PELAGIC AND EARLY BENTHIC STAGES
AS DETERMINANTS OF THE DISTRIBUTION AND ABUNDANCE
OF THE ASCIDIAN
PODOCLAVELLA MOLUCCENSIS SLUITER

Andrew Randall Davis
M. Sc. Hons (Auckland)

A thesis submitted in partial
fulfilment of the requirements
of the degree of
Doctor of Philosophy in Zoology,
University of Adelaide,
March 1987.

Awarded 16/10/87

"Give me a fruitful error any time, full of seeds,
bursting with its own corrections.
You can keep your sterile truth for yourself"

Vilfredo Pareto

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr Alan Butler, for his critical input during all phases of this project and for his willingness to discuss my ideas, plans and findings. Alan also had the misfortune of wading through early drafts of this manuscript. During Alan's year-long absence in 1984, Dr Dave Paton took the helm and continually challenged my ideas and preconceptions; his lack of experience with marine systems was by no means apparent. Discussions with Drs Mike Kokkinn and Steve McKillup helped improve my half-baked ideas. Mike Cappo kindly edited a late draft of this manuscript.

A project of this nature entails considerable field work and this work would have been far more difficult without the companionship, good-humour and assistance of my friends: Greg Powell, Andy Bennett, Jane Davis, Martin Robinson, Mike Cappo, Craig Proctor, Helen Chernoff, Andy Cichon, David "The Hulk" Peake-Jones, Brian Pierce, and Jean Jackson.

The chemical aspects of this project were done in collaboration with Dr Ian van Altena. I thank Phil Leppard and Dr Keith Walker for patient advice on statistical matters. Technical assistance and endless technical suggestions were provided by Terry MacKenzie and Phil Kempster. Ruth Evans ably assisted with the production of many of the figures. Sandra Lawson juggled documents on the word processor and the laboratory manager, David Williams, assisted me in many subtle but important ways.

Permission to work within the Port Noarlunga aquatic reserve was granted by the South Australian Department of Fisheries.

During this project I was supported by a University of Adelaide Postgraduate Scholarship. I also gratefully acknowledge financial assistance from the Victorian Institute of Marine Science and the Ecological Society of Australia.

Finally, I extend my heartfelt thanks to Jane Davis, for without her support, encouragement, and Moussaka, this thesis may never have come to fruition.

DECLARATION

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

ABSTRACT

The colonial ascidian Podoclavella moluccensis Sluiter (Aplousobranchia: Clavelinidae) inhabits subtidal hard substrata in temperate and tropical Australian waters. Colony densities span more than two orders of magnitude between sites in St Vincent's Gulf and Investigator Strait, South Australia. This thesis investigates the role of pelagic and early benthic phases of the life history in determining the distribution and abundance of adult colonies.

P. moluccensis lends itself to an investigation of early life history stages because larvae are highly conspicuous. The size (4mm in length) and bright blue pigmentation of P. moluccensis larvae render them easily observable under water.

Population dynamics were examined at two sites; Edithburgh Jetty and Port Noarlunga Reef. Life history attributes differed between these sites. At Edithburgh, colony densities were the highest observed at any site and colonies were semelparous annuals. Densities at Port Noarlunga were approximately 7-fold lower than at Edithburgh and this population was perennial and iteroparous. Associated with these differences in life histories were differences in the population dynamics and the fecundity of colonies at each site. Fecundity was higher at Edithburgh, with a higher proportion of each colony brooding and significantly larger broods.

The number of recruits at each site showed a strong positive relationship with the size of the adult population. Recruitment at Edithburgh was an order of magnitude higher than at Port Noarlunga. A strong relationship between adult density and recruitment is to be expected given the short distances over which P. moluccensis larvae disperse.

Dispersal was quantified by following 270 larvae after their release from the parental colony. One hundred larvae were followed successfully to settlement. The distance that larvae dispersed from the parent colony was represented by a negative binomial function, following smoothing of the data. On average, larvae moved a little over two metres after swimming for less than two minutes. Estimated larval mortality was, on average, less than 11%.

Larvae did not settle at random on available substrata. They selected subtrata at settlement on the basis of light, gravitational, and chemical cues (textural cues were not examined). Settling larvae showed a preference for substrata on which early post-settlement mortality was low. In a regression of settlement against recruitment, settlement explained 86% of the variation in the relationship. Hence, the number of settlers could be confidently inferred from estimates of recruitment.

Post-settlement mortality was dependent on substratum type. Overgrowth by neighbouring animals and the dislodgement of epifauna upon which larvae had settled were significant sources of post-settlement mortality. Juvenile colonies were shown not to survive high levels of artificial damage, indicating that predators were a potential source of mortality. Indeed, recruit survival and growth rate were significantly enhanced in crab exclosures. Crabs were not consuming recruits but rather 'trampling' them.

An interplay between adult population size, the distance of dispersal, and the availability of sites suitable for settlement adequately explain the distribution and abundance of adult colonies. These findings underscore the significance of early pelagic and benthic stages in determining the distribution and abundance of species which have dispersive larvae.

CONTENTS

CHAPTER TWO: Spatial and temporal Patterns of Distribution and Abundance

CHAPTER THREE: Dispersal and Larval Mortality

CHAPTER FOUR: Patterns of Recruitment: settlement and post-settlement mortality

4.3 Settlement Preferences and Post-settlement Survival on Naturally Occurring Substrata

4.4 Settlement Preferences and Post-settlement Survival on Vertical and Horizontal Substrata

CHAPTER FIVE: The Effect of Predators

LIST OF FIGURES

LIST OF TABLES

CHAPTER ONE

General Introduction

Complex interactions are likely to be common place in marine and other communities. In an attempt to deal with the complexity inherent in natural systems some ecologists have, for some time, been advocating a reductionist or mechanistic approach to communities (Andrewartha & Birch, 1954; Harper, 1982; Schoener, 1986). They suggest that it is necessary to gain a better understanding of the components of communities - the dynamics of populations, their life histories and aspects of the behaviour and physiology of individuals. Indeed, natural selection, the driving force of evolution, operates on variation between individuals, and only indirectly on populations or communities.

The examination of this complexity may be pursued at any of several ecological levels. Excluding evolutionary ecology there are four levels or subdisciplines in the study of ecology; individual ecology, population ecology, community ecology and ecosystem ecology. These levels are not simply arbitrary but constitute a hierarchy (Schoener, 1986). Schoener develops a strong case for considering the first three levels as a "perfect" hierarchy (sensu Beckner, 1974). He excludes ecosystem ecology from this hierarchy because, by definition, it includes the physical environment and therefore is not a strict sum of lower levels. It could be argued, however, that rarely will a community, in the sense used by most workers, be a strict sum of populations. As the study of ecology can be regarded as hierarchical, Allen & Starr (1982) have suggested that it should be studied at all levels. However, much of it is directed at one level, the community (but see Lubchenco & Gaines, 1981).

