrounded by fast growing species will obviously be overgrown more rapidly than one which is larger or surrounded by slower growing species. In the second experiment, patches were cleared which were surrounded by one of two species whose growth rate varied by a factor of two. Patch size was varied simultaneously.

The results of the two experiments are used to identify some of the factors which are important in the organization of the epifaunal community of Edithburgh pier and to predict differences in the structure of communities on substrata of different sizes. Data from small and large substrata at Edithburgh are included as a preliminary test of these predictions.

MATERIALS AND METHODS

Study area

The wooden pier at Edithburgh (137°45'E 35°5'S; Fig. 1) extends 173 metres in an easterly direction from a low rocky cliff. Field work on the pier was (and is) conducted under the outer half of the pier. Piling diameter is between 30 and 40 cm, and most of the pilings are at least 68 years old (some are 80). Depth around the pier varies from 4.5 to 5.5 m below Mean Lower Low Water.

To the south of the pier lies a dense bed of the seagrass Posidonia australis var. angusta Hook. Underneath the pier and to the north and east the seagrass is less abundant and the most conspicuous benthic species is Pinna bicolor Gmelin, a fan-shell which has the anterior half of the shell embedded in the sand (see Butler and Brewster 1979). The shell provides a substratum for various sessile species. The alga Scaberia argardhii Greville and the seagrass Halophila ovalis (R.Br.) are also common.

The area is sheltered by land from the prevailing south-west winds and is not subject to oceanic swells. Water temperature varies between 22°C in late January and 11-12°C in July and August, although these extremes vary by one or two degrees in individual years.

Species in the community

This study focussed on those species that are capable of adhering to hard substrata within the study area, and includes only sessile species. Both the pier pilings and Pinna shells bear an assemblage of species from a number of phyla. The most common are tunicates, sponges, bryozoans and serpulid polychaetes, but attached molluscs and coelenterates also occur. Most species are colonial. Table 1 lists the commoner species. We excluded species which occupied

less than 0.05% of space on the pilings. The epifauna of Pinna shells is composed of essentially the same species pool. Two species, the coral Scolymia Homophyllia australis (Milne-Edwards and Haime) and a stalked barnacle Scalpellum peronii, were occasionally found on Pinna shells, but do not occur on pier pilings.

Taxonomic problems exist for many invertebrate groups in South Australia, necessitating the use of code numbers for some species. The code numbers correspond to catalogues of colour transparencies and specimens held in the Zoology Department, University of Adelaide. Further details of this procedure appear in Keough and Butler (1979).

Natural patches are formed on the pilings, and vary in size from 1 cm^2 to 1 m^2. Personal observations suggest that all large patches are formed through senescence of old colonies or by wave damage. Small patches are formed by the foraging activities of predators, mainly the asteroids Tosia australis Gray and Petricia vernicina (Lamarck).

General methods

All field work was conducted using either SCUBA or SSBA, and collection of data was made with Nikonos cameras and electronic flash, using Ektachrome 64 ASA film. Photographs were taken from distances between 1 and 0.15 metres. Patches were thus censused repeatedly and non-destructively. Work on the pilings was done using only piling surfaces which do not face outwards, and in the zone from 0.5 to 2.5 metres above the bottom. This was to minimize physical heterogeneity within the working area.

Experiment I

Five patches of size 20 cm x 30 cm were created at randomly selected positions on those pilings within the study area. Sessile organisms were removed with a knife and chisel, and the wood scrubbed with a stiff brush to remove all fragments of living tissue. Each patch was outlined with orange nylon rope. The procedure was repeated at 3 later times as follows: "February" group 26.II.76; "May" group 18.V.76; "August" group 26.VIII.76; "December" group 6.XII.76. Each patch was then photographed at monthly intervals for one year from the time of creation.

Experiment II

A two-factor experimental design was used to investigate the effects of surrounding species (2 levels) and initial patch size (3 levels). The sponges Mycale sp. and Crella sp. were used as the levels for the first factor, and together with three sizes of patch: 10 cm x 10 cm; 25 cm x 25 cm; and 50 cm x 50 cm. Patches were chosen so that at least 20 cm of sponge tissue bounded each side. Sponge colonies were selected at random and the corners of the patches within them marked with nails. Replicate numbers were ten for each of the smaller size and four and three for the largest patches for Mycale and Crella respectively. The small replicate numbers for the largest size were due to the small number of very large sponge colonies on the pilings.

The two sponge species were selected because they are two of the three most common species in the community and Mycale sp. has a growth rate approximately twice that of Crella sp. Growth rate is defined as the distance travelled by the growing edge of an isolated colony per unit time.

Data processing and analysis

Space is frequently postulated as the potentially limiting resource in marine benthic communities, and we therefore measured species abundances as the percentage of two-dimensional space occupied. Only those parts of colonies or individuals actually adherent to the piling surface were considered. In most cases this was simply the two dimensional projection of the organism onto a film surface. Three species could not be treated in this way, and their areas of attachment were determined by direct examination of colonies in the field. The tunicate Podoclavella cylindrica has an upright bushy growth form with basal attachment area of 0.5 cm^2; the bivalve Chlamys asperrimus is attached by a byssus of the same size, while the sponge Callyspongia sp. (SP 13) has a runner-like growth form (sensu Jackson 1979b) which necessitated examination of each colony individually.

Colour slides were projected onto white paper and the outlines of colonies traced. Percent areas were then measured by planimetry. The number of new recruits was determined by counting those colonies which were present at time t which were not present at time t-1 month. Overgrowth was measured as the amount of live tissue in a patch which was covered at time t+1. All measurements were standardized to a period of 30 days.

A contact matrix based on the overgrowth records from experiment I was also constructed. For all pairwise interactions where overgrowth occurred the winner was recorded. If the number of observations for a given species pair was equal to or exceeded 6, the competitive relationship between the two species was assessed in the following manner.

Consider a species pair in which species A has a probability p of winning in an encounter with species B; B wins with probability q = 1 - p.

Set: H_0 p = q = 0.5 A and B are competitively equivalent

vs. H_1 p ≠ 0.5, since there is a priori no good reason for suggesting that one species will win.

The exact probability of the observed result given H_0 may then be calculated (Siegel 1956), and if H_0 is rejected, the species winning more of the encounters is designated competitively dominant to the other. Otherwise, they are designated "competitively equivalent".

Russ (pers. comm.) and Harris (1978) have reported that colonies may stop growing at their interface. They have recorded this frequently at Portsea, Victoria. Jackson (1979a) also reports this, but in his case such "ties" were uncommon. If an encounter has three possible outcomes (i.e. if there are ties), some modification of the above test is necessary. Consider the interaction between species A which has a probability r of winning an encounter, and B which wins with probability s . t of the encounters result in ties . r + s + t = 1.

Set p = max (r,s)

q = min (r,s) + t

H_0 p = 0.5

vs. H_1 p > 0.5 This becomes a one-tailed test, since the lower tail (p < 0.5) means that neither species is dominant, since p is thue proportion of wins of the more successful of the two.

As before, if H_0 is rejected, the species winning the greater number of encounters is designated dominant. Otherwise, they are designated "competitively equal".

RESULTS

Experiment I

Patches were reoccupied by vegetative growth of adjacent colonies and by colonization from the plankton (Fig. 2). The total percent cover in patches showed no heterogeneity between groups (Kruskal-Wallis non-parametric analysis of variance, $H = 5.31$, $P > 0.05$). Similarly, the amount of growth due to vegetative extension and to growth of colonists did not show heterogeneity between groups ($H = 3.12$ and 5.6 respectively, $P > 0.05$). Vegetative extension accounted for a significantly greater part of the total occupation of patches than colonist growth (Wilcoxon matched-pairs signed-ranks test on pooled data from four groups, $T = -16$, $p < 0.005$). After twelve months vegetative growth made up more than 75% of total growth in most patches.

If the species occupying patches are grouped into phyla, sponges are seen to occupy the greatest proportion of space (Fig. 3). This occurs almost exclusively by vegetative extension. Tunicates and bryozoans were far less abundant, and bryozoans invaded patches almost entirely by larval colonisation. Tunicates invaded patches by both methods (Fig. 4). The common tunicates in the community (Table 1) are annual colonial species, with peaks of abundance in July-September of each year (Kay 1980). They die off in late spring-early summer, and settlement of larvae occurs in summer.

Species belonging to other phyla were almost always below 1% cover, with the exception of the February group, where the stony coral *Culicia* sp. reached 3.6%.

During the year following the creation of the patches no one species occupied a high percentage of space in one group and not in another (Fig. 5). In view of the minor role of colonisation events

this was not surprising. After twelve months the two sponges, Crella sp. and Mycale sp. were clearly the most abundant species in all groups (Fig. 5). Crella sp. and Mycale sp. both form encrusting sheets up to 1 m^2 in size. Both species have high growth rates: the growing edge of Mycale sp. may travel 15 cms in thirty days, and that of Crella sp. 5-7 cms in thirty days.

Within all groups there was considerable variation in the species composition of patches. This was partly due to the heterogeneous nature of the piling community, since patches varied widely in the species which surrounded them.

The number of recruits varied widely between patches within groups. Both the numbers and species composition of the recruits were variable. Our experiments were not designed to investigate the causes of this variation.

Both total and partial overgrowth of colonies was observed frequently in all groups. Chance juxtapositions of species of differing overgrowth capacities and variation in species composition of patches accounted for much of this variation.

Patterns of overgrowth

Amongst the common species on the pilings, there were 324 possible pairwise interactions, but only 98 of these were observed, and only 40 occurred sufficiently frequently to be analysed. Analysis of the contact matrix (Fig. 6) showed that many species were equivalent to each other. Deterministic reversals in the sense of Buss and Jackson (1979) were not observed, but some species were equivalent to species which would have been expected to beat them. Two examples are shown in Figure 7. The sponge SP 48 is overgrown by the sponge Aplysilla rosea (SP 1) which is in turn overgrown by Crella sp. SP 48, however,

is equivalent to Crella sp. Didemnid sp.b (T 18) overgrows both Mycale sp. and Crella sp., and is equivalent to Didemnum sp.a (T 9). Didemnum sp.a., however, is equivalent to both Mycale sp. and Crella sp.

If the patterns between phyla are examined, it can be seen that tunicates were able to overgrow ("dominant to") bryozoans and serpulids in all cases. They were dominant to sponges (5 cases) or equivalent (2 cases). Sponges were dominant (8 cases) to or equivalent (3 cases) to bryozoans. Serpulids were overgrown by all colonial species. Overgrowth of bryozoans and serpulids occurred in all patches, but the duration of the experiment was such that complete exclusion only occurred in one patch.

Experiment II

Small patches were reoccupied by the vegetative growth of the surrounding sponge more rapidly than were large patches. Patches of the same size were reoccupied more rapidly by Mycale sp. than by Crella sp. (Fig. 8).

No recruitment was observed in the 10 x 10 cm and 25 x 25 cm patches surrounded by Mycale sp. Bryozoans and serpulids did colonise the 50 x 50 cm patches surrounded by Mycale sp., but they were overgrown completely by the end of the experimental period. The bryozoans which colonised the 10 x 10 cm patches which were surrounded by Crella sp. were similarly excluded. Mean percent cover for colonising bryozoans, sponges and tunicates increased with time for Crella sp. patches of medium and large sizes even though some colonisers were overgrown.

We were thus able to identify a number of attributes of a patch which affect its occupation.

1. Position determines which species are adjacent to the patch and thus the rate at which it is reoccupied, and has a major influence on later species composition.

2. Age. Species composition and percent cover both change with time, although not in a deterministic manner. The usual fate of a patch is monopolisation by sponges and tunicates. The identities of the final species vary considerably.

3. Time of clearance. Seasonal and between-year variation in larval abundance will affect species composition, although this effect is minor.

4. Size of patch. Small patches are generally occupied more rapidly than are large, although this may vary according to surrounding species.

DISCUSSION

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 fauna at Edithburgh, where the established fauna had considerable influence over the fate of newly cleared substratum because of the rapid vegetative growth of colonies next to bare patches. Most of the bare substratum in the epifaunal community occurred in patches that were smaller than the largest patches in Experiment II (Kay 1980). 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.

When patches are completely closed, the resultant combination of species may persist for some time. In the case of long-lived sponges such as Crella sp. or Mycale sp., persistance times of up to five years are common (Kay 1980). Patches occupied by colonial tunicates such as Botrylloides leachii persist for shorter periods such as five or six months. Events within patches are predictable only in the sense that colonising bryozoans and serpulids will in most cases be overgrown by sponges or tunicates.

There is a large amount of between patch variation, as was mentioned earlier. Part of this can be accounted for by the different combinations of species which surround patches. The observed patterns of overgrowth are also of some importance. Most of the "equivalences" occur between species which are good overgrowth competitors, i.e. sponges and tunicates. Thus, even if two patches have the same species composition, the events within the two patches may differ greatly, depending on the result of various pairwise interactions between occupants. As the number of species within a patch increases, so does the possible number of final compositions of the patch. A large amount of between patch variation can be generated by this alone. It may also be an underlying cause for the variation in the composition of the species surrounding a patch; we know nothing of the past history of the particular sections of pilings in which the patches were created.

Most of the equivalences occur between species which can be regarded as good competitors (sponges, tunicates); few occur between sponges or tunicates and bryozoans or serpulids (poor competitors)

(Fig. 6). The survival of bryozoans and serpulids thus increases with size of patch on the pilings, since large patches remain open for longer (Fig. 8). The time for a superior competitor to reach a colonising bryozoan is thus longer.

If patches were isolated (habitat islands), occupation by vegetative growth would be prevented, and the abundance of bryozoans and serpulids should increase. However, the relationship between patch size and survival time of poor competitors may be reversed, for the following reasons.

In small patches, fewer species settle (Jackson 1977a; Keough, unpubl. obs.). Thus, on small substrata (isolated patches), the probability of deleterious competitive interactions is decreased. At Edithburgh, few species were observed to settle on live tissue, so that on small isolated substrata, poor competitors may be able to monopolize the substratum and prevent further colonisation.

On larger substrata, the probability of colonisation by a good competitor is higher, and overgrowth interactions become more important. Bryozoans and serpulids would thus be expected to decrease in abundance as the size of substrata increased. Such small isolated substrata have been designated "spatial refuges" (Jackson 1977a).

The bivalve Pinna bicolor occurs at densities of around 1 m^{-2} beneath and around Edithburgh pier. The broad, posterior end of each valve protrudes above the sand, providing small substrata of the habitat island type. Mean area of valves above the sand at Edithburgh is 170 cm^2. Individual shells may be regarded as patches where vegetative extension from outside does not occur, and comparisons between events on piling patches and on Pinna may prove useful. Patterns of overgrowth on Pinna do not differ from those among species on the pilings (Keough, unpubl. obs.). There are potential problems

with this comparison: Pinna occur on the bottom where sand scour may modify species abundances or growth forms (see Wilkinson and Vacelet 1979 for example with sponges); Pinna are not shaded and algae may form an important part of the epibiota. However, it happens that colonisation events on Pinna and pilings are similar, and algae occupy less than 0.1% of space on Pinna shells at Edithburgh. This situation is not true for Pinna in other parts of Gulf St Vincent.

In order to test whether sand scour strongly influences the abundance of the various taxa, a series of random photographs were taken of the lower 0.3 m of the pilings. Percent cover was calculated for sponges, bryozoans and tunicates and compared with unmanipulated areas of the pilings which were sampled by Kay (1980) at the same times of the year (June). Total cover was lower, due to a major storm immediately preceding the sampling. This storm eroded sand from the base of pilings, leaving a 2-4 cm band of clear space. We were thus not able to compare total abundance of the major groups, and our comparison was made to examine relative abundances. Variances were heterogenous (F-max test, $p << 0.001$) and the data were pooled for all quadrats to give total abundances for each phyletic group. The data were combined into a two-way table with times and phyla as variables. A χ^2 test for homgeneity was performed, and was not significant ($\chi^2_4 = 3.48$, $P > 0.3$). Accordingly, we conclude that sand scour appears not to be a strong influence on relative abundances.

Comparisons of phyletic abundances between pilings and Pinna (Fig. 9) show that bryozoans and serpulids are much more abundant on Pinna shells and sponges and tunicates are correspondingly less abundant.

The good competitors are limited by substratum size and by their relatively low densities of larval settlement, as can be seen by

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TABLE 1. Species in the epifaunal community of Edithburgh pier. See text for criteria of inclusion.

Porifera	
SP1	*Aplysilla rosea* Schulze
SP2	*Aplysilla sulphurea* Schulze
SP3	*Dysidea fragilis* (Montagu)
SP46	Royal blue spiky sponge
SP20	*Mycale* sp.
SP47	Yellow encrusting sponge
SP30	*Crella* sp.
SP48	Red encrusting sponge
SP49	Off-white/grey encrusting sponge
SP11	Grey volcano sponge
SP50	*Tendania* sp.A
SP51	*Tendania* sp.B
SP13	*Callyspongia* sp.
Bryozoa	
B1	*Celleporaria fusca* (Busk)
B2	*Celleporaria valligera* Harmer
B3	*Celleporaria pigmentaria* (Waters)
B4	*Smittina raigii* (Audouin)
B5	*Cryptosula pallasiana* (Moll)
B6	*Biflustra* sp.
B7	Mustard encrusting bryozoan
Tunicata	
T5	*Podoclavella cylindrica* (Quoy and Gaimard)
T11	*Botrylloides leachii* (Savigny)
T9	*Didemnum* sp.A
T18	Grey encrusting tunicate (Didemnidae)
Cnidaria	
J5	*Culicia* sp.
Mollusca	
M18	*Chlamys asperrimus* (Lamarck)
Annelida	
TW3+4	*Galeolaria* spp.

TABLE 2. Comparison of total percentage cover on all *P. bicolor* shells with mean percentage cover when only shells bearing a particular phyletic group are considered. Bryozoan and serpulid total percentage covers were determined from 42 shells; frequency of occurrence for all phyletic groups and percentage covers for tunicates and sponges had a sample size of 220. Samples were taken in October 1978.

Phyletic group	Total % cover	Percentage of shells with group present	Mean % cover when present
Serpulids	1.2	>98	1.2
Bryozoans	22.9	97	22.9
Sponges	9.9	10	44
Colonial tunicates	0.1	6	78

CAPTIONS FOR FIGURES

Figure 1a. Gulf region of South Australia showing the location of Edithburgh.

1b. Edithburgh pier seen from above.

Figure 2. Change in percentage cover after initial patch clearance. Graphs show mean and standard deviation of total percentage cover (X), percentage cover due to vegetative extension ( ), and percentage cover due to growth of colonization ( ) for all four groups in Experiment I.

Figure 3. Vegetative and colonizer growth for sponges after initial patch clearance. Bar diagrams show mean (bar) and standard deviation (line) of percentage cover due to vegetative extension (solid bars) and due to growth of colonizers (open bars) for all four groups in Experiment I. Month of patch clearance indicated by , last sample taken indicated by .

Figure 4. Vegetative and colonizer growth for bryozoans (top 4 diagrams) and tunicates (lower 4 diagrams) after initial patch clearance for all four groups in Experiment I. For meaning of symbols see caption to Figure 3.

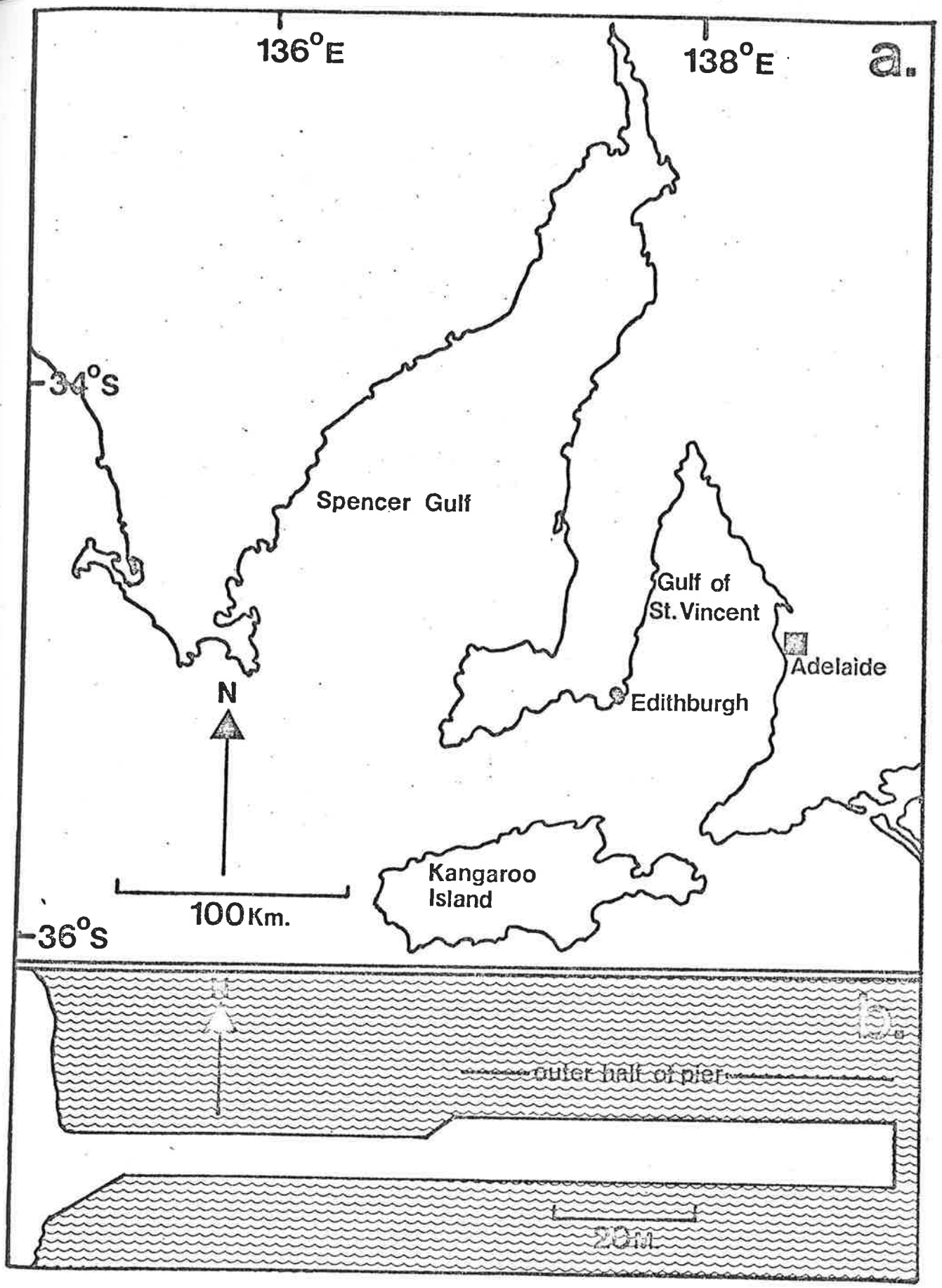
Figure 5. Bar diagrams showing the mean (bar) and standard deviation (line) of percentage cover for individual species on sample dates corresponding as nearly as possible to 3, 6, 9 and 12 months after initial patch clearance in all four groups in Experiment I.

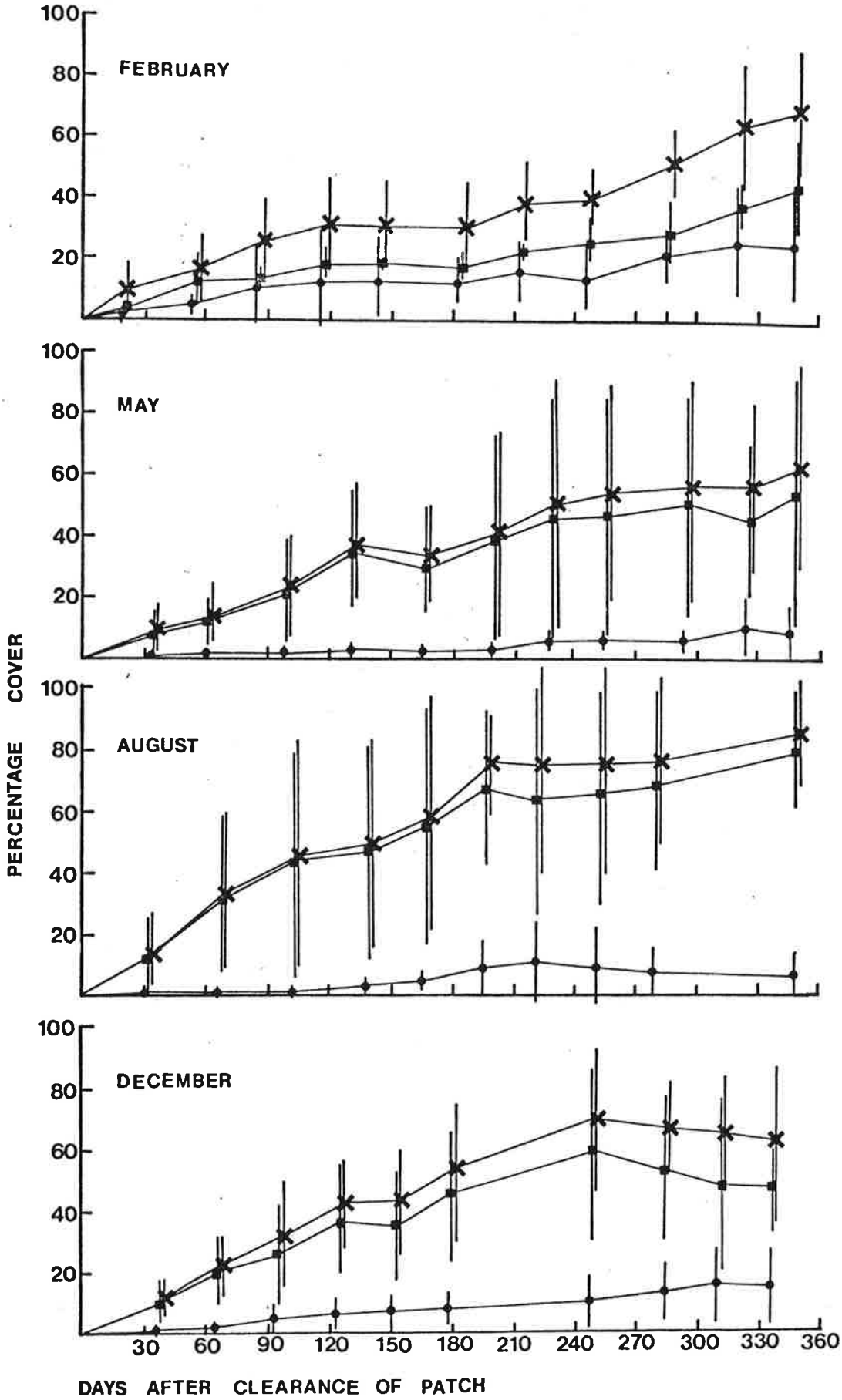
Figure 6. Contact matrix of competitive interactions for species pairs where the number of observations ≥ 6. In each cell, the left hand number is the number of wins to the "column" species, the right hand number is the wins to the "row" species. Arrows point in the direction of the dominant of each 2-species pair, and asterisks indicate competitive equivalences. Further explanation appears in text.