The reductionist approach assumes that communities can be considered simply as the sum of their parts, plus their interactions (Harper, 1982). With workers identifying 'emergent properties' in some communities this assumption is apparently violated (Richmond et al., 1975; Salt, 1979). The existence of emergent properties is not in contention, but there is disagreement over their significance. Edson et al., (1981) consider emergent properties to be embroiled in semantics and "irrelevant" to ecology, and Schoener (1986) believes that these properties do not "rule out reducibility". The most convincing demonstration of the power of the reductionist approach stems not from rhetoric, in my opinion, but from the examples that Schoener (1986) cites.

To demonstrate the complexity and subtlety of interactions which may be overlooked if levels below that of the community are not studied, consider the following examples. Dayton (1971) documented a deleterious effect of limpets on barnacles. He found that limpets in the course of their foraging crushed, dislodged ("bulldozed"), and accidently consumed barnacles. More recent work has demonstrated that under certain circumstances limpet grazing may enhance barnacle survival. In a series of experiments using a range of limpet densities, Underwood et al. (1983) were able to show that on occasions limpets did have a detrimental effect on barnacle numbers. They found also that limpets could enhance barnacle survival by grazing away algae that otherwise was capable of smothering the barnacles. The outcome of this limpet - barnacle - algal interaction was predictable. It was dependent upon a complex interaction between the rates of settlement and growth of the two spatial competitors and the density of limpets. Futhermore, these interactions were mediated by prevailing environmental conditions.

In the absence of investigations directed at the appropriate level, utilizing carefully designed and interpreted experiments, such complexity would pass unnoticed. I am not advocating an investigation of complexity inherent in systems merely for complexity's sake. Biologists often do not require a precise (quantitative) answer: a qualitative result may be adequate to disprove a null hypothesis. From the example above it is clear, however, that there is a danger of generalizations appearing in the literature without adequate consideration of alternative hypotheses (also see Underwood & Denley, 1984).

The development of models in ecology, be they mathematical, graphical, or verbal, must continually compromise between precision, realism and generality. One must be sacrificed if the other two are to be maximized (Levins, 1966). Studies of epifaunal communities in South Australia provide a good example of the trade-off between precision, realism and generality. Ecologists studying this community have sacrificed precision in an attempt to attain realism and generality. These communities are diverse. As a direct result of this diversity, and the poorly known taxonomic status of some groups (e.g. sponges), workers have grouped organisms into broad taxonomic categories (e.g. sponges, bryozoans, colonial ascidians, etc.) (Kay & Keough, 1981; Kay & Butler, 1983; Keough, 1983, 1984a, 1984b; Butler, 1986). These categories represent a convenient means of handling this diverse fauna and reflect real biological subdivisions, as they identify different body plans and growth forms. However, they suffer from the shortcoming of masking many of the interactions and much of the complexity inherent in the system. Nevertheless, these studies have served to identify, as these workers intended, the broad scale patterns, and to a lesser degree the processes operating, at the community level. To understand more fully the processes responsible for producing these patterns it is necessary to adopt the approach that Andrewartha & Birch (1954), Harper

(1982) and Schoener (1986) advocate. That is, to investigate the life cycle and dynamics of the component species.

An examination of interactions among component species in the cryptic communities beneath foliaceous reef-building corals resulted in a model proposing that species diversity was maintained in these communities by a network of interactions (Jackson & Buss, 1975) rather than a simple competitive relationship in which species A beats species B, which in turn beats species C, as had been documented for other marine communities (Paine, 1966, 1974; Dayton, 1971; Connell, 1975, 1978). The outcome of interactions among species in temperate epifaunal communities was dependent on the taxonomic level considered. Competitive interactions among closely related nonconspecific colonies of taxa had an unpredictable outcome resulting from stand-offs between neighbouring species (Kay & Keough, 1981; Russ, 1982; Keough, 1984a). At a higher taxonomic level the outcome of interactions was much less variable; "colonial tunicates overgrow most other species, sponges overgrow bryozoans and serpulids, encrusting bryozoans overgrow serpulids, and serpulids are overgrown by all other common sessile taxa" (Keough, 1984a, p.685)

With few exceptions studies of benthic interactions have been concerned with adult organisms. It is clear, however, that interactions among larvae and recently settled recruits, and interactions between these early life history stages and adult organisms, may be complex and important determinants of the subsequent distribution and abundance of adults (Grosberg, 1981; Young & Chia, 1981, 1984; Woodin, 1985; Davis, in press).

In this study I set out to investigate the population dynamics of one component of the South Australian epifaunal community, an ascidian exhibiting modular growth. Particular attention was focussed on the interactions of larvae and recently settled recruits with adult organisms.

Modular growth entails the iteration of building blocks, analogous to individuals of solitary organisms (Jackson, 1977). This growth form provides these clonal organisms with ecological and evolutionary opportunities that are not available to aclonal (solitary) animals, including: indeterminant growth, the ability to invade patches rapidly by reproducing asexually, and an ability to regrow following large scale colony damage. Clonal growth also presents problems for study of the population dynamics of these animals (Harper, 1977). No relationship exists between size and age, owing to partial mortality, fission and fusion . Hence age-related demographic traits, commonly used to characterise the demography of aclonal species, are not applicable.

This study focusses on the colonial ascidian <u>Podoclavella moluccensis</u> Sluiter*, hereafter referred to as <u>Podoclavella</u>. This ascidian is a member of the family Clavelinidae (Order: Aplousobranchia) and is widely distributed in Australia, ranging from Rottnest Island, Western Australia to the Great Barrier Reef, Queensland (Kott, 1972). In St Vincent's Gulf and Investigator Strait, South Australia, <u>Podoclavella</u> is a common and conspicuous member of the epifaunal community. Colonies are sessile and attach to rocky reefs and artificial substrata, such as jetty pilings, and often grow epizooically

---

* Voucher specimens lodged at the Department of Zoology, University of Adelaide bear the code (T5); duplicates are also in the South Australian Museum, Adelaide. Until recently this species had been misidentified as <u>Podoclavella cylindrica</u> (Quoy & Gaimard) - Kott, pers. comm.

on other invertebrate species. These colonies are pigmented pale blue and the repeated units, or zooids, arise from a spreading stolon.

The life history of ascidians is straightforward. They are typically hermaphrodites and in most colonial species the ova are fertilized in the peribranchial cavity and are retained, or brooded, by the maternal colony (Berrill, 1931). Larvae are tadpole-like (they are often referred to as ascidian tadpole larvae), freeswimming, and non-feeding (lecithotrophic). After release larvae usually spend a few hours, or less, swimming and then settle (Berrill, 1975). Metamorphosis soon follows and involves considerable reorganization, including resorption of the larval tail. This process marks the transition between a larval planktonic existence and the sessile filter-feeding mode of life characteristic of the adult. The colony grows by the budding of zooids from the newly metamorphosed larva and the cycle is complete upon the zooids reaching reproductive status .

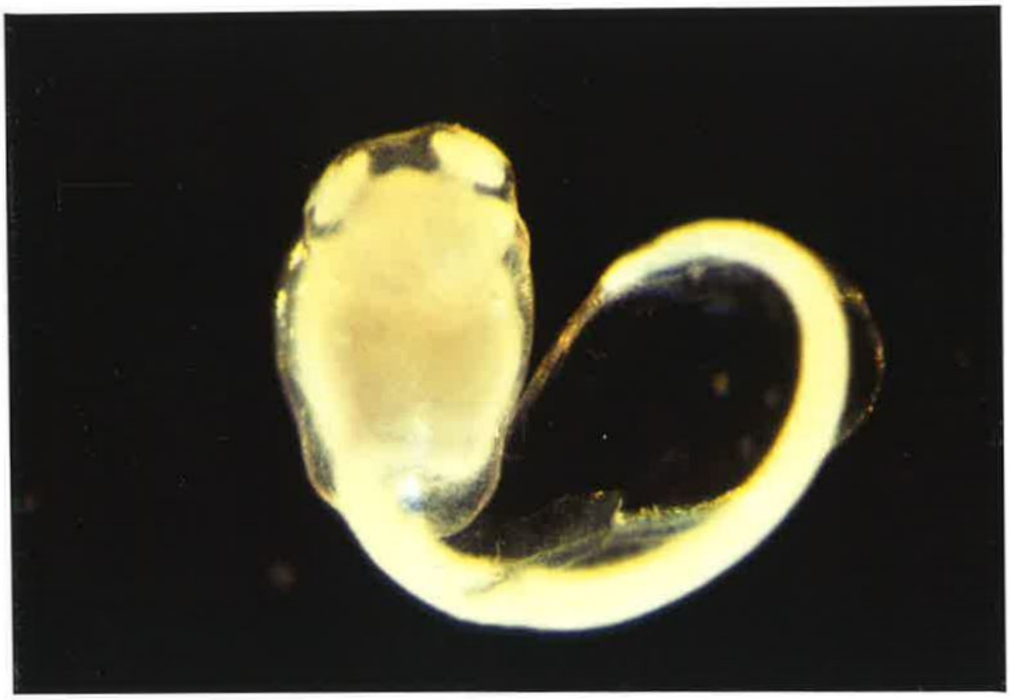
Podoclavella was selected for study for two reasons: First, adult colonies were conspicuous and counts of the large zooids (upto 45mm high) provided a convenient estimate of colony size. Second, and more importantly, this species possesses large larvae (Kott, 1972), facilitating a direct examination of factors influencing the settlement of larvae and their subsequent survival.

Larvae were first observed in the field in the spring of 1983. They were over three times larger than Kott had recorded, measuring 4mm in length. Their size and blue pigmentation rendered them easily visible underwater and allowed observations of larval movements and settlement behaviour (Plate 1).

In this thesis I examine the spatial and temporal patterns of distribution and abundance of adult Podoclavella. Particular emphasis is placed on the role played by pelagic and early benthic stages of the life history in producing these patterns. Chapter 2 examines the spatial and temporal patterns of distribution and abundance. In the remaining chapters I consider the effect of settlement and early post-settlement mortality on these patterns of distribution and abundance. Specifically: Chapter 3 examines larval dispersal and mortality, Chapter 4 the role of settlement and post-settlement mortality in determining patterns of recruitment and Chapter 5 addresses the influence of predators on early post-settlement mortality. In the final chapter, the general discussion, I couple the patterns observed in Chapter 2 with the processes examined in the other chapters.

Logistically, it was not feasible to undertake an intensive study of larvae at more than one site. A site with reliable diving conditions was selected for this task. To facilitate comparisons between sites the confidence with which settlement may be inferred from levels of recruitment was assessed also in Chapter 4.

Plate 1. Larva of Podoclavella moluccensis. This specimen was preserved and the blue pigmentation is not apparent. The trunk is 1mm in length and the tail 3mm. Note the large adhesive papillae at the anterior of the larva.



CHAPTER TWO

Spatial and Temporal Patterns of Distribution and Abundance

2.1 INTRODUCTION

Ascidians are widely distributed geographically and often remarkably abundant, even numerically dominant, in some communities (Millar, 1971). As this group is largely restricted to the sublittoral, observations of ascidian population dynamics stem from, and are usually incidental to, investigations of epifaunal community development and stability (Osman, 1977; Sutherland & Karlson, 1977; Sutherland, 1981; Russ, 1980; Kay & Butler, 1983; But see Svane, 1983, 1984; Svane & Lundalv, 1981, 1982a, 1982b).

Although many of these studies have recorded population densities of ascidians and the magnitude of change in density over time, few have identified the factors producing these changes. Most workers have introduced biases into their investigations by examining small areas of substratum, submerged for only short periods of time (usually less than four years).

The size and age of substrata have an important influence on the species that settle on them and, in turn, the community that develops there. Small substrata submerged for short periods will tend to be dominated by short lived species heavily reliant on larval recruitment. They are therefore unlikely to be representative of epifaunal communities and their component species (Kay & Keough, 1981; Keough, 1984a).

A second bias stems from the suspension of these experimental surfaces above the seabed, thereby excluding crawling invertebrates. Many of these invertebrates, including crabs, grazing gastropods and urchins, remove or kill epifaunal organisms (Ayling, 1981; Sebens, 1983b, 1985; Young & Chia, 1984).

Unfortunately some of the studies on large substrata, submerged for long periods of time, may also suffer from a lack of generality. In their long term, photogrammetric study of ascidian populations on the Swedish west coast, Svane (1983, 1984) and Svane & Lundalv (1981, 1982a, 1982b) considered one patch of rock wall only at each of their sites - there was no replication. Despite the large area of this patch ($1.5m^2$), relative to many of the studies listed above, it is nevertheless unwise to use one replicate as a basis for comparison (Hurlbert, 1984).