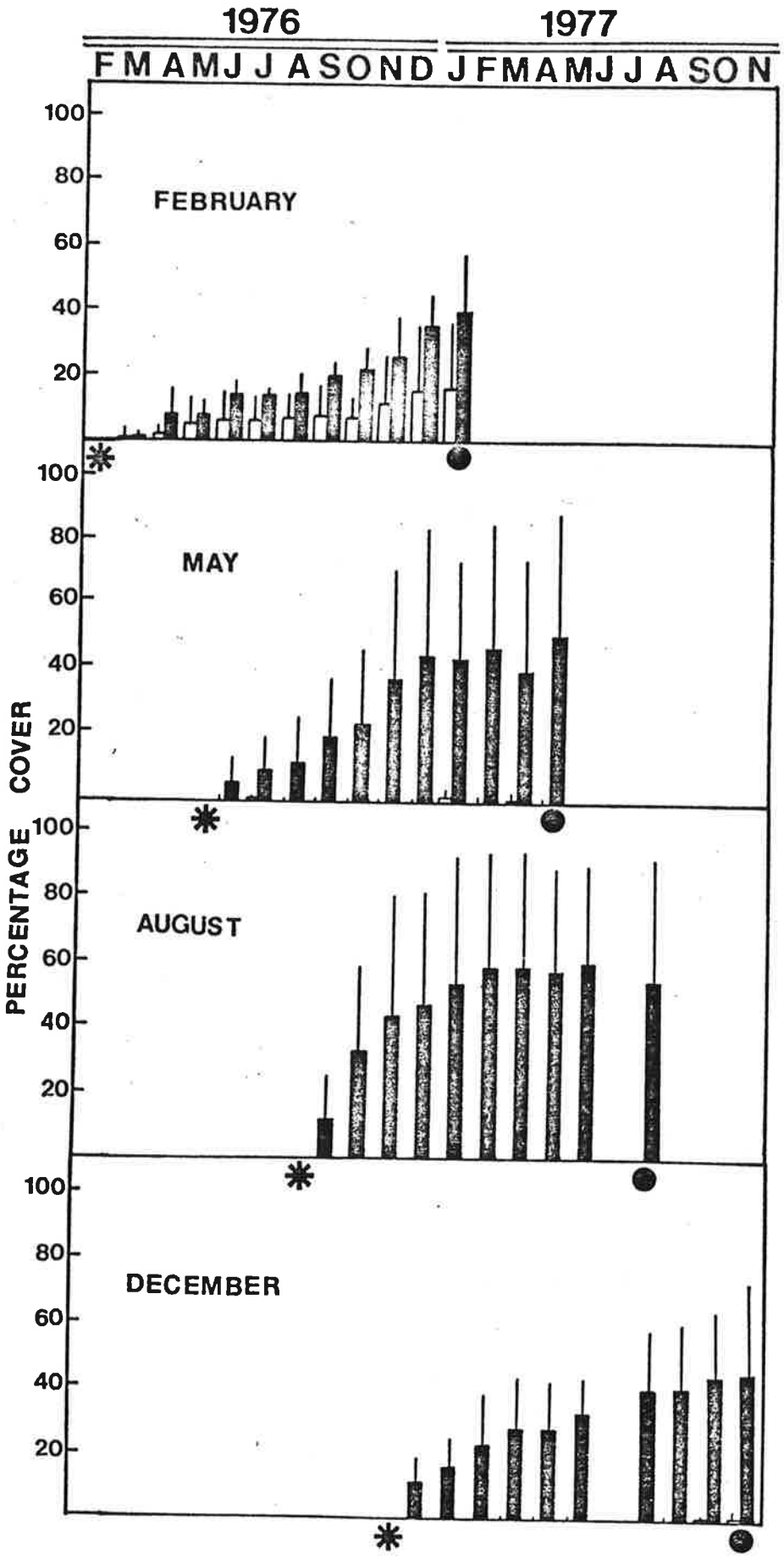
Figure 7. Non-hierarchical overgrowth patterns. Arrows indicate the direction of dominance, half-arrows indicate competitive equivalences. SP1 is Aplysilla rosea, SP20 Mycale, SP30 Crella, and SP48 an unidentified sponge species. T9 is Didemnum sp.A, T18 is a didemnid species.

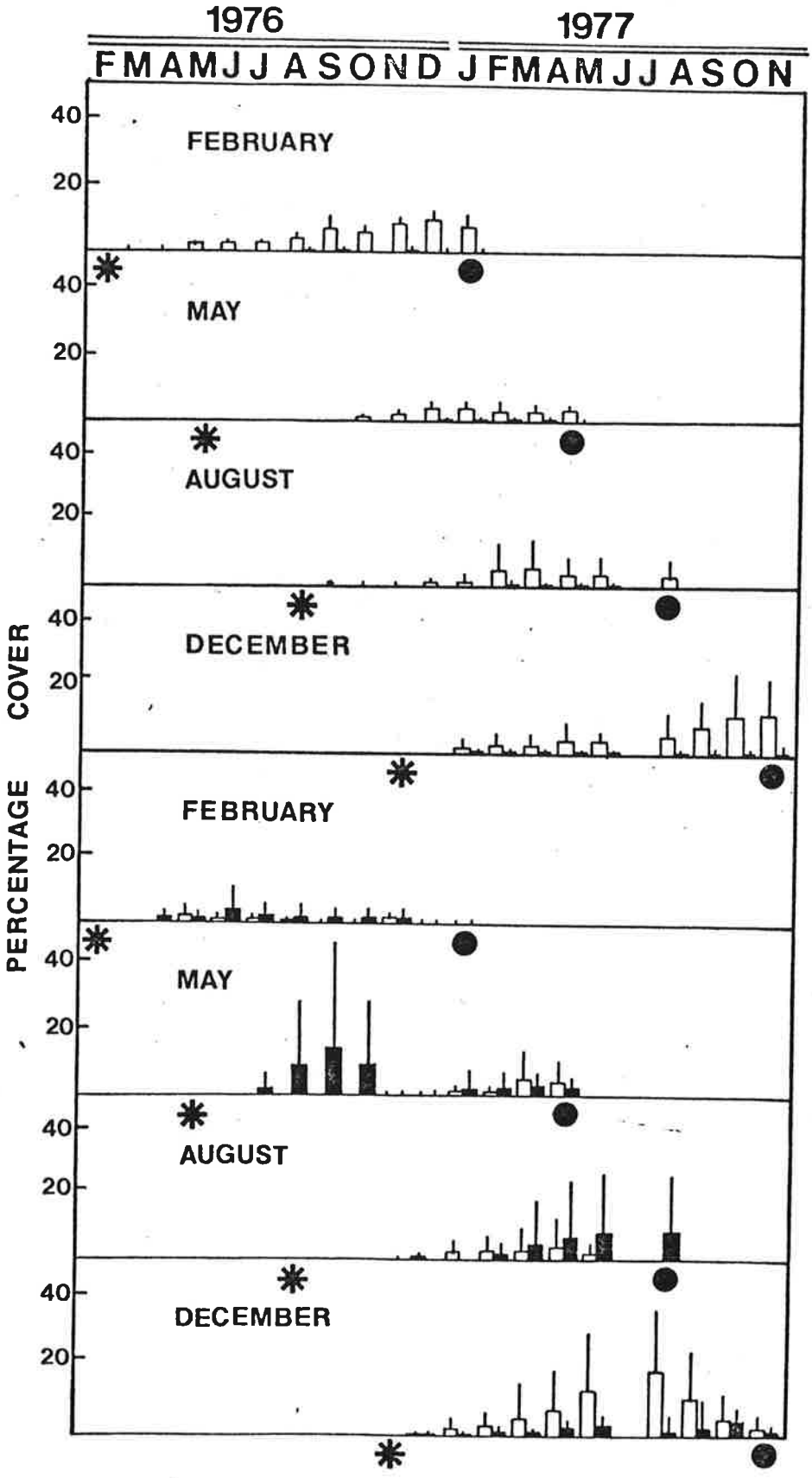
Figure 8. Mean and standard deviation of percentage cover for the vegetative extension of surrounding sponge tissue after initial patch clearance in all six groups in Experiment II. SP30 is Crella sp.

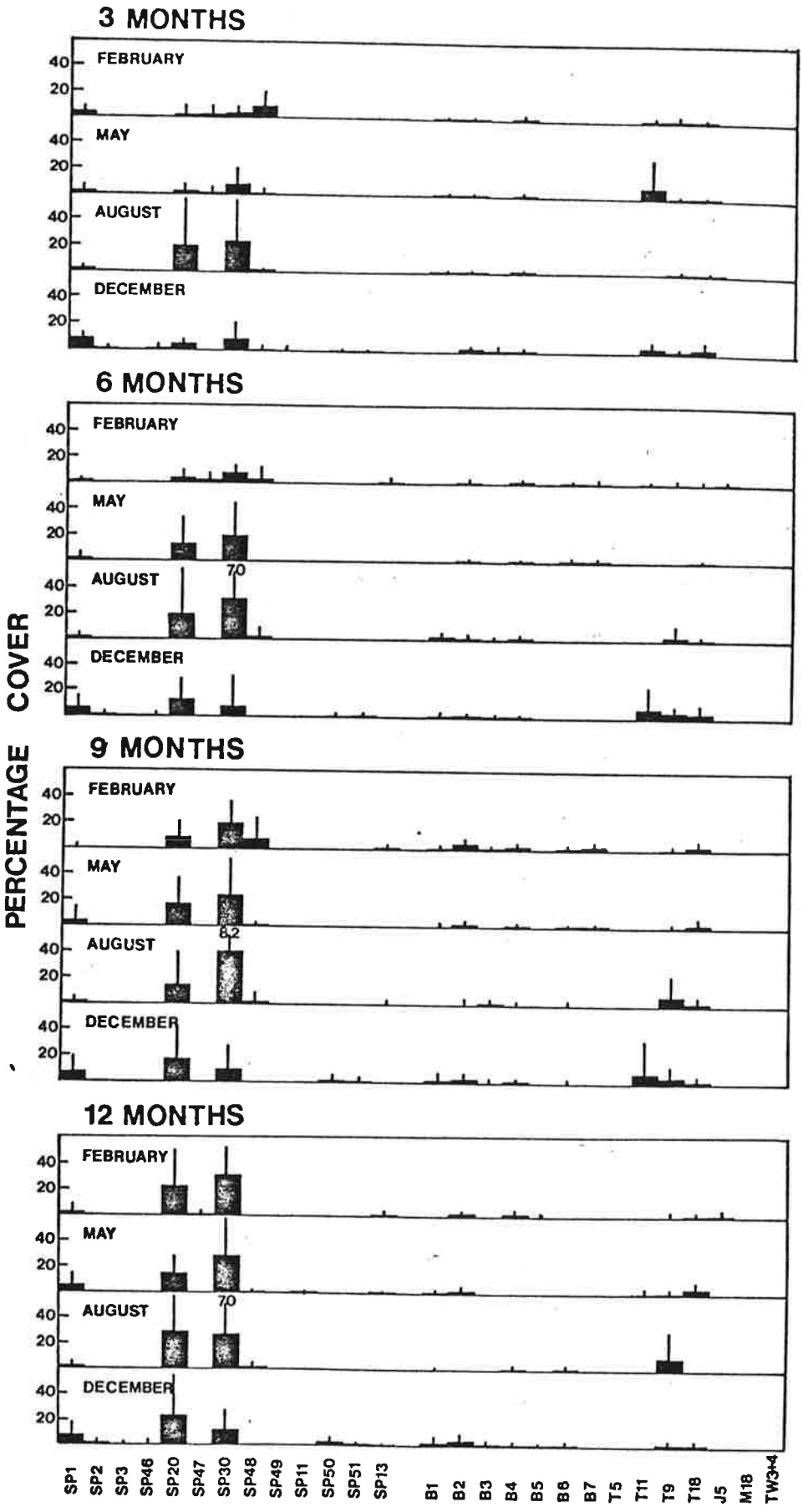
Figure 9. Comparison of pier pilings (a) and Pinna bicolor shells (b). Bar diagrams show the mean percentage cover of the four major faunal groups. Sponges, solid bar; bryozoans, spotted bar; tunicates, open bar; serpulids, striped bar. Pier piling data was calculated from 20 randomly allocated 20 cm x 30 cm quadrats. P. bicolor data were calculated from 42 shells.

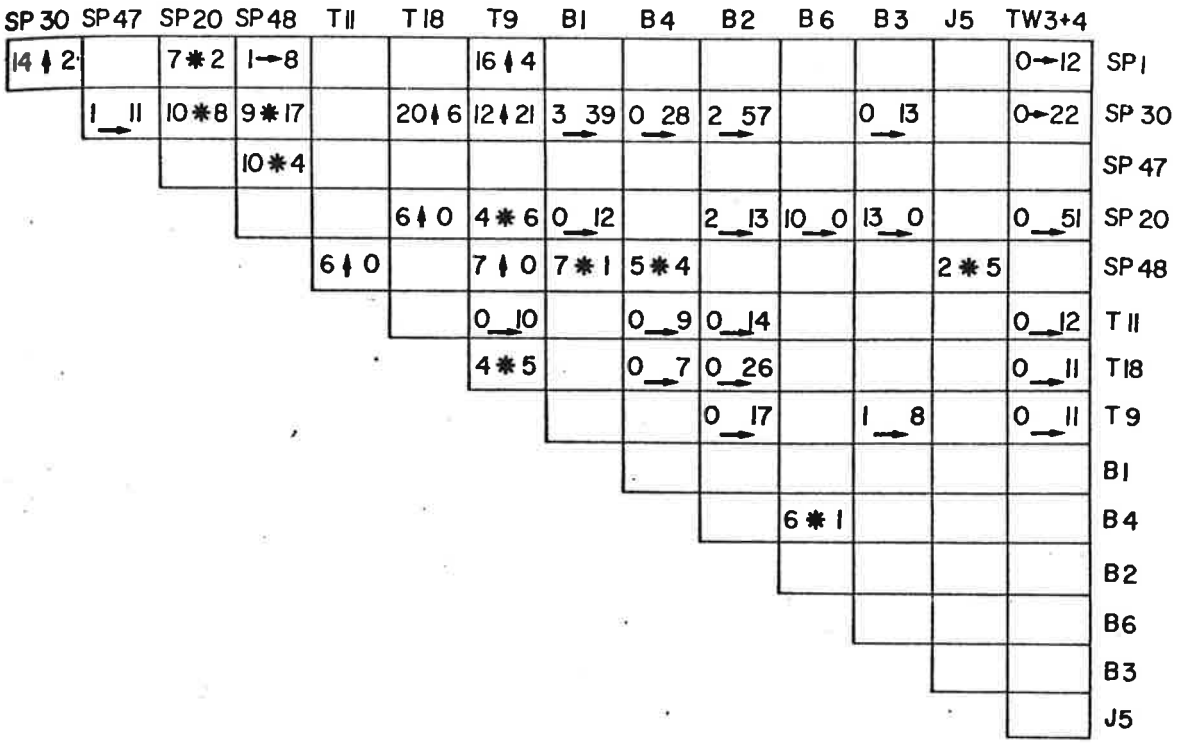

136°E
138°E
a.
34°S
Spencer Gulf
Gulf of
St. Vincent
Adelaide
Edithburgh
N
100 Km.
Kangaroo
Island
36°S
outer half of pier
20m


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


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


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
FEBRUARY
MAY
AUGUST
DECEMBER
FEBRUARY
MAY
AUGUST
DECEMBER
40
20


3 MONTHS
FEBRUARY
MAY
AUGUST
DECEMBER
6 MONTHS
FEBRUARY
MAY
AUGUST
70
DECEMBER
9 MONTHS
FEBRUARY
MAY
AUGUST
82
DECEMBER
12 MONTHS
FEBRUARY
MAY
AUGUST
70
DECEMBER
40
20
PERCENTAGE COVER
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


SP 30 SP 47 SP 20 SP 48 T II T 18 T 9 B I B 4 B 2 B 6 B 3 J 5 TW3+4
14 ↓ 2
7 * 2
1 → 8
16 ↓ 4
0 → 12
SP I
1 → 11
10 * 8
9 * 17
20 ↓ 6
12 ↓ 21
3 → 39
0 → 28
2 → 57
0 → 13
0 → 22
SP 30
10 * 4
SP 47
6 ↓ 0
4 * 6
0 → 12
2 → 13
10 → 0
13 → 0
0 → 51
SP 20
6 ↓ 0
7 ↓ 0
7 * 1
5 * 4
2 * 5
SP 48
0 → 10
0 → 9
0 → 14
0 → 12
T II
4 * 5
0 → 7
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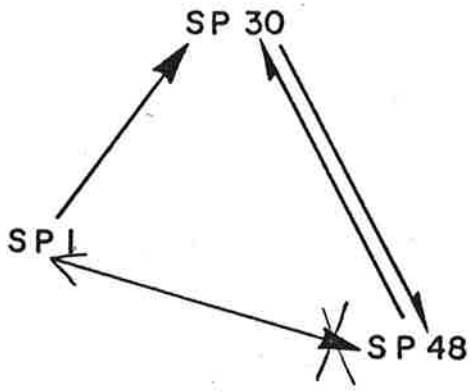
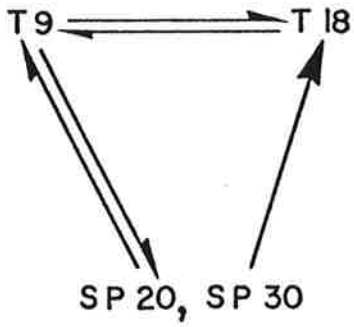
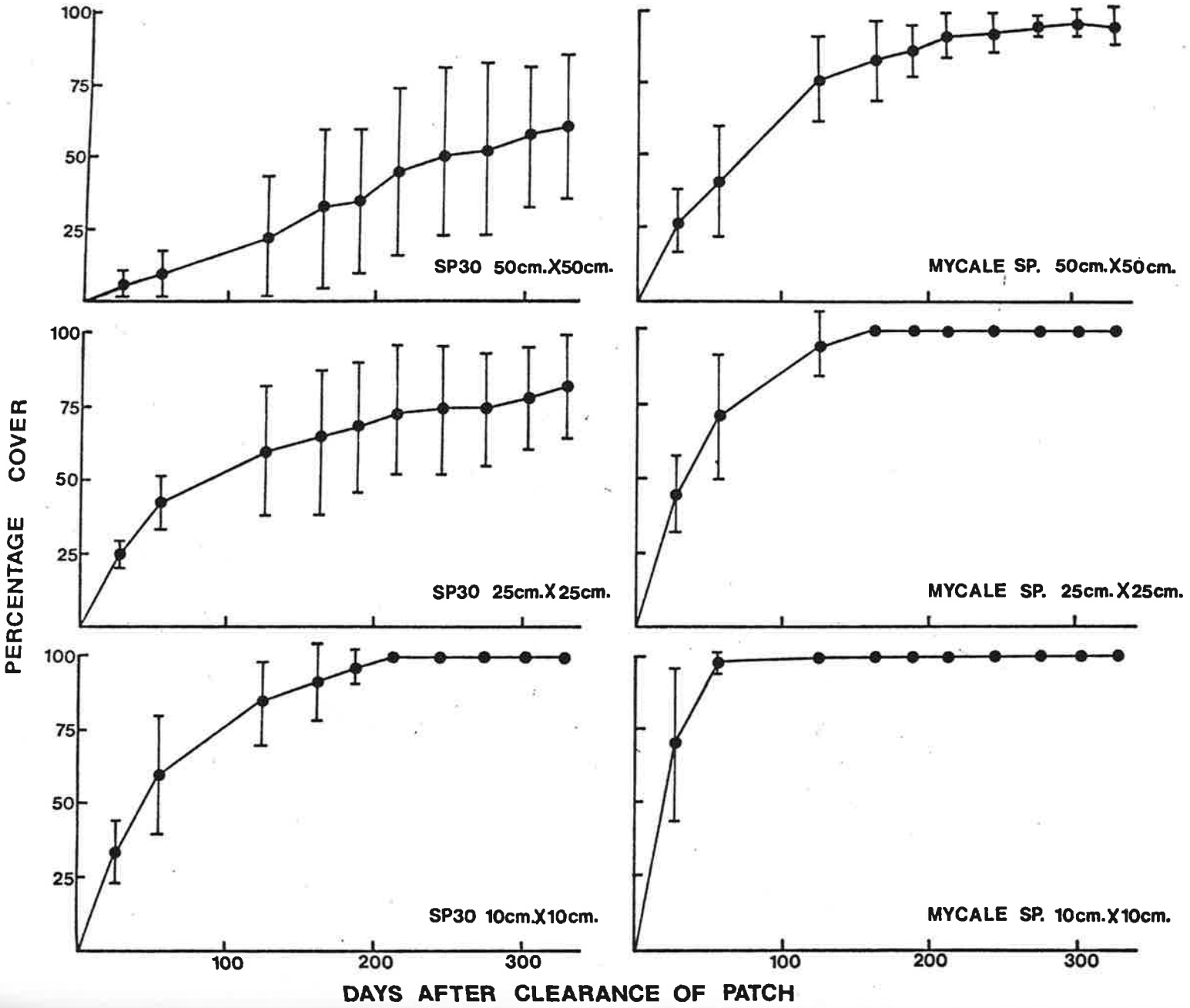
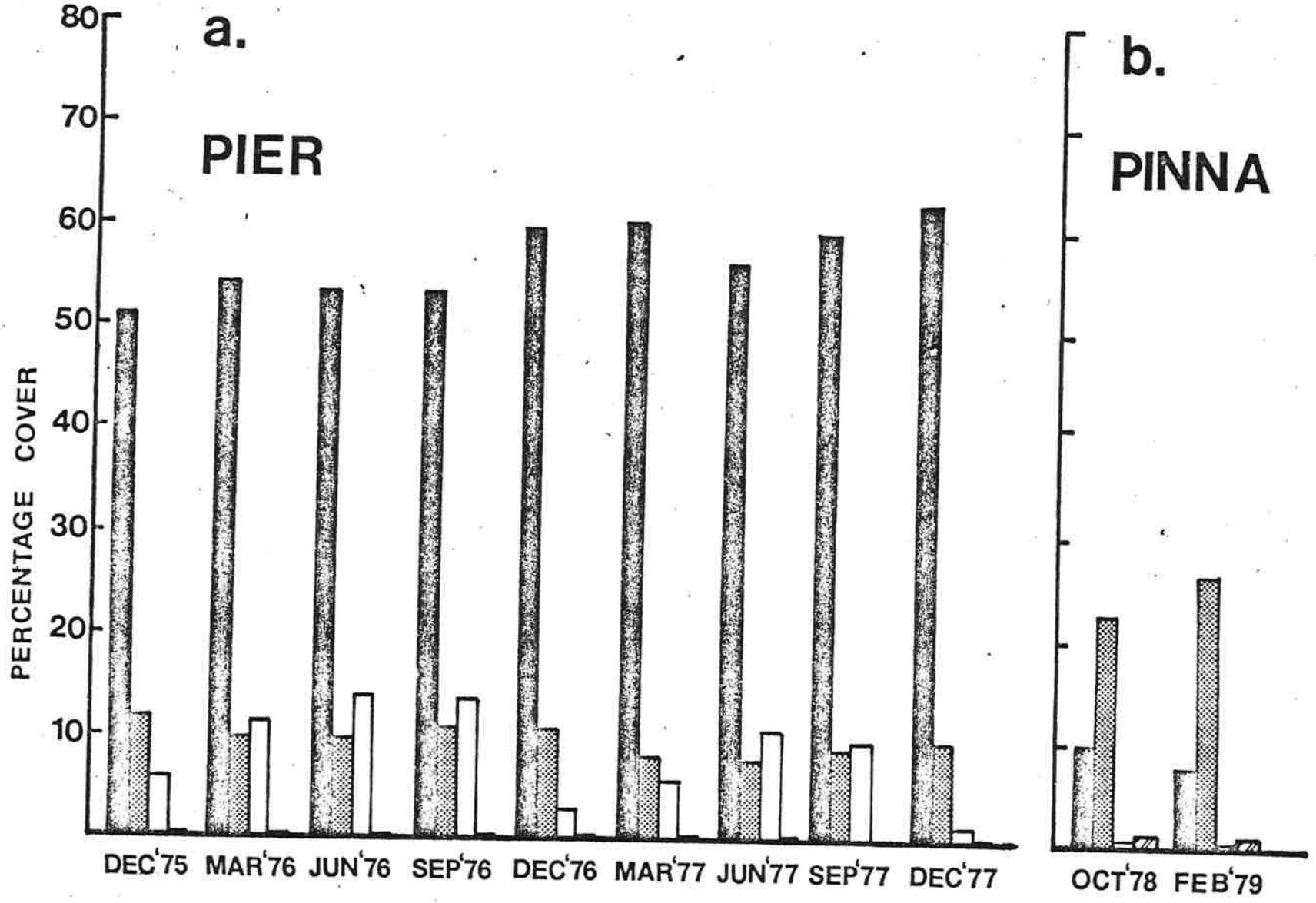
B I
6 * 1
B 4
B 2
B 6
B 3
J 5


SP 30
SP 1
SP 48


T 9
T 18
SP 20, SP 30


PERCENTAGE COVER
100
75
50
25
SP30 50cm.X50cm.
MYCALE SP. 50cm.X50cm.
SP30 25cm.X25cm.
MYCALE SP. 25cm.X25cm.
SP30 10cm.X10cm.
MYCALE SP. 10cm.X10cm.
100
200
300
DAYS AFTER CLEARANCE OF PATCH


a.
PIER
b.
PINNA
PERCENTAGE COVER
80
70
60
50
40
30
20
10
DEC'75
MAR'76
JUN'76
SEP'76
DEC'76
MAR'77
JUN'77
SEP'77
DEC'77
OCT'78
FEB'79

APPENDIX 3

This contains the complete ANOVA tables from the analysis of recruitment patterns in Chapter 3.

In all cases, ns denotes non-significant statistic; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Where an F-statistic was significant, a Student Newman-Keuls procedure was performed. The results to this appear beneath the relevant ANOVA table. Treatments are displayed in decreasing order of means. Homogeneous subsets of means are underlined.

3.1 Analyses of Recruitment and Densities

The following tables are one-way ANOVA's to test for differences in the number of recruits per $180cm^2$ per 60 days between the three panel sizes. In the following section, the "groups" are panel sizes. Each ANOVA table will be headed with a dependent variable, as follows:

(a) total recruits - all species pooled

(b) serpulids - all serpulid species pooled

or (c) an individual species, which will be named where relevant.

The heading also contains the time period to which the data apply.

Data are presented for two sites. 3.1.1 contains Edithburgh data; 3.1.2 those for West Lakes.

3.1.1 Edithburgh

One-way ANOVA on total recruits. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	575.61	287.80	0.872 ns
Within groups; error	45	14845.88	329.91	
Total	47	15421.48		

F-max = 5.76, **

One-way ANOVA on total recruits. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	504.93	252.47	1.522 ns
Within groups; error	57	9454.4	165.87	
Total	59	9959.33		

F-max = 3.15, ns

One-way ANOVA on total recruits. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	62.52	31.26	0.54 ns
Within groups; error	26	1508.93	58.04	
Total	28	1571.45		

F-max = 3.895, ns

One-way ANOVA on total recruits. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	25.77	12.89	0.86 ns
Within groups; error	52	783.06	15.06	
Total	54	808.84		

F-max = 4.366, *

One-way ANOVA on total recruits. Time period 5/79 -7/79.

Source of variation	df	SS	MS	F
Between groups	2	19.32	9.66	0.63 ns
Within groups; error	50	771.52	15.43	
Total	52	790.83		

F-max = 4.332, *

One-way ANOVA on total recruits. Time period 7/79 - 9/79.

Source of variation	df	SS	MS	F
Between groups	2	82.16	41.08	2.112 ns
Within groups; error	48	933.77	19.45	
Total	50	1015.92		

F-max = 1.964, ns

One-way ANOVA on total recruits. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	2433.76	1216.88	7.303 **
Within groups; error	41	6832.12	166.64	
Total	43	9265.89		

F-max = 7.23, **

One-way ANOVA on total recruits. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	172.36	86.18	0.384 ns
Within groups; error	55	12331.86	224.22	
Total	57	12504.22		

F-max = 2.57, ns

One-way ANOVA on total recruits. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	151.98	75.99	3.50 *
Within groups; error	55	1195.54	21.74	
Total	57	1347.52		

F-max = 3.43, *

One-way ANOVA on total recruits. Time period 3/80 - 5/80.

Sourse of variation	df	SS	MS	F
Between groups	2	59.25	29.62	0.71 ns
Within groups; error	35	1452.23	41.49	
Total	37	1511.47		

F-max = 1.96, ns

One-way ANOVA on serpulids. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	284.38	142.19	0.49 ns
Within groups; error	45	13029.54	289.55	
Total	47	13313.92		

F-max = 5.783, **

One-way ANOVA on serpulids. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	400.83	200.42	1.31 ns
Within groups; error	57	8713.75	152.87	
Total	59	9114.58		

F-max = 2.73, ns

One-way ANOVA on serpulids. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	61.28	39.64	0.534 ns
Within groups; error	26	1492.86	57.42	
Total	28	1554.14		

F-max = 3.895, ns

One-way ANOVA on serpulids. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	27.12	13.56	0.91 ns
Within groups; error	52	776.59	14.93	
Total	54	803.71		

F-max = 4.606, *

One-way ANOVA on serpulids. Time period 5/79 -7/79.

Source of variation	df	SS	MS	F
Between groups	2	20.41	10.21	0.67 ns
Within groups; error	50	765.52	15.31	
Total	52	785.93		

F-max = 4.578, *

One-way ANOVA on serpulids. Time period 7/79 - 9/79.