The problems associated with sampling ascidian populations are further complicated by the body plan of some ascidian species. Ascidians fall into two broad groupings; 1) Solitary animals and 2) Colonial animals made up of repeated, physiologically connected, units. These units (zooids) are analogous to individual solitary organisms and impose a modular construction on these ascidians. Zooids, or more commonly groups of zooids, are often capable of operating independently of the parent colony, even after separation from it. These physiologically independent sub-units of colonies, referred to as ramets by plant ecologists (Harper, 1977), result from the settlement and subsequent budding of one larva: collectively they represent one genotype, a genet. Colonies may be split and separated by fission, but they may also be joined by fusion. Compatible ramets, usually derived from a single genet, may coalesce or fuse (Hughes & Jackson, 1980; Heyward & Stoddart, 1985).

Assessment of population size will be hampered if colony fission and fusion occurs regularly and rapidly (Bak <u>et al.</u>, 1981). These processes also decouple the relationship between colony size and age. As a direct result, concepts of demography derived from solitary animals, such as age at first reproduction, are not applicable (Hughes and Jackson, 1985).

Clearly, the study of population dynamics in colonial organisms will be confused if the products of colony fission and fusion cannot be distinguished from those of larval settlement and colony mortality. The degree of confusion will depend on the organisms studied and the intensity of sampling. In colonial organisms possessing a mineralized skeleton, such as corals, traces of their fission and fusion remain and annual sampling may be sufficient to distinguish these patterns (Hughes & Jackson, 1985). In constrast, soft bodied organisms require more regular sampling if these patterns are not to be confused (Bak et al., 1981). In extreme cases, such as that observed by Ryland et al. (1984), observations every few hours may be necessary.

In this thesis I follow Jackson's (1985) definitions and consider colonies that are physically separate, and therefore countable, to be individuals, irrespective of whether they represent ramets or genets. This represents an oversimplification and will be further discussed later in this chapter. Reproduction will be considered a means by which the number of individual colonies is increased. Reproduction may be sexual, through the production of larvae and their subsequent settlement or, alternately, it may be asexual by the fission of a colony into separate entities.

The aim of this chapter was to investigate patterns of spatial and temporal distribution and abundance of one species, Podoclavella moluccensis (Clavelinidae), within St Vincent's Gulf. Initially the number and size of colonies were examined at two spatial scales; first at a broad scale (between sites) and second at a finer scale within sites. All sampling was replicated and restricted to large substrata, submerged for periods in excess of 20 years.

Owing to technical and financial constraints, population dynamics were investigated at only two sites. The intention was to determine the magnitude of change with time and then investigate the factors likely to produce these changes. These factors include: the production and recruitment of sexually produced propagules, fission, fusion and finally mortality. Here I describe patterns of distribution and abundance and then address the underlying processes producing them in the following chapters.

2.2 MATERIALS AND METHODS

Study sites

Patterns of distribution and abundance were investigated at ten sites within St Vincent's Gulf and Investigator Strait, South Australia (Fig 2.1). Four of these were rocky reefs and the remainder jetties. Many of these sites were sampled only once and do not warrant a detailed description. For brevity relevant details of each site and a subjective ranking of wave exposure are given in Table 2.1.

Sampling was intensive at two sites and they will be described in detail. Port Noarlunga Reef (35°09'S 138°29'E) is a consolidated pleistocene sand dune. This reef runs parallel to the coast, approximately 350m offshore, and is partially exposed on low tides. Access to the flat reef top was provided by a jetty. The inner (sheltered) side of the reef dropped almost vertically to sand at around 7m depth (MLLW), whereas the outer reef fell less abruptly to sand and was deeper (10m at MLLW). A dense forest of the laminarian, Ecklonia radiata (C. Ag.) J. Ag., and fucoid algae, Sargassum spp., cloaked sunlit rock surfaces, while the undersides of overhangs and vertical rock faces were dominated by a number of sponge and ascidian species. The solitary ascidian Pyura irregularis (Herdman) was particularly common.

Edithburgh Jetty (35° 5'S 137° 45'E) faces east and was sheltered from the prevailing south-westerly winds. Constructed last century, this 173m long structure is supported on pilings of one, or a combination of, Eucalyptus species: E. marginata (Jarrah), E. fibrosa (Red Ironbark) and E. paniculata (Grey Ironbark).

Edithburgh Jetty stands in approximately 6m of water (MLLW) and is flanked on three sides by seagrass meadows of *Posidonia australis* var. *angusta* Hook. Fauna common in the meadows and underneath the jetty include the razorfish, *Pinna bicolor* Gmelin and the solitary tunicates *Phallusia depressiuscula* (Heller) and *Polycarpa pedunculata* Heller.

The jetty pilings were dominated by sponges (over 19 species have been recorded - Kay and Butler, 1983) and a seasonally abundant colonial ascidian, *Botrylloides leachii* (Savigny). A number of bryozoan and ascidian species, in addition to the stony coral, *Culicia tenella* Dana, were also common.

Port Noarlunga Reef was exposed to the prevailing south-westerly winds and diving was always weather dependent. On the other hand, diving at Edithburgh jetty was seldom precluded by rough conditions. The wave exposure of each site had a profound influence on water clarity. Visibility at Port Noarlunga rarely exceeded 5m, whereas better visibility was common at Edithburgh.

Seawater temperatures varied between 23°C in summer (January and February) to around 10°C in winter (July and August)

Spatial patterns

The distribution and abundance of *Podoclavella* was assessed at two scales. The first was between reefs and jetties within St Vincent's Gulf and the second at a much finer scale, within a reef.

The apparency of animals (that is, the ease with which they may be distinguished from their environment) is an important consideration when sampling their patterns of distribution. Winter 'blooming' of colonial ascidians commonly occurs in South Australian epifaunal communities (Kay & Butler, 1983), thereby altering their apparency. *Podoclavella* bloomed in winter and was therefore most apparent in this season (A.M. Kay, pers. comm.). So, where possible, sampling was restricted to this time of year.

During this monitoring two variables were measured; colony density and colony size. Size of colonial organisms has been estimated in two ways. Colony area may be measured (e.g Hughes & Jackson, 1985) or the number of repeated units, within a colony, counted (e.g. Karlson, 1983). Measurements of colony area are advantageous as they are indicative of an organism's ability to obtain and hold space, a limiting resource in epifaunal communities. However, such measurements of area are often difficult to obtain and, unless the organism grows as a thin sheet, they may also be inaccurate. Counts of zooids more directly reflect the population dynamics of a modular organism, and counts of the zooids of Podoclavella proved to be the most convenient means of estimating colony size. To ensure that counts of zooids were a good predictor of colony size (dry weight) and the area of substratum occupied by a colony, the relationship between these three measurements was established.

i) Relationship between zooid number, colony size and attachment area.

To establish these relationships a sample of colonies (n=56), representing the size range available, was collected from Edithburgh Jetty in the winter of 1983. Zooids were removed from the stoloniferous basal 'mat' of a colony, with a razor blade, and placed in a plastic bag. The outline of this basal 'mat' was traced onto an acetate sheet with a chinagraph pencil, then the mat was prised from the piling and also placed in the plastic bag. All colonies were assigned numbers and kept in separate plastic bags.