Source of variation	df	SS	MS	F
Between groups	2	75.48	37.74	1.94 ns
Within groups; error	48	934.88	19.48	
Total	50	1010.35		

F-max = 1.96 ns

One-way ANOVA on serpulids. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	2326.43	1163.22	7.50 **
Within groups; error	41	6359.46	155.11	
Total	43	8685.89		

F-max = 1.940, ns

90 45 180

One-way ANOVA on serpulids. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	132.96	66.48	0.30 ns
Within groups; error	55	12097.06	219.95	
Total	57	12230.02		

F-max = 2.596, ns

One-way ANOVA on serpulids. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	149.92	74.96	3.41 *
Within groups; error	55	1207.46	21.95	
Total	57	1357.38		

F-max = 1.65, ns

One-way ANOVA on serpulids. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	42.23	21.12	0.68ns
Within groups; error	35	1093.25	31.30	
Total	37	1135.48	31.	

F-max = 1.73, ns

One-way ANOVA on Galeolaria spp. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	238.09	119.04	0.477 ns
Within groups; error	45	11237.9	249.73	
Total	47	11476.0		

F-max = 6.477, *

One-way ANOVA on Galeolaria spp. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	396.23	198.12	1.538 ns
Within groups; error	57	7344.35	128.85	
Total	59	7740.58		

F-max = 2.82, ns

One-way ANOVA on Galeolaria spp. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	46.10	23.05	0.84 ns
Within groups; error	26	715.14	27.51	
Total	28	761.24		

F-max = 1.916, ns

One-way ANOVA on Galeolaria spp. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	10.68	5.34	0.41 ns
Within groups; error	52	670.95	12.90	
Total	54	681.64		

F-max = 5.666, *

One-way ANOVA on Galeolaria spp. Time period 5/79 - 7/79.

Source of variation	df	SS	MS	F
Between groups	2	7.681	3.841	0.281 ns
Within groups; error	50	665.526	18.311	
Total	52	673.208		

F-max = 5.625, **

One-way ANOVA on Galeolaria spp. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	241.88	120.94	6.32 **
Within groups; error	41	785.10	19.15	
Total	43	1027.00		

F-max = 9.68, **

One-way ANOVA on Galeolaria spp. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	92.32	46.16	0.338 ns
Within groups; error	55	7516.58	136.67	
Total	57	7608.90		

F-max = 1.56, ns

One-way ANOVA on Galeolaria spp. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	30.34	15.17	2.23 ns
Within groups; error	55	373.54	6.79	
Total	57	403.88		

F-max = 2.26, ns

One-way ANOVA on *Galeolaria* spp. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	0.63	0.31	0.21 ns
Within groups; error	35	52.42	1.50	
Total	37	53.05		

F-max = 1.90, ns

One-way ANOVA on Spirorbis convexis. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	2.365	1.162	0.499 ns
Within groups; error	45	106.635	2.37	
Total	47	109.0		

F-max = 2.353, ns

One-way ANOVA on Spirorbis convexis. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	0.300	0.150	0.022 ns
Within groups; error	57	380.95	6.683	
Total	59	381.25		

F-max = 2.994, *

One-way ANOVA on Spirorbis convexis. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	6.894	3.45	0.278 ns
Within groups; error	26	322.07	12.39	
Total	28	328.97		

F-max = 9.09, ns

One-way ANOVA on Spirorbis convexis. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	4.65	2.32	1.75 ns
Within groups; error	52	69.06	1.33	
Total	54	73.71		

F-max = 13.684, **

One-way ANOVA on Spirorbis convexis. Time period 7/79 - 9/79.

Source of variation	df	SS	MS	F
Between groups	2	8.261	4.13	1.30 ns
Within groups; error	48	152.56	3.18	
Total	50	160.82		

F-max = 7.18, **

One-way ANOVA on Spirorbis convexis. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	14.50	7.25	0.23 ns
Within groups; error	55	1735.73	31.56	
Total	57	1750.22		

F-max = 5.89, **

One-way ANOVA on Spirorbis convexis. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	149.92	74.96	3.41 *
Within groups; error	55	1207.46	21.95	
Total	57	1357.38		

F-max = 3.558, ns

One-way ANOVA on Spirorbis convexis. Time period 3/80-5/80.

Source of variation	df	SS	MS	F
Between groups	2	16.50	8.25	0.89 ns
Within groups; error	35	324.86	9.28	
Total	37	341.37		

F-max = 7.99, ns

One-way ANOVA on Spirorbis pagenstecheri. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	4.90	2.45	0.49 ns
Within groups; error	45	224.01	4.98	
Total	47	229.00		

F-max = 2.63, ns

One-way ANOVA on Spirorbis pagenstecheri. Time period 1/79 - 3/79

Source of variation	df	SS	MS	F
Between groups	2	23.44	11.72	1.67 ns
Within groups; error	26	182.36	7.01	
Total	28	205.79		

F-max = 1.28, ns

One-way ANOVA on Spirorbis pagenstecheri. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	1086.67	543.33	4.85 *
Within groups; error	41	4597.88	112.14	
Total	43	5684.55		

F-max = 1.875, ns

90 180 45

One-way ANOVA on Spirorbis pagenstecheri. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	14.18	7.09	0.93 ns
Within groups; error	35	266.16	7.60	
Total	37	280.34		

F-max = 1.97, ns

One-way ANOVA on Didemnum sp A. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	63.45	31.72	2.534 ns
Within groups; error	45	563.37	12.52	
Total	47	626.81		

F-max = 6.86, **

One-way ANOVA on Didemnum sp A. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	0.779	0.389	1.110 ns
Within groups; error	41	14.380	0.351	
Total	43	15.159		

F-max = 1.26, ns

One-way ANOVA on bryozoans. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	3.24	1.62	0.43 ns
Within groups; error	35	132.34	3.78	
Total	37	135.58		

F-max = 6.25, ns

3.1.2 West Lakes

One-way ANOVA on total recruits. Time period 6/78 - 8/78.

Source of variation	df	SS	MS	F
Between groups	2	502.296	251.15	0.231 ns
Within groups; error	57	62063.9	1088.84	
Total	59	62566.2		

F-max = 1.27, ns

One-way ANOVA on total recruits. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	769.7	384.85	0.65 ns
Within groups; error	49	42801.1	873.49	
Total	51	43570.8		

F-max = 5.13, *

One-way ANOVA on total recruits. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	2280.8	1140.4	1.09 ns
Within groups; error	51	53580.1	1056.6	
Total	53	55860.8		

F-max = 3.499, ns

One-way ANOVA on total recruits. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	137094.0	68547.0	1.546 ns
Within groups; error	45	1995743.0	44349.3	
Total	47	2132837.0		

F-max = 2.177, ns

One-way ANOVA on total recruits. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	91.76	45.88	0.281 ns
Within groups; error	43	7022.1	163.30	
Total	45	7113.83		

F-max = 6.428, **

One-way ANOVA on total recruits. Time period 5/79 - 7/79.

Source of variation	df	SS	MS	F
Between groups	2	1542.2	771.1	1.648 ns
Within groups; error	33	15442.6	468.0	
Total	35	16984.8		

F-max = 4.828, ns

One-way ANOVA on total recruits. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	7988.2	3994.1	0.164 ns
Within groups; error	42	1022866.2	24354.0	
Total	44	1039854,3		

F-max = 5.207, *

One-way ANOVA on total recruits. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	1674.3	837.2	0.269 ns
Within groups; error	32	99703.8	3115.7	
Total	34	101378.2		

F-max = 9.347, **

One-way ANOVA on total recruits. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	1187.0	593.5	3.687 *
Within groups; error	26	4185.7	161.0	
Total	28	5372.8		

F-max = 6.051, ns

One-way ANOVA on total recruits. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	254119.5	127059.7	1.997 *
Within groups; error	36	2290003.2	63611.2	
Total	38	2544122.7		

F-max = 14.805, **

One-way ANOVA on serpulids. Time period 6/78 - 8/78.

Source of variation	df	SS	MS	F
Between groups	2	699.36	349.7	0.337 ns
Within groups; error	57	59154.3	1037.8	
Total	59	59853.65		

F-max = 2.31, ns

One-way ANOVA on serpulids. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	595.7	297.8	0.728 ns
Within groups; error	49	20035.0	408.9	
Total	51	20630.7		

F-max = 6.049, **

One-way ANOVA on serpulids. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	413.8	206.9	1.15 ns
Within groups; error	51	8143.6	179.3	
Total	53	9557.3		

F-max = 1.41, ns

One-way ANOVA on serpulids. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	13998.0	6999.0	0.891 ns
Within groups; error	45	353561.4	7856.9	
Total	47	367559.5		

F-max = 1.974, ns

One-way ANOVA on serpulids. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	94.87	47.43	0.291 ns
Within groups; error	43	7001.5	162.83	
Total	45	7096.37		

F-max = 6.6, **

One-way ANOVA on serpulids. Time period 5/79 - 7/79.

Source of variation	df	SS	MS	F
Between groups	2	1542.15	771.03	1.65 ns
Within groups; error	33	15442.6	467.96	
Total	35	16984.75		

F-max = 4.826, ns

One-way ANOVA on serpulids. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	7254.74	3627.37	0.149 ns
Within groups; error	42	1025898.5	24426.16	
Total	44	1033153.2		

F-max = 5.219, *

One-way ANOVA on serpulids. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	1695.97	847.98	0.283 ns
Within groups; error	32	95821.58	2994.42	
Total	34	97517.54		

F-max = 9.185, **

One-way ANOVA on serpulids. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	408.3	204.16	2.596 ns
Within groups; error	26	2045.1	78.66	
Total	28	2453.4		

F-max = 8.755, *

One-way ANOVA on serpulids. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	255465.6	127732.8	2.01 ns
Within groups; error	36	2287412.3	63539.2	
Total	38	2542877.9		

F-max = 15.16, **

One-way ANOVA on Hydroides. Time period 6/78 - 8/78.

Source of variation	df	SS	MS	F
Between groups	2	390.65	195.3	0.291 ns
Within groups; error	57	38292.75	671.8	
Total	59	38683.4		

F-max = 5.04, **

One-way ANOVA on Hydroides. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	18.005	9.003	1.332 ns
Within groups; error	49	331.072	6.757	
Total	51	349.077		

F-max = 5.87, **

One-way ANOVA on Hydroides. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	10524.0	5262.0	0.756 ns
Within groups; error	45	313149.9	6958.9	
Total	47	323674.0		

F-max = 2.015, ns

One-way ANOVA on Hydroides. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	90.522	45.26	0.28 ns
Within groups; error	43	6897.2	160.4	
Total	45	6987.7		

F-max = 6.28, **

One-way ANOVA on Hydroides. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	12260.6	6130.3	0.298 ns
Within groups; error	42	862974.7	20547.0	
Total	44	875235.2		

F-max = 5.422, *

One-way ANOVA on Hydroides. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	1783.29	891.65	0.669 ns
Within groups; error	32	42673.85	1333.56	
Total	34	44457.14		

F-max = 5.596, *

One-way ANOVA on Hydroides. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	355.77	177.89	2.33 ns
Within groups; error	26	1984.98	76.35	
Total	28	2340.76		

F-max = 8.71, *

One-way ANOVA on Hydroides. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	247279.1	123639.5	1.974 ns
Within groups; error	36	2254355.7	62621.0	
Total	38	2501634.8		

F-max = 15.49, **

One-way ANOVA on Spirorbis convexis. Time period 6/78 - 8/78.

Source of variation	df	SS	MS	F
Between groups	2	493.88	246.94	1.13 ns
Within groups; error	57	12505.1	219.39	
Total	59	12993.98		

F-max = 16.84, **

One-way ANOVA on Spirorbis convexis. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	445.31	222.66	0.632 ns
Within groups; error	49	17257.77	352.20	
Total	51	17703.08		

F-max = 6.029, **

One-way ANOVA on Spirorbis convexis. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	237.1	118.6	0.759 ns
Within groups; error	51	7972.5	156.3	
Total	53	8209.6		

F-max = 1.137, ns

One-way ANOVA on Spirorbis convexis. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	273.5	136.75	1.695 ns
Within groups; error	45	3629.75	80.66	
Total	47	3903.25		

F-max = 7.26, **

One-way ANOVA on Spirorbis convexis. Time period 5/79 - 7/79.

Source of variation	df	SS	MS	F
Between groups	2	1760.24	880.12	1.891 ns
Within groups; error	33	15359.40	465.44	
Total	35	17119.64		

F-max = 5.006, ns

One-way ANOVA on Spirorbis convexis. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	18599.94	9299.97	0.216 ns
Within groups; error	42	180801.98	4304.81	
Total	44	199401.91		

F-max = 3.01, ns

One-way ANOVA on Spirorbis convexis. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	195.10	97.55	0.122 ns
Within groups; error	32	25679.30	802.48	
Total	34	25874.40		

F-max = 8.19, **

One-way ANOVA on Spirorbis convexis. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	80.23	40.12	0.662 ns
Within groups; error	36	2180.69	60.58	
Total	38	2260.92		

F-max = 3.19, ns

One-way ANOVA on Ciona. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	47.44	23.72	2.17 ns
Within groups; error	26	283.74	10.91	
Total	28	331.17		

F-max = 1.994, ns

One-way ANOVA on Ascidia. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	63.24	31.62	2.898 ns
Within groups; error	26	284.63	10.95	
Total	28	347.86		

F-max = 5.493, ns

One-way ANOVA on bryozoan BX1. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	5.23	2.62	0.30 ns
Within groups; error	49	424.8	8.67	
Total	51	430.1		

F-max = 3.41, ns

One-way ANOVA on Elminius modestus. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	109.6	54.8	0.48 ns
Within groups; error	49	5581.8	113.9	
Total	51	5691.4		

F-max = 29.24, **

One-way ANOVA on Scrupocellaria. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	5.59	2.80	0.143 ns
Within groups; error	51	964.94	18.92	
Total	53	970.54		

F-max = 2.885, ns

One-way ANOVA on Electroma. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	810.82	405.41	1.05 ns
Within groups; error	51	19711.78	386.51	
Total	53	20522.59		

F-max = 20.96, **

One-way ANOVA on Bugula sp. A. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	5.48	2.74	0.133 ns
Within groups; error	51	1050.89	20.61	
Total	53	1056.37		

F-max = 4.373, *

One-way ANOVA on Bugula sp. A. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	6.41	3.21	2.18 ns
Within groups; error	32	47.13	1.47	
Total	34	53.54		

F-max = 1.523, ns

One-way ANOVA on Bugula sp. A. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	1.34	0.67	0.63 ns
Within groups; error	36	38.26	1.06	
Total	38	39.59		

F-max = 13.37, **

One-way ANOVA on Galeolaria. Time period 6/78 - 8/78.

Source of variation	df	SS	MS	F
Between groups	2	15.24	7.62	1.41 ns
Within groups; error	57	308.49	5.41	
Total	59	323.73		

F-max = 32.61, **

3.2 Similarity Analyses

Fifty random pairs of panels were selected and a similarity between each pair calculated. This was done for each of three panel sizes. These similarities ("between-panel similarities") are the dependent variable in the following tables. One-way ANOVA was used to test whether the level of similarity varied with panel size. The results are discussed in Chapter 3, and the full ANOVA tables are presented below. Each ANOVA tables is headed by site (West Lakes/Edithburgh) and time period.

Data are presented for Edithburgh in 3.2.1, and for West Lakes in 3.2.2.

3.2.1 Edithburgh

One-way ANOVA on Edithburgh data. Time period 9/78 - 11/78.

Source of variation	df	SS	MS	F
Between groups	2	0.077	0.039	0.097 ns
Within groups; error	138	2.252	0.016	
Total	140	2.329		

F-max = 1.139, ns

One-way ANOVA on Edithburgh data. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	0.117	0.059	0.057 ns
Within groups; error	138	2.772	0.020	
Total	140	2.889		

F-max = 2.185, ns

One-way ANOVA on Edithburgh data. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	0.629	0.315	4.373 *
Within groups; error	57	4.102	0.072	
Total	59	4.732		

F-max = 9.727, *

180	90	45

One-way ANOVA on Edithburgh data. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	0.939	0.470	9.038 ***
Within groups; error	144	7.483	0.052	
Total	146	8.423		

F-max = 1.472, ns

180 90 45

One-way ANOVA on Edithburgh data. Time period 5/79 - 7/79.

Source of variation	df	SS	MS	F
Between groups	2	0.096	0.048	0.773 ns
Within groups; error	138	8.582	0.062	
Total	140	8.678		

F-max = 2.16, ns

One-way ANOVA on Edithburgh data. Time period 7/79 - 9/79.

Source of variation	df	SS	MS	F
Between groups	2	1.438	0.72	10.707 ***
Within groups; error	138	9.276	0.067	
Total	140	10.716		

F-max = 8.04, *

180 90 45

One-way ANOVA on Edithburgh data. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	0.311	0.156	3.44 *
Within groups; error	144	6.518	0.045	
Total	146	6.829		

F-max = 3.693, **

180 90 45

One-way ANOVA on Edithburgh data. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	0.042	0.021	0.671 ns
Within groups; error	144	4.494	0.031	
Total	146	4.536		

F-max = 5.25, *

One-way ANOVA on Edithburgh data. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	0.047	0.024	0.507 ns
Within groups; error	140	4.830	0.034	
Total	142	4.877		

F-max = 2.92, ns

One-way ANOVA on Edithburgh data. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	0.519	0.259	7.494 **
Within groups; error	69	2.388	0.035	
Total	71	2.907		

F-max = 4.212, ns

180 90 45

3.2.2 West Lakes

One-way ANOVA on West Lakes.data. Time period 6/78 - 8/78.

Source of variation	df	SS	MS	F
Between groups	2	0.223	0.111	3.565 *
Within groups; error	144	4.502	0.031	
Total	146	4.725		

F-max = 3.428, **

45 180 90

One-way ANOVA on West Lakes data. Time period 8/78 - 10/78.

Source of variation	df	SS	MS	F
Between groups	2	0.213	0.107	2.94 ns
Within groups; error	144	5.228	0.036	
Total	146	5.441		

F-max = 2.61, *

One-way ANOVA on West Lakes data. Time period 11/78 - 1/79.

Source of variation	df	SS	MS	F
Between groups	2	0.110	0.055	3.190 *
Within groups; error	144	2.488	0.017	
Total	146	2.598		

F-max = 1.259, ns

90 180 45

One-way ANOVA on West Lakes data. Time period 1/79 - 3/79.

Source of variation	df	SS	MS	F
Between groups	2	0.002	0.001	0.033 ns
Within groups; error	144	4.106	0.029	
Total	146	4.108		

F-max = 1.249, ns

One-way ANOVA on West Lakes data. Time period 3/79 - 5/79.

Source of variation	df	SS	MS	F
Between groups	2	0.403	0.202	3.298 *
Within groups; error	144	8.800	0.061	
Total	146	9.204		

F-max = 1.710, ns

90 180 45

One-way ANOVA on West Lakes data. Time period 7/79 - 9/79.

Source of variation	df	SS	MS	F
Between groups	2	0.154	0.077	1.097 ns
Within groups; error	87	6.091	0.070	
Total	89	6.244		

F-max = 1.849,ns

One-way ANOVA on West Lakes data. Time period 9/79 - 11/79.

Source of variation	df	SS	MS	F
Between groups	2	0.551	0.275	11.054 ***
Within groups; error	144	3.586	0.025	
Total	146	4.137		

F-max = 2.56, ns

180 90 45

One-way ANOVA on West Lakes data. Time period 11/79 - 1/80.

Source of variation	df	SS	MS	F
Between groups	2	0.112	0.056	2.444 ns
Within groups; error	144	3.294	0.023	
Total	146	3.406		

F-max = 2.043, *

One-way ANOVA on West Lakes data. Time period 1/80 - 3/80.

Source of variation	df	SS	MS	F
Between groups	2	0.248	0.124	4.52 *
Within groups; error	57	1.563	0.027	
Total	59	1.811		

F-max = 2.60, ns

180 90 45

One-way ANOVA on West Lakes data. Time period 3/80 - 5/80.

Source of variation	df	SS	MS	F
Between groups	2	0.094	0.047	2.710 ns
Within groups; error	144	2.497	0.017	
Total	146	2.591		

F-max = 2.114, *

Distribution of *Pinna bicolor* Gmelin (Mollusca: Bivalvia) in South Australia with observations on recruitment

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SUMMARY

BUTLER, A.J. & KEOUGH, M.J. (1981) Distribution of Pinna bicolor Gmelin (Mollusca : Bivalvia) in South Australia with observations on recruitment. Trans. R. Soc. S. Aust.

A diving survey was conducted in January 1980 at 43 sites from Port Broughton in Spencer Gulf to Ceduna in the Great Australian Bight to observe the distribution of the bivalve Pinna bicolor Gmelin, its density, habitat-types and associated species. Earlier records from Investigator Strait, the Gulf of St Vincent and Spencer Gulf are also reported. At 11 sites samples were taken to determine distributions of shell length, counts of growth checks and gonad states.

Although P. bicolor is widespread in suitable habitats throughout South Australia, its distribution is "patchy" on large and small scales. Recruitment is shown to vary in space and time and the significance of this in the ecology of the species is discussed.

INTRODUCTION

The ecology of *Pinna bicolor* is of intrinsic and practical interest (Butler and Brewster 1979) and we have been studying both the population ecology of the bivalve itself (Butler and Brewster 1979) and the epibiota on its shells (Kay and Keough 1981, Keough 1980[1]) at a few sites in the Gulf of St Vincent. However, there is no systematically collected information about the distribution and habitat-types of this species throughout the rest of the State.

It is well known that the "recruitment" of many marine organisms, especially those with pelagic larvae, is variable in both space and time. (By "recruitment" we mean entry to the population at a size such that they can be detected or captured - in this case, seen by a diver. This is not the same as "settlement" from the plankton, because newly-settled larvae may die before they are detectable.) Variability in recruitment may be extremely important in the ecology of such species (e.g. Bowman & Lewis 1977, Keough 1980, Sutherland 1974, Sutherland & Karlson 1977). Although variability in recruitment is reasonably well-documented for certain commercially important species (eg. Loosanoff 1966, Andrews 1979) there is a paucity of published data about its occurrence in a wide variety of organisms, and a paucity of detail about the spatial and temporal scales of "patchiness" in recruitment. Such data are needed for the development of methods for investigating patchy recruitment, and for the development of models, and management policies, for species which have large random variation in certain components of their environments.

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[1]Keough, M.J. (1980) Dynamics of the epifauna of the bivalve *Pinna bicolor* Gmelin. Ph.D. thesis, University of Adelaide (in preparation)

Pinna bicolor is such a species, and in South Australia it is at the southern edge of its tropical and subtropical range (Rosewater 1961), so it is especially interesting to know how its recruitment varies between places and times in South Australia.

Finally, the spatial distributions of sessile, benthic animals may be "patchy" in the sense that their density appears to be non-uniform and to vary non-randomly over areas that appear to an observer to be uniformly suitable (e.g. various papers in Coull 1977). It is of course possible that the area is not in fact uniformly suitable, but also possible that the animals are indeed absent from some habitable sites, perhaps as a result of "patchy" recruitment. Again, this phenomenon requires documentation as a first step in its study[it is important to produce distribution maps showing confirmed absences as well as records of a species.

This paper reports a survey designed to provide general observations on the distribution of P. bicolor in South Australia, the habitat-types in which it occurs (or does not), the organisms associated with it and the regularity of its recruitment. Certain conclusions can be drawn from these general observations made at one time[detailed explanations must depend upon long-term observations and experimental tests of hypotheses.

METHODS

Pinna has been recorded from depths as great as 30m on the floor of Gulf St Vincent (Shepherd and Sprigg 1976) but this survey was confined to areas within 2km of the shore and depths no more than 18m. Our object was to visit as many as possible of those sites where Pinna had been reported or where it might have been expected to occur from the

type of bottom and degree of exposure. (Our assumption here was simply that Pinna requires a soft bottom and no more than moderate wave-exposure.) Cotton (1961) records P. bicolor from Beachport but we know of no other record of the species in South Australia east of Backstairs Passage, nor is it likely to occur inshore on that exposed coast. That part of the State is not discussed here. Before this survey we had many records from Gulf St Vincent and some from Spencer Gulf and Investigator Strait; those records are summarised here, and in particular we discuss data from eight sites scored within two months of the main survey and using the same procedures (sites 1 - 8 in Table 2). The survey itself covered 43 sites from Port Broughton in Spencer Gulf to Ceduna in the Great Australian Bight in January, 1980.

Subtidal sites were surveyed using SCUBA from an inflatable dinghy, intertidal sites on foot. The observations in list A, Table 1, were made at all sites. At certain sites, random samples of P. bicolor were collected by clearing a 1m-wide transect in a randomly-chosen direction and the observations in list B, Table 1, were made on the collected animals in the dinghy or on shore. Table 2 shows the sites and the types of observations made at each. Note that in addition to visiting widely spaced locations, we commonly sampled several sites separated by short distances within one area or embayment. Since one object of the survey was to investigate the small-scale 'patchiness' of P. bicolor, and since one object of this paper is to allow future workers to investigate changes over time, the locations of our sites are given in some detail in Table 2. Table 1 gives sufficient detail on methods excepting the following.

The density of P. bicolor in each of two size-classes was estimated by the diver in number per square metre with the aid of an aluminium rod 1m long. The observer had extensive prior experience

of measuring density using a 1 m^2 quadrat and so the estimates can be taken as sufficiently reliable for use as an index of density. The smaller size-class is likely to have settled within the last year (Butler & Brewster 1979); it was scored separately so as to give an index of recruitment at sites where samples were not taken.

The densities of the animals under item A.12 were scored on the following qualitative scale; none seen, rare, common, abundant. These categories were based on previous experience of "typical" densities for these species and have different meanings for each group. The reasons for scoring them also differ, as follows. The three species of bivalves M. meridianus, C. asperrimus and C. bifrons are ecologically similar to Pinna. Certain asteroids prey on P. bicolor. The gastropods Polinices spp. and probably some muricids are thought to do so. Some fish and cephalopods may do so, especially on small Pinna. Holothurians and echinoids may influence the survival of recently-settled postlarvae. We were interested in any hint of associations (positive or negative) between the presence of P. bicolor, particularly of recent recruits, and the abundance of any of these species. Under each of the headings Muricids, Urchins and Asteroids, and commonly under the other headings, it was possible to identify the particular species recorded.

The length and height of the shell were measured in cm as described by Butler and Brewster (1979). Scars left by the posterior adductor muscle in the nacreous layer of the shell can be counted, although with error. The number of "major" scars appears to be an index of age (Butler and Brewster 1979) and it is likely that they represent winter growth-checks although this awaits confirmation from tagged animals (work is in progress). They were always counted by the same observer in this study. A crude index of age is also available

from the epibiota of the shell, given a knowledge of the biology of the epibiotic species (Keough 1980) which were recorded in this study on the qualitative scale used by Butler and Brewster (1979) with notes on species-composition. The reproductive tissue in Pinna spreads diffusely under the mantle anterior to the posterior adductor muscle and is not always detectable macroscopically. Its development is as yet poorly understood. In this study it was scored qualitatively on the following scale; 0, none visible; P, poorly developed, a thin layer of what appears to be gonad visible; M, moderately developed, undoubtedly gonad tissue present obscuring underlying organs; W, well developed, massive gonad concealing large area of underlying organs.

DISTRIBUTION OF P. BICOLOR IN SOUTH AUSTRALIA

Pinna bicolor has been recorded by us at the locations listed in Table 3 and from Fishery Beach (Fleurieu Peninsula), American River Inlet near Muston (Kangaroo Island), Rapid Bay (Gulf St Vincent), Aldinga Reef (Gulf St Vincent), Price (Gulf St Vincent), Goose and Wardang Islands (Spencer Gulf). Shepherd and Sprigg (1976) recorded it at many spots on the floor of Gulf St Vincent (their Fig. 3) and Cotton (1961) recorded it from 'Beachport to Fremantle'. Thus, the species is widespread on sheltered shores or in deeper water throughout the State. However, note that not all the locations in Table 2 are listed in Table 3 and that sites close to one another often differ (e.g. Chinaman Creek, sites 10 - 14; Franklin Harbour, sites 17 - 21; Tumby Bay, sites 22 - 25; Port Lincoln, sites 26 - 30). Note also that in some embayments which appeared suitable for Pinna, we found none (Kellidie Bay, sites 31 - 38; Venus Bay, sites 40 - 47; Elliston,

site 39) or very few (Franklin Harbour, sites 17 - 21; Port Lincoln, sites 26 - 30). Thus, the distribution of P. bicolor appears "patchy".

MORPHOLOGY

A few shells found at various sites were similar to the form which Cotton (1961) called Subitopinna virgata but almost all were typical of his Pinna dolabrata. Both of these were referred by Rosewater (1961) to the variable species Pinna bicolor Gmelin. The relationship between shell length and shell height will be discussed elsewhere, but on preliminary analysis it appears not to differ significantly amongst all the locations sampled. At any location some shells bore more subtubular spines than others; these were more prominent in young individuals; the typical form at all locations is fairly smooth-shelled (Cotton 1961 Figs 68 & 69; Rosewater 1961 Plates 147, 151 & 152).