In the laboratory colonies were removed from the bags, the zooids counted and dry weights determined after drying for 48 hours at 50°C. The attachment area of each colony was calculated by digitizing tracings of the area of the basal mat with a microcomputer. The regression of zooid number on the area of attachment and colony dryweight was then calculated. Owing to the present uncertainty surrounding the application of model II regression (Sokal & Rohlf, 1981 p.555), in this and other chapters model I regression analysis will be used.

ii) Comparison of density between sites

The density of Podoclavella was established by counts in quadrats positioned haphazardly. Quadrats were varied in size depending upon the nature of the substratum investigated. On most jetty pilings, quadrats measuring 2.5m^2 were used. The circumference of each piling was measured with a tape and the appropriate quadrat height, to give an area of 2.5m^2, was calculated. Hence, counts were performed on all sides of a piling. The base of each quadrat was positioned 0.5-2m above the seabed.

A smaller quadrat size was adopted on Edithburgh Jetty. Densities of Podoclavella at this site were so high that a quadrat of 0.17m^2 (30x56cm) was more appropriate. The bases of these quadrats were positioned about 1.5m above the seabed.

The area of quadrats positioned on rocky reefs was reduced to 1.25m^2. Quadrats were positioned on vertical faces devoid of large brown algae, which was, incidently, equivalent to the sampling procedure used underneath jetties.

iii) Comparison of density within sites

Variation in the distribution and abundance of Podoclavella within sites was investigated at Edithburgh Jetty and on two rocky reefs, Pinnacle Beach Reef on Yorke Peninsula and the Inner Reef at Port Noarlunga. At Edithburgh Jetty the density of adult Podoclavelia colonies on encrusting animals and naturally occurring bare space was estimated with 97 quadrats, each measuring 0.044m^2 (17.5x25cm). This quadrat size was small enough to be occupied by one substratum type (e.g. an ascidian colony) yet large enough to yield an adequate number of adult colonies. To simplify the analysis, colonies were not counted unless an estimated 95% of the quadrat was covered by one type of substratum. To facilitate the satisfaction of this criterion, the quadrat was rotated around one of its corners until the dominant substratum covered more than 95% of the quadrat. If this criterion was not met after rotating the quadrat through a maximum of 45°, then the quadrat was placed elsewhere. Following placement the number of adult colonies in the quadrat was counted and the type of substratum recorded.

Expected frequencies of colonies for a substratum were calculated by multiplying the mean number of colonies within all quadrats by the number of quadrats falling on that substratum. Observed and expected frequencies were then compared for goodness of fit.

On the rocky reefs colony density and size were determined in 1.25m^2 quadrats placed haphazardly on vertical and horizontal rock faces, in the presence and absence of brown macro-algae.

The abundance of Podoclavella on the undersides of overhangs and boulders was investigated at Port Noarlunga Reef also. Despite overhangs being a common feature of this dissected reef it was necessary to reduce quadrat size to 0.17m^2 to facilitate these measurements.

Podoclavella is restricted to hard substrata, but not exclusively jetty pilings or rocky reefs. In South Australia Podoclavella also attaches to the valves of the large bivalve, Pinna bicolor (Keough, 1984b). Pinna lives partially buried in sand from the intertidal zone to a depth of 30m (Butler & Brewster, 1979). The density of Podoclavella on Pinna shells was estimated along 5, 30m transects positioned approximately 50m north east of Edithburgh Jetty. A 30m line was fixed to a stake and payed out five times along random compass bearings. The number of Pinna shells, irrespective of whether the mollusc was alive or dead, and the density of Podoclavella they supported were counted in a 1m strip each side of the line. Thereby each transect surveyed 60m^2 of seabed.

Temporal patterns

Sampling intervals are the window through which population dynamics are viewed. Sampling intervals that are too long may miss important events, while shorter intervals may give a false impression of stasis in a population. Ideally a sampling programme should accord with the life history of the animal under investigation. However, if the generation time of the organism is long or the life history is poorly understood, this may prove very difficult. The ultimate constraint on sampling intensity in most projects is economy of time and money; this study was no exception. Monitoring was set at monthly intervals at Port Noarlunga and six weekly intervals at Edithburgh Jetty.

Temporal changes in abundance were monitored for over two years at two sites, Edithburgh Jetty and the Inner Reef at Port Noarlunga (Fig. 2.1). These sites were selected for their accessibility.

Photographs were taken and counts made in permanently marked quadrats measuring 0.17m^2 at each site. Quadrat size was determined by the area on a piling which could conveniently be photographed. Quadrats were delineated by a nail driven into the top left hand corner. Ramset concrete nails were used at the reef site and were fixed in place with a two part epoxy putty - Expocrete. Relocation of quadrats was facilitated by the attachment of a short strand of Nichrome wire to the nails. At Edithburgh Jetty a galvanized clout was driven through a small plastic or antifouling-coated steel plate to mark the quadrats. A strand of Nichrome wire was also attached.

Quadrats were photographed with a Nikonos III camera and electronic flash. The camera was mounted in a specially constructed frame to ensure that quadrats were accurately framed and to maintain a distance from subject to camera of 0.8m. Ektachrome 64 ASA or 100 ASA film was exposed at a shutter speed of 1/60 second at f5.6 or f8 respectively.

In addition to photographic sampling, changes in the size frequency distribution of colonies and survivorship were assessed at Edithburgh Jetty. At each sampling date, approximately every six weeks, the sizes of 200 colonies were measured. On each occasion the number of zooids was counted in 20 haphazardly selected colonies, on 10 pilings chosen randomly.

Estimates of survivorship were obtained at Edithburgh by monitoring 90 permanently marked colonies in 1983 and 10 colonies in 1984. Colonies were marked by nailing a numbered 'Dymo' tag next to a colony and attaching a short strand of Nichrome wire to aid in relocation. In 1985 survivorship of 22 colonies was obtained from photographs of permanent quadrats. The presence of colonies was assessed at roughly six weekly intervals in 1983 and 1984, and on three occasions during 1985.

Initially, sampling at Port Noarlunga was restricted to photographing permanent quadrats. Some data proved difficult to obtain from these photographs and quadrats were then visually assessed as well.

The availability of vacant space at each site was estimated from photographs of permanent quadrats. Slides were projected onto a grid of 464 evenly spaced dots. The number of dots on vacant space and on the colonial ascidian Botrylloides leachii were counted and converted to percentages of the total area. Vacant space was considered to be bare areas of piling at Edithburgh but at Port Noarlunga the removal of animals rarely produced bare rock; encrusting coralline algae usually covered the rock surface. At this site bare rock or encrusting coralline algae were considered vacant space.

iv) Reproductive status

Most colonial ascidian species are viviparous; eggs are retained and develop within the oviduct or peribranchial cavity. Larvae are subsequently released at an advanced stage of development (Berrill, 1975). To determine the number of larvae produced by Podoclavella at each site three parameters were examined; the frequency of sexual reproduction, the number of zooids brooding and the size of those broods.

To determine how often Podoclavella reproduced, the reproductive status of adult colonies was determined with destructive sampling at Edithburgh Jetty. Ten colonies were marked with numbered 'dymo' tags and Nichrome wire, as described earlier. At approximately 6 weekly intervals samples of 5 zooids were removed from each colony, preserved in formalin and examined in the laboratory. Some of these samples were sectioned at 7 microns, stained (Ehrlich's Haematoxylin and Eosin) and examined under a microscope at 20x to affirm visual assessment of reproductive status. The assessment of reproductive status at Port Noarlunga was restricted to non-destructive field observations.

The number of zooids brooding and the size of their broods were estimated by sampling at both sites in 1985 and 1986. The number of zooids possessing brood pouches was determined by counting the total number of zooids in 10-14 colonies on each sampling date and recording the presence or absence of a brood pouch on each zooid. Brood pouches were blue and were usually counted easily in the field without destruction of colonies (Plate 2). The presence of larvae within the pouch was not determined. The number of brood pouches in 36 colonies was counted at both sites in 1985. Counts were made on 12 colonies at each site in 1986. Although the sample sizes between years are unequal, they are proportional and are therefore orthogonal (Huitema, 1980 p.198).

Measurements of brood size per pouch required destructive sampling and were only made once at each site in each year. Zooids from brooding colonies were removed to the laboratory. The heights of these zooids were measured, they were dissected and the number of larvae per pouch counted. Between 5 and 10 zooids were removed from each colony.

Differences in the number of brood pouches per colony and brood sizes between sites and years were examined with a two factor ANCOVA. The factors, each with two levels, were site and year. Estimates of brood number are likely to be influenced by the size of the colonies while zooid height may influence the number of larvae per brood. Both of these variables were included in the analyses as covariates. Several assumptions are made by ANCOVA (Huitema, 1980). One of the most important of these is that the regression slopes for the groups are not significantly different. Equality of the regression slopes was examined with BMDP program 1V before proceeding with the two factor analyses. The presence of heterogeneity among the variances was examined with Cochran's test for homogeneity.

If the size of larvae does not vary significantly between sites then the number and size of broods equates to reproductive effort. In 1985 a sample of larvae collected at each site were dissected from brood pouches and their sizes (maximum trunk diameter) measured with a graticule at 20x.

Plate 2. A brood pouch (arrowed) within a zooid of *Podoclavella moluccensis* at Edithburgh Jetty. Bulges within the pouch are brooded larvae. The scale bar is 2.5mm in length.

2.3 RESULTS

Spatial patterns

i) Relationship between zooid number, colony biomass and the area of attachment

The number of zooids in a colony showed a significant relationship with colony biomass (dry weight)($t=21.4$ $df=54$ $P<.001$, $r^2=.89$, Fig 2.2) as did the area of substratum occupied by a colony ($t=12.5$, $df=51$, $P<.001$, $r^2=.75$, Fig 2.3). In both relationships the best fit of the data to the model, as judged by r^2 values, was obtained with the raw data. Only 53 colonies, of the 56 collected were used in the regression of zooid number on attachment area, as area measurements were not obtained for 3 colonies.

ii) Variation in abundance between sites

Densities of _Podoclavella_ spanned more than two orders of magnitude within St Vincent's Gulf (Table 2.2). Densities on jetties showed considerably more variation than those on rocky reefs, following adjustment of densities to a quadrat size of $2.5m^2$. _Podoclavella_ attained high densities on the jetties at Edithburgh ($\bar{x}=236$ per $2.5m^2$, $n=20$) and Stenhouse Bay ($\bar{x}=36$ per $2.5m^2$, $n=12$), yet was completely absent from Wool Bay Jetty. On rocky reefs densities were not observed to exceed 7 per $2.5m^2$. The rank of sites by density was not correlated with the rank of exposure ($N=-22$ $n=10$ $P>.05$, N is the numerator of Kendall's tau, tabulated values for this statistic are given by Sokal & Rohlf, 1969 p.537).

The size of colonies also varied considerably between sites within St Vincent's Gulf (Table 2.3). On average, colonies were almost

5 times larger at Port Giles Jetty than at either Stenhouse Bay Jetty or Pinnacle Beach Reef. Usually colonies were, on average, between 40 and 90 zooids in size, although one colony comprising 1000 zooids was observed at Port Giles Jetty. Colony size showed a significant rank correlation with wave exposure ($N=44$ $n=9$ $P<.05$, Wool Bay Jetty was omitted as Podoclavella was absent).

iii) Variation in abundance within sites

At Edithburgh Jetty colonies of Podoclavella were not randomly distributed on encrusting animals and bare space ($G=104.5$ $df=7$ $P<.001$, Fig. 2.4). Colonies were at higher densities than expected on the sponge species Dendrocia sp. (SP30), Tedania sp B (SP51) and the ascidian, Botrylloides leachii. Colonies were in lower numbers than expected on the sponges Dendrilla rosea Lendenfeld (SP1) and Mycale sp. (SP20) and vacant space. Podoclavella was not observed on the bryozoan Celleporaria sp., the cnidarian Culicia tenella, or the sponge Ulosa sp. (SP48) (Letters and numbers in parentheses are the codes of voucher specimens lodged at the University of Adelaide).

On rocky reefs Podoclavella was almost completely restricted to vertical surfaces devoid of fucoid and laminarian algae (Table 2.4). Podoclavella was not recorded in quadrats from horizontal surfaces (Table 2.4), but colonies were occasionally observed on these surfaces when large algae were not present. Although these patterns have only been quantified on two reefs, casual observations at other sites lend support to them.

Podoclavella was absent on the underside of overhangs at the Port Noarlunga Inner Reef. Quadrats were placed haphazardly on the horizontal (or near horizontal) undersides of overhangs close to the sand (roughly -6m, n=10) and near to the top of the reef (approximately

-2m, n=10). Again, observations on other reefs lend support to these findings.

On Pinna shells the density of Podoclavella was low, on average, with one colony on every 25 shells (mean per shell =.04 SE=.02 n=5, 60m^2 transects). With densities of Pinna, on average, of 0.5 per m^2 (SE=0.1) at this site, Podoclavella approached a density of about one colony per 50 square metres of seabed. It is noteworthy that this figure probably overestimates the density of Podoclavella within Gulf St Vincent as these estimates are close to a large source of larvae, Edithburgh Jetty.