DENSITY IN DIFFERENT HABITATS

This survey did not provide data suited for powerful tests of null hypotheses about the relationship between P. bicolor density and such variables as bottom type, depth, current and the presence of other organisms. Nevertheless, some extreme possibilities can be eliminated from the available data. Table 3 shows estimated densities at those sites where P. bicolor was found, and implies zero density at all other sites. P. bicolor occurred in bottom sediments ranging from very fine sand to very coarse sand; we could detect no relationship between our qualitative notes on sediment type and the presence, or density, of P. bicolor. The "prevailing" or "average" conditions of temperature and

current could only be estimated roughly from our measurements and notes on a single dive, but again we could not see a possible explanation for the presence, density, or estimated age-distribution (see below) of P. bicolor in either of these variables.

There is no significant correlation between P. bicolor density and depth (data in Table 3 for positive P. bicolor densities; zero densities included for all other sites in Table 2; $r = -0.17$, $n = 51$, $P > 0.05$), nor between P. bicolor density and the percentage cover of seagrasses (the latter transformed to angles, Rohlf & Sokal 1969, p. 129; $r = 0.02$, $n = 51$, $P > 0.05$). Since we already had reason (unpublished data) to suspect a negative correlation between P. bicolor and seagrasses, this was rechecked by excluding data pertaining to embayments where P. bicolor was rare or absent and where one might argue larvae have, for some reason, failed to arrive (namely Pt Lincoln, Kellidie Bay, Venus Bay and Elliston). The correlation between P. bicolor density and seagrass cover remained non-significant ($r = -0.17$, $n = 29$, $P > 0.05$).

The densities of other species which might conceivably influence P. bicolor, or have similar requirements, were scored on qualitative scales. Inspection of a table of these scores showed no obvious relationships with P. bicolor density. Most of the data do not warrant statistical analysis, but the association between the bivalves P.bicolor, Malleus meridianus, Chlamys asperrimus and C. bifrons was examined further. Scores for each were grouped into two categories - 'low' (= 0 + rare) and 'high' (= common + abundant) - and the scores for P. bicolor were tested for independence of each of the other species in three 2x2 contingency tables; none was significant at the 5% level (Table 4). This is not a powerful test; it merely indicates that the other species are not strongly associated with P. bicolor.

GONAD CONDITION AT DIFFERENT SITES

The scoring of gonad development as None, Poorly, Moderately or Well Developed is a very crude index not only because it is somewhat subjective but also because the histology of gonad development in P. bicolor has not yet been worked out and related to these scores (this work is in progress). Nevertheless, if the populations at different sites were predominantly in different stages of the reproductive cycle, this might be expected to be reflected in the scores, whatever their detailed histological meanings. To test this, we first determined for each of the 12 sites at which gonads were examined within the time-period December 1979-January 1980 the minimum number of adductor muscle scars at which any animal was scored "moderately" or "well developed" (M or W). Next, we considered only animals with that number of scars or more, and calculated the proportion of them scored M or W. This was done because at some sites the proportion of the whole sample with developed gonads would be depressed by the presence of a large number of very small, prereproductive animals. (Scar counts are used here as an index of age - see below - but very similar results are obtained if shell length, instead of scars, is used to determine which animals are potential breeders.)

The results are shown in Table 5. The proportions scored M and W show highly significant heterogeneity between sites when the whole set is tested as a 2x12 contigency table. However, this may possibly be due to the length of time - over a month - between sampling the first and last sites. Therefore, consider only the seven sites sampled over 10 days between 5.i.80 and 15.i.80 and sampled sequentially from Franklin Harbour to Ceduna so that latitude rose and then fell during the 10 days. This set is also highly significantly heterogeneous.

There are three pairs of sites sampled close together in both time and space; sites 13 & 16 in upper Spencer Gulf, sites 23 & 25 in Tumby Bay and sites 48 & 50 in Streaky Bay. Tested by a 2x2 contingency table, each of these pairs is homogeneous for the proportion M or W. In summary, despite our crude method of scoring gonad condition, it is clear that sites spatially far apart, even if sampled at about the same time, differ in the proportion of animals in breeding condition. Sites close together in space and time receive similar scores.

COUNTS OF ADDUCTOR MUSCLE SCARS

Adductor muscle scars are counted with error, but Butler and Brewster (1979) argued, for site 6, Table 2, that major scars probably represent winter growth checks. In interpreting the scar counts from this survey we must remember that variables which cause a slowing of growth, such as temperature, food supply, breeding or various kinds of stress (Clark 1974), may be distributed differently at different sites. At one site, scar counts are probably an index of age, but they do not necessarily estimate chronological age in the same way at all sites. We know that the relationship between shell length and scar count differs between sites. For example, the average length of animals with five scars from site 3 is 31.5cm; that from site 5 (which is intertidal) is 20.0cm. We have at present no way to test whether indertidal animals produce more scars per unit time, or simply grow more slowly. However, from the data available to Butler and Brewster (1979) and various observations obtained subsequently (Butler, unpublished) it seems likely that scars do provide an estimate of age in years, in several different habitats (sites 3,5,6,7 in Table 2). We shall therefore base our interpretation of scar counts on this assumption.

If the number of major adductor scars is an estimate of age in years, then even though scars are counted with error a comparison of the distributions of scar counts from two sites should test whether the age distribution is the same at the two sites. The distributions of scar counts at 13 sites are shown in Table 6. They are highly significantly heterogeneous when the whole set is tested, or when only the set sampled in January 1980 is tested (see G-values in Table 6). Comparing pairs of sites close together in space and sampling date, we find that one is homogeneous (sites 48 & 50), the other two heterogeneous (sites 23 & 25, sites 13 & 16).

The scar distributions were examined further to make inferences about recruitment. First, we considered the density of recent recruitment. Because of the difficulty in scoring the first, faint scar the categories 0 and one scar were pooled, and assumed to represent "1978-9 recruits". The size of this class relative to the rest of the sample was scored for each site into one of three categories: 0, no animals with zero or one scar; minor, $0 < p \leqslant 20$ where p = percentage of the sample having zero or one scar; major, $20 < p \leqslant 100$. The results are shown in Table 7. As for most animals with planktonic larvae, the density of recruitment is not expected to be constant from year to year, even if some recruitment always occurs, and this appears to be borne out by Table 6. Further, the fluctuations in density of recruitment do not seem to be in phase at all sites. If fluctuations in recruitment were in phase, and if subsequent age-specific mortality rates were also the same, the conspicuous modes should be in the same scar-classes at all sites. They are not. This can be seen by inspection of Table 6. To test this, we considered only the first six scar-classes (0 - 5) because for older animals we have less confidence in the assumption of a constant schedule of

age-specific mortalities. The results of tests for homogeneity are shown in Table 6. The whole set is highly significantly heterogeneous; so is the set of nine sites sampled in January 1980. More importantly, two of the pairs of nearby sites sampled close together in time are highly significantly heterogeneous (sites 13 & 16 and sites 23 & 25).

Next, we asked whether recruitment appears to be "regular" at each site, that is, whether some recruits appear each year, albeit at varying densities. To do this, high scar-classes were ignored, because mortality may have reduced their numbers so much that sampling error becomes important. The first six scar-classes (0 - 5) were examined; recruitment at a site was called "irregular" if there were any zero frequencies in the first six classes, otherwise it was "regular". Table 7 shows the result.

Table 7 also shows a ranking of the diver's estimate of density of small Pinna. Note that this is an "absolute" index based on the number of small animals per m^2 of bottom, whereas the above method is based on the proportion of the sample which was young. Also, an animal 7cm in shell height may, at some sites, be several years old. The index based on density of small animals is thus of limited value, but is included because it is available where samples were not collected.

The magnitude of the "1978-9 recruitment", on either index, appears to have differed between sites. Many have "irregular" recruitment. In one case a pair of sites which differed in scar-frequency distributions above (sites 23 & 25) also differ in their 1978-9 recruitment and in their "regularity" of recruitment.

The data collected concurrenty with the samples give no suggestion of explanations for these variations. Neither depth nor percentage cover of seagrass was significantly associated with

"regularity" of recruitment using either the Fisher exact test (assigning seagrass or depth values to two categories) or a two-sample runs test (ordering the depth or seagrass values and then counting "runs" of "regularity" scores); in both cases, $P > 0.05$. Similarly if the scores for 1978-9 recruitment were grouped into two categories (0+m, M) then they were not significantly associated at the 5% level with either depth or seagrass cover using either test.

The magnitude of 1978-9 recruitment (grouped into two categories) was not significantly associated with "regularity" of recruitment (Fisher exact probability test: $P = 0.085$).

When the notes on associated species were grouped into two categories (0 + rare; common + abundant) and tabulated against the scores for 1978-9 recruitment or for "regularity", no positive or negative associations were apparent on inspection, and certainly none were statistically significant at the 5% level using Fisher exact tests.

The density of small animals ($H \leq 7$cm) is positively correlated with that of larger ones (both estimated in situ by the diver). For sites where any P. bicolor were found, Pearson's $r = 0.49^{*}$, $P < 0.05$; Spearman's $\rho = 0.76^{***}$, $P < 0.001$.) This test was repeated, excluding sites 5,7,13,21,23,25,48,49 because their length-scars relationship showed that animals of H = 7cm may have more than two scars, and thus the density of "small" animals may not be an estimate of the density of recent recruitment. The conclusion remained the same (Pearson's $r = 0.54^{*}$, $P < 0.05$; Spearman's $\rho = 0.75^{**}$, $P < 0.005$).

However, "regularity" of recruitment was not significantly associated with total density either by a 2x2 contingency table with density classified as $\leq 2\ m^{-2}$ or $> 2\ m^{-2}$ (Fisher exact test: $P = 0.085$) or by a runs test as used above for depths ($P > 0.05$).

DISCUSSION

This survey has provided a 'distribution map' for Pinna bicolor in South Australia. It is based on visits to many, but not all, sites apparently suitable - that is, sites of low wave-action with soft bottoms. There is a temptation to assume that when a species has been recorded at two points, it may be expected to occur in suitable habitats in between (thus, distribution maps are often shaded in), but that seems not to be so in this case. The distribution is 'patchy'; P. bicolor is absent from some apparently suitable sites. The 'patchiness' occurs on a local scale; P. bicolor may be found on some but not other dives on apparently similar bottoms within a kilometre or so - e.g., sites 10 - 14, 17 - 21, 22 - 25, 26 - 30. But it is also evident on a larger scale; the species seems to be absent from certain large and apparently habitable embayments (Kellidie Bay, Venus Bay, Elliston), though present in others north and south of them. Note that these are well-enclosed embayments; perhaps the current patterns are such that the arrival of planktonic larvae there from outside is a rare event. If so, then by chance a recruitment might occur from time to time and establish a temporary "population". This seems to have happened at Port Lincoln (site 26). The reason for giving the details in Table 2 is to document this patchiness; later workers might want to check the same locations.

Organisms are rarely if ever distributed evenly. Some of the unevenness in their distributions can be explained by an understanding of their ecology - we can say why the unoccupied sites are unsuitable or have not been colonised - but there may remain a component which cannot be explained, even tentatively, with existing knowledge. The possibility remains that the vacant sites are unsuitable or

inaccessible, but the reasons are not at present known. We shall call this "unexplained patchiness"; P. bicolor provides an example.

There is no detectable relationship between density of P. bicolor and sediment type, current regime, water depth (Table 3), cover of seagrass, or associated animal species, especially other ecologically similar bivalves (Table 4). One might not have expected a competitive interaction of any importance between these bivalves (Stanley 1977), but perhaps their ecological similarity - or even the fact that Malleus and C. asperrimus use P. bicolor for attachment - might have led to a positive association. None is evident. We note in passing that the other three species of bivalves, like P. bicolor, were more often scored "low" than "high" in density even though many sites appeared suitable, and any diver knows they can be very abundant. These species, too, appear "patchy".

Species which are either predators or "malentities" (Andrewartha 1970) might be expected a priori to have most of their influence on younger stages of P. bicolor; still, we note that they showed no association with the density of P. bicolor large enough to be seen by a diver.

The above is based on imprecise data - mostly subjective rankings - and so there is a possibility that real associations exist but were not detected. However, one might have expected such associations to be at least noticeable in the kind of data we collected even if they were not statistically significant; no trends, however slight, were apparent. Thus we conclude for the present that with respect to the presence and density of P. bicolor we are observing unexplained patchiness.

The proportion of the population with developed gonads appears less "patchy". It differs between sites even considering only those

sampled close together in time, but spatially-close sites - pairs of sites in the same embayment - do not differ significantly (Table 5). We cannot infer that these populations are in the same phase (because we do not know, for example, whether a gonad scored 'P' is developing or spent) but it seems likely.

Counts of adductor-muscle scars were heterogeneous between sites, including some nearby pairs. These scars surely represent checks in the growth of the animal but the reasons for the checks, and their periods, are not known with certainty. Nevertheless there is reason to assume that they represent winter growth checks and our interpretation of the counts was based on that assumption. On that assumption, the age-distributions of the standing populations of P. bicolor at different sites - including some nearby pairs - differ. We examined those distributions in more detail and found that the proportion of the population with low scar counts - recent recruits - differs between sites including nearby ones (Table 6). In other words, the density of recruits relative to that of adults varies. Further, the presence or absence of whole classes - interpreted as "regularity" of recruitment - differs between sites. Note that the absence of an entire class is a stringent criterion of "irregularity", given the error in counting rings. It seems clear that recruitment fluctuates from year to year, and the fluctuations are not in phase at all sites, nor necessarily even at nearby sites. This contrasts with the proportions with developed gonads, which were similar at nearby sites.

Recent recruitment and the regularity of recruitment were not correlated with depth, cover of seagrass, nor with each other. "Regularity" was not significantly associated with total density of P. bicolor as estimated in $no.m^{-2}$.

No relationships could be detected between recruitment and the densities of associated species. This is not to say that the associates have no effects. Firstly, it is possible that their abundance is correlated with the recruitment of P. bicolor but our data are too imprecise to detect it. Secondly, they may move about, so that their abundance at a particular place and time bears little relationship to their effects on P. bicolor there at some earlier time. Thirdly, their effects may be masked by other variables, especially the density of settlement of P. bicolor. The lack of correlations in our data does eliminate the grossest hypotheses, e.g. that dense holothurians will, by killing newly-settled larvae, lead to sporadic recruitment.