Temporal Patterns

i)Sexual versus asexual reproduction

Reproduction was predominantly sexual at both sites. Fission occurred but was passive and did not appear to be a significant life history attribute. Colony fusion was not observed, even among ramets of a single genet.

Podoclavella is hermaphroditic and gonads became apparent within the gut loop of colonies in early to mid August. Histology revealed that by early September some colonies had functional gonads and were producing sperm and ova simultaneously. In late September and early October brood pouches developed at the base of the branchial basket. Blue in colour these pouches were very conspicuous particularly when distended with developing larvae. Larvae were released from late October through early December at both sites. Larvae were 4mm in length and possessed a blue pigment spot that rendered them highly conspicuous.

Colony fission occurred at both sites though at very different frequencies. It was rare at Edithburgh Jetty, with only 4.5% of the colonies observed (n=66) undergoing fission in 1983 and 7.6% (n=79) in 1984. At Port Noarlunga 39% of the colonies observed (n=33) produced daughter colonies. The number of daughter colonies produced in one fission event was also significantly larger at Port Noarlunga (Table 2.5).

Fission resulted from the fragmentation of colonies so daughter colonies were never separated from the parent colony by more than a few centimetres. In addition daughter colonies were usually small, rarely exceeding 10 zooids in size, and had a low probability of surviving for more than 3-4 months (Fig 2.5). It is instructive to examine the process by which colony fission occurs.

ii) The formation of daughter colonies

Fission was intimately linked with the degeneration of colonies. Colonies at each site went through a phase of colony degeneration, followed by rapid regeneration. In all but one case, at both sites, fission was preceded by colony degeneration (n=22). It appears that some stolons within the basal mat are damaged or 'atrophy' during the degeneration process, resulting in the production of one or more daughter colonies.

Degeneration was characterized by siphon closure and the shrinkage of a zooid within its test. Ultimately this shrinkage produced a small whitish 'blob', measuring only 2-3mm in height, on the blue stoloniferous basal mat. A flaccid piece of test remained after shrinkage of the zooid. This was usually dislodged by wave action, and the 'white blob' regenerated into a functional zooid. The whole process usually took less than one month to complete.

Sometimes zooid degeneration within a colony was synchronous, with all zooids degenerating at once. On other occasions only a proportion of the colony would degenerate leaving some functional zooids. The degeneration of these functional zooids occurred a short time later.

Colony degeneration occurred at different rates at the two sites, hence the rate of daughter colony formation also differed. At Edithburgh Jetty degeneration occurred during the winter months of May and June and later, following the appearance of recruits in October and November (Fig. 2.6). So, at this site, the majority of colonies degenerated twice, although occasionally colonies degenerated twice during the winter months and then once again during the late spring (Fig. 2.7). Degeneration in November and December was rarely followed by regeneration; it often resulted in colony fission and was almost invariably followed by the death of colonies.

Degeneration was not periodic at Port Noarlunga, occurring year round and with a higher frequency than seen at Edithburgh (Fig. 2.6). Colonies at this site degenerated and subsequently regenerated between 3 and 9 times over two years of monitoring (Fig. 2.7). Records of degenerate colonies are likely to be underestimates owing to the frequency of monitoring. Daughter colonies were produced throughout the year with a larger number of daughter colonies produced, on average, per fission event than at Edithburgh (Table 2.5). Degeneration on this reef seldom culminated in colony death.

iii) Population dynamics

Marked temporal changes in colony abundance and size frequency were apparent at one site and not the other. The patterns observed at each site will be described in turn.

Edithburgh: The Edithburgh population was maintained at a higher density than that at Port Noarlunga, but showed marked fluctuations with time (Fig. 2.8). Heavy recruitment accounts for the increase in density observed in late spring (November and December) of 1984 and 1985. This pulse of recruits was also observed in the spring of 1983 but was not quantified.

Recruitment was followed by a steady decline in numbers through the year, the last colonies dying in December, or January and February of the following year (Fig. 2.9). The mortality of mature colonies and the influx of large numbers of recruits markedly reduced mean colony size in late spring and early summer. Growth produced a shift toward larger colonies in the following months (Fig. 2.10a).

Port Noarlunga Reef: Very different patterns were apparent in the Port Noarlunga population. Colony density was much lower and remained far more stable than the Edithburgh population, in the two years of monitoring (Fig. 2.8).

Much of the variation in colony density observed in this population is non-significant and can be attributed to changes in the number of quadrats monitored rather than real changes in number. When sampling was initiated only a low number of quadrats were monitored, with considerable variation apparent in the density estimates obtained (Fig. 2.8). This was rectified in March 1984 with the marking and photographing of 17 quadrats. By May 1985 it was apparent that results from only a subsample of these quadrats could be reliably interpreted from the photographs. The quadrats most difficult to interpret were those containing the most colonies. So, beginning in July 1985, visual censuses of all quadrats were made in addition to photographic monitoring. This allowed the inclusion into the data set of quadrats that previously had been difficult to monitor photographically, thereby raising the estimated densities.

Pulses of recruitment occurred at Port Noarlunga in all years, but the resolution of my photographic monitoring rendered estimates unreliable. Visual censusing of all quadrats produced reliable estimates of recruitment in the spring of 1985. Although these pulses were synchronized with those seen at Edithburgh, they were of much lower magnitude. In addition, most recruits soon died.

The lower rates of recruitment at Port Noarlunga, and the frequent production of small daughter colonies, produced a colony size frequency distribution that was very different from that seen at Edithburgh. Colony sizes were relatively small year round, rather than during just the settlement season (Fig. 2.10b).

Some colonies at Port Noarlunga fragmented into daughter colonies while others were not observed to undergo fission. As most daughter colonies were small and ephemeral, and as genets could readily be identified at this site, I considered genet rather than colony mortality. Genets were long-lived at Port Noarlunga. In more than two years only 6 of the 21 permanently marked colonies (28.5%) disappeared, despite a severe storm that did considerable damage to Port Noarlunga Jetty in March 1983 (Fig. 2.9). Although cause of death could not be ascertained for most of the genets that disappeared, one genet was lost following removal of a solitary ascidian (Herdmania momus), upon which it had been growing. Casual observations at this site indicate that the longevity of some Podoclavella genets is greater than four years.

iv) Comparison of the number of larvae produced at each site

Colonies at both sites reproduced sexually during the spring, November through to early December. Significant differences were observed in the number of brood pouches per colony and the number of larvae in each brood pouch at the two sites. No significant differences in the size of larvae were detected.