The above discussion concerns recruits as a proportion of the population. Actual densities of recruits would be of interest. The only relevant data we have are the diver's in situ estimates of the densities of two size-classes. The density of small animals is positively correlated with that of large ones, considering all sites where P. bicolor were found. However, this may be an artefact, because although an animal of $H \leqslant 7$cm at site 3 would very likely be under two years old and probably under one (Butler and Brewster 1979), this will not necessarily be true at all sites (above). However, if we eliminate sites where animals have a large scar count for a given length, we still find the same conclusion; density of small P. bicolor is positively correlated with that of large ones. This seems to be rather in contrast to the conclusions drawn above from the scar counts. However, it is consistent with them if the events leading to recruitment are viewed as follows.

Larvae of Pinnidae can travel long distances in the plankton (R.S. and A. Scheltema, pers. comm.). Thus, the fact that animals breed at all sites does not guarantee that settlement - still less,

recruitment - will occur at all sites, and those larvae which settle at a site may not have been spawned there. Larvae move about with the currents and may well be distributed patchily within the water (see reviews in Steele 1978). Thus, their probability of successful recruitment at a given benthic site depends firstly on their being carried there on a current of suitable strength, etc. for settlement, and secondly on subtle properties of the bottom (which may vary from time to time), the presence or absence of mobile or ephemeral predators, the availability of food for newly settled postlarvae (which itself may depend upon planktonic patchiness and on the vagaries of the currents), and so on. We stress the term probability. The mere fact that recruitment is partly dependent on currents, on the shapes of land-masses and channels and on the topography of the bottom, will mean that sites differ consistently in the probability that larvae will settle. This can account for some very well-enclosed embayments apparently containing few or no P. bicolor, and for a correlation between the densities of adults and young, but it leaves recruitment as a random variable with a large variance which, on the present state of our knowledge, we cannot explain. Most sites receive variable, and some even irregular, recruitment and we cannot explain or predict this using depth, associated species, sediment type or latitude.

Recruitment is a major "mystery stage" (Spight 1975) in the ecology of many species with pelagic larvae (e.g. Andrews 1979, Mileikovsky 1971, Sastry 1979, Underwood 1979). It is important because it varies so widely. We can hope to understand the ecology of the species after successful recruitment, but recruitment itself is the main event that determines the density of such a species at a given site. Whilst it may be possible in some cases to predict recruitment from independent variables which influence larval survival, our data -

especially the very small-scale "patchiness" - give no encouragement that it will be possible in this case. For purposes of a general understanding of the ecology of the system (or for long-term planning, if the species were a commercially important one) we may make use of a probability distribution for recruitment. For purposes of short-term prediction, the only course is to monitor recruitment directly, as done for commercial species (e.g. Lewis, in prep.).

The above should not be taken as an assertion that nothing can be known about the recruitment of Pinna. Knowledge of a probability distribution can be powerful. Those species which interact with Pinna - feed on its young, live on its shells, etc, - must be adapted to that probability distribution. It is a challenge to ecology to produce useful models for systems in which many of the important events have probability distributions with large variances.

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Table 1. A. Observations recorded at each site surveyed.
B. Additional observations made on random samples of *Pinna bicolor* at sites marked * in Table 2.

A.

1. Position by landmarks and bearings. Record map reference.
2. Depth (m, by shot line).
3. Surface and bottom water temperatures (°C by mercury thermometer).
4. State of tide and current.
5. Estimated prevailing wave and current conditions.
6. Distance covered by diver.
7. Notes on bottom type and macrobiota.
8. Estimated percentage cover of each of the seagrass genera *Zostera*, *Posidonia*, *Amphibolis*, *Halophila*.
9. Density (m^{-2}) of *Pinna bicolor* of dorso-ventral shell height $\leq$ 7cm.
10. Density (m^{-2}) of *Pinna bicolor* of dorso-ventral shell height > 7cm.
11. Diver's *in situ* notes on size distribution, spatial distribution, morphology and epibiota of *Pinna*.
12. Qualitative scores of the abundance of the following animal species or groups: *Malleus meridianus*, *Chlamys asperrimus*, *Chlamys bifrons*, *Polinices* spp., muricid gastropods, holothurians, echinoids, asteroids, fish and cephalopods.

B. For each animal in a random sample:

1. Antero-posterior shell length (cm).
2. Dorso-ventral shell height (cm).
3. Number of adductor muscle scars, left shell valve.
4. Appearance of gonad.
5. Shell damage due to breakage or sponge boring.
6. Presence of shell spines.
7. Epibiota.

Table 2. Sites inspected for Pinna bicolor. Observations in list A (Table 1) were recorded at all sites. Those in list B were also recorded at sites marked with an asterisk.

Site number	Location	Depth (m) (I=intertidal)	Latitude °S/ Longitude °E
1	1-2km W of Semaphore jetty	7	34.83/138.45
2*	3km NW of St Kilda	3	34.73/138.48
3*	2km E of Ardrossan	15	34.43/137.95
4	Ardrossan: beacon N of bulk loading jetty	7-8	34.43/137.93
5*	Stansbury: on intertidal sand-spit	I	34.92/137.83
6*	Edithburgh: site used by Butler & Brewster (1979)	7	35.11/137.78
7	Troubridge Island: intertidally on SW side	I	35.13/137.82
8	Wallaroo: out to 150m W from site of old jetty	0-7	34.93/137.61
9	Port Broughton: over 4km travelled in channel and around mangrove island	0-3	33.56/137.92
10	Chinaman Creek: 2km WSW of shacks	10.5	32.23/137.80
11	Chinaman Creek	4	32.65/137.80
12	1.5-2km WSW of Chinaman Creek	4.5	32.65/137.78
13*	400m WSW of Chinaman Creek	3-4	32.68/137.83
14	Chinaman Creek	2-3	32.65/137.82
15	Port Augusta: Playford Power Station jetty	7-10	32.54/137.78
16*	Port Augusta: first normal channel marker S from Power Station	7.5	32.55/137.78
17	Franklin Harbour: about 400m S of Cowell jetty	3	33.70/136.94
18	Franklin Harbour	3-4	33.70/136.94
19	Franklin Harbour: 500-600m E of jetty	4	33.68/136.95
20	Franklin Harbour: Cowell jetty	4-5	33.68/136.94
21*	Franklin Harbour: may be locally called Dr Thompson's Reef	0.5	33.71/136.94
22	Tumby Bay: 600m ESE of jetty	5.5	34.39/136.12
23*	Tumby Bay: jetty	4	34.39/136.11
24	Tumby Bay: 200m off end of jetty	5	34.39/136.12
25*	Tumby Bay: 100m off entrance to caravan park	I	34.38/136.11
26*	Port Lincoln: 300m E of caravan park jetty	13.5	34.73/135.89
27	Port Lincoln: Kerton Point jetty	9	34.72/135.88
28	Port Lincoln: 150m off caravan park	3-5	34.73/135.89
29	Port Lincoln: 300m WSW of 1st port channel marker	15-18	34.70/135.88
30	Port Lincoln	13	34.72/135.87
31	Coffin Bay: between jetty and point to NW	2.5	34.63/135.47
32	Coffin Bay: in channel leaving Coffin Bay	4	34.62/135.46
33	Coffin Bay	1	34.62/135.46

34	Coffin Bay: between Goat Is and other side of bay	5	34.62/135.47
35	Coffin Bay: point at entrance to Coffin Bay	2.5	34.62/135.46
36	Kellidie Bay	1-2	34.61/135.48
37	Kellidie Bay	1	34.61/135.47
38	Coffin Bay jetty	4	34.62/135.47
39	Elliston: near jetty	5	33.64/134.89
40	Venus Bay: near jetty	3-4	33.23/134.68
41	Venus Bay	I	33.23/134.72
42	Venus Bay: downstream from 2nd upstream channel marker	3	33.22/134.68
43	Venus Bay: side channel on way back to jetty	4	33.23/134.68
44	Venus Bay: 1st upstream channel marker from jetty	0.5-4	33.22/134.67
45	Venus Bay: channel SW of Germein Island	0.5-3	33.22/134.66
46	Venus Bay	5-6	33.23/134.64
47	Venus Bay: 1st downstream channel marker from jetty	3	33.23/134.66
48*	Streaky Bay	I	32.80/134.21
49	Streaky Bay: 100m inshore from 48	I	32.80/134.21
50*	Streaky Bay: 200m S of 1st outgoing channel marker, near Crawford Landing	6.5	32.78/134.23
51	Ceduna jetty	3	32.13/133.67

Table 3. Water-depth and estimated density of *P. bicolor* at those sites where it was found in summer, 1979-80. Site numbers correspond to those in Table 2. *Densities at these sites were measured using a $1m^2$ quadrat.

Site	Depth (m)	*P. bicolor* of H ⩽ 7cm $no.m^{-2}$	*P. bicolor* of H > 7cm $no.m^{-2}$
1	7	1.8	2.5
2	3	0	<<0.1
3*	15	1.87	0.97
4	7.5	0	0.2
5*	Intertidal	1.71	1.41
6*	7	0.20	1.54
7	Intertidal	0.30	>1
8	0-7	2	5
13	3	10	5
15	7-10	<0.01	4
16	7.5	0.01	0.8
19	4	0	<0.01
21	0.4-0.5	0.01	0.85
23	4	0.05	0.15
25	Intertidal	2	7
26	13.5	0	0.7
27	9	0.001	0
30	13	0	0.001
48	Intertidal	14	3.5
49	Intertidal	3.5	1
50	6.5	1.5	1.5
51	3	1	1

Table 4. Association between qualitative scores for the densities of *P. bicolor* and three species of epibenthic bivalves. Each figure in the Table is the number of sites at which that combination of scores occurred.

Density of *P. bicolor*	*Malleus meridianus*		*Chlamys asperrimus*		*Chlamys bifrons*	
	low	high	low	high	low	high
low $\leq 1m^{-2}$	34	5	39	0	37	2
high $>1m^{-2}$	5	3	7	1	6	2
χ^2_1 for 2x2 contingency table	1.38		0.79		1.30	
P	>0.05		>0.05		>0.05	

Table 5. Gonad development in Pinna bicolor sampled at 12 sites. Site numbers correspond to Table 2. Gonads were visually scored as '0' - not apparent; 'P' - poorly developed; 'M' - moderately developed and 'W' - well developed and these have been pooled into two categories here. Only animals in the reproductive "age"-class, as determined by adductor muscle scars, are included (see text).

Site	Date Sampled	Number O + P	Number M + W
3	18.xii.79	0	49
5	20.xii.79	27	131
6	13.xii.79	20	130
13	24.i.80	16	39
16	23.i.80	19	57
21	5.i.80	0	74
23	7.i.80	11	19
25	6.i.80	23	42
26	9.i.80	24	25
48	13.i.80	11	43
50	13.i.80	6	22
51	15.i.80	5	43

χ^2_1 tests for homogeneity:

Whole 2x12 table:	$\chi^2_{11} = 84.92^{***}$	($P < 0.001$)
Sites 21,23,25,26,48,50,51:	$\chi^2_6 = 54.13^{***}$	($P < 0.001$)
Sites 13,16:	$\chi^2_1 = 0.10$	($P > 0.05$)
Sites 23,25:	$\chi^2_1 = 0.01$	($P > 0.05$)
Sites 48,50:	$\chi^2_1 = 0.01$	($P > 0.05$)

Table 6. Frequencies of counts of adductor-muscle scars in samples of *Pinna bicolor* from 13 sites in South Australia.

Site	Number of Scars													No. of animals in sample
	0	1	2	3	4	5	6	7	8	9	10	11	≥12	
2		3	24	17	3	3	1	1	2		2			56
3	105		3	4	1	1	1	3	1	2	3	3	27	154
5	6	6	22	29	21	16	14	21	9	10	4	3	3	164
6		33	28	15	21	9	17	7	8	11	1			150
13		7		3	2	12	10	13	7		6	2		62
16		3	4	11	21	16	10	7	3	5	2		1	83
21		1	3	4	15	20	14	12	3	1	1	1		75
23			1	10	2	5	3	1	3	2	1	1	2	31
25	2	2	14	7	15	22	9	9	2	1	1			84
26									1	1	4	13	30	49
48	12	9	8	8	6	8	12	8	2	2				75
50	9	13	1	3	4	3	3	6	1	2	4		1	50
51	9	13	7	7	12	3	4	3	3	3	2	3	1	70

Log-likelihood rates tests for heterogeneity:

Whole 13x13 table:	G = 1156***	d.f. = 144	P < 0.001
Sites 13-51:	G = 499.9***	d.f. = 96	P < 0.001
Sites 13&16:	G = 24.15**	d.f. = 7	P < 0.005
Sites 23&25:	G = 28.57***	d.f. = 6	P < 0.001
Sites 48&50:	G = 14.87	d.f. = 8	P > 0.05
Scar classes 0-5 (0 & 1 pooled)			
All sites except 26	G = 463.8***	d.f. = 44	P < 0.001
Sites 13-51 (except 26)	G = 153.5***	d.f. = 28	P < 0.001
Sites 13 & 16	G = 18.42**	d.f. = 4	0.001 < P < 0.005
Sites 23 & 25	G = 16.73**	d.f. = 4	0.001 < P < 0.005
Sites 48 & 50	G = 7.45	d.f. = 4	P > 0.05

Table 7. Inferences about density of recent recruitment and regularity of recruitment over the previous 5-6 years, based on counts of adductor muscle scars (Table 7) on the assumptions that the scars represent winter growth checks, and that post-recruitment mortality rates and their year-to-year variations are the same at all sites. See text for methods. O, no recruitment; m, minor recruitment; M, major recruitment; I, irregular; R, regular. The table also shows inferences about density of recent recruitment based only on the diver's estimate of density of Pinna of H ≤ 7cm at sites where Pinna density was > 0. (Table 4). 0, density = 0; S, sparse, 0 < density ≤ 0.1 m^{-2}; D, dense, density > 0.1 m^{-2}.

Site	1978-9 Recruitment from scar counts	Recent recruitment from density of small animals	Regularity of Recruitment from Scar Counts
1		D	
2	m	0	I
3	M	D	I
4		O	
5	m	D	R
6	M	D	I
7		D	
8		D	
13	m	D	I
15		S	
16	m	S	I
19		O	
21	m	S	I
23	O	S	I
25	m	D	R
26	O	O	I
27		S	
30		0	
48	M	D	R
49		D	
50	M	D	R
51	M	D	R

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