Brood pouches per colony: The number of zooids with brood pouches in each colony was divided by the total number of zooids, yielding the proportion of each colony brooding. A plot of these proportions revealed that on average more than half of each colony at Edithburgh was brooding in 1985 and 1986 (Fig. 2.11). In contrast the mean proportion brooding at Port Noarlunga in 1985 was less than 0.1. In 1986, however, this figure rose to almost 0.4, and considerable variability was apparent in the proportion brooding. Indeed, one colony at Port Noarlunga in 1986 had the highest proportion of brood pouches observed; 0.96 of the zooids in that colony possessed brood pouches.

The proportion of each colony with brood pouches was analysed with a two factor ANCOVA. Proportions were often smaller than 0.3 and larger than 0.7, so they were arcsine transformed prior to analysis. Zero proportions were replaced with the term 1/4n as recommended by Snedecor & Cochran (1980, p.290). A test for the equality of regression slopes revealed no significant differences between groups ($F=0.29$ $df=3.88$ $P > .5$). The ANCOVA revealed significant differences between sites and years, and the covariate, colony size, was also highly significant. The interaction of site and year was not significant (Table 2.6). An examination of the marginal adjusted means (as there are only two levels for each factor of the ANCOVA, a multiple comparison test is not required, Huitema, 1980) revealed that a significantly higher proportion of colonies were brooding at Edithburgh. In addition, a significantly higher proportion of colonies were brooding in 1986 than in 1985.

Number of larvae in each pouch: The brooding of larvae was dependent upon zooid height. Zooids of less than 15mm in height were rarely observed to brood larvae (Fig. 2.12). The ANCOVA of number of larvae in each brood pouch showed the same pattern as was observed in the number of brood pouches per colony. The assumption of equality of slopes was not violated (F=2.1 df=3,168 $P > .05$). After a log transformation to homogenize the variances, the two factor ANCOVA revealed differences between sites and years, while the interaction term was non-significant. The covariate, zooid height, was also significant. The marginal adjusted means indicated that colonies at Edithburgh had larger broods and that broods in 1986 were larger than those in 1985.

Comparison of larval size: Measurements of the diameter of larvae in brood pouches were not significantly different between sites in 1985 (t= 1.34 df=118, $P >.05$). On average, brooded larvae at Edithburgh measured 0.90mm (SE=0.03), while at Port Noarlunga the average size was 0.86m (SE=0.01).

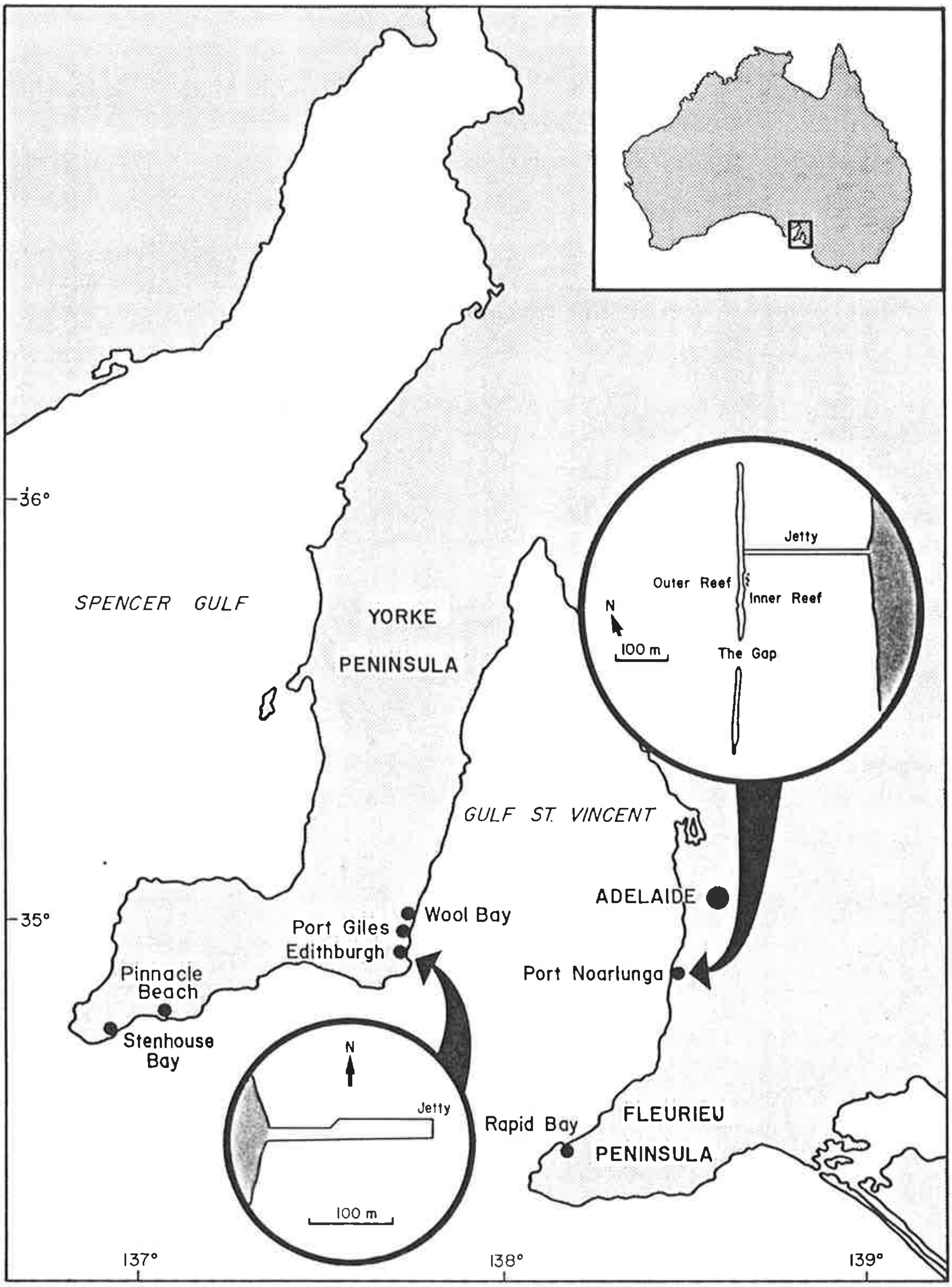
v) The availability of vacant space

Changes in the availability of vacant space at Edithburgh, expressed as a percentage of the total area, showed consistent differences over time which were inversely related to the cover of Botrylloides leachii. The mean cover of vacant space was higher during the summer months than in winter (Fig. 2.13). Variation around the mean was also noticeably higher in summer. Botrylloides is an annual ascidian which exhibits indeterminate growth. This species covers large areas of pilings in winter and early spring, then reproduces and dies. On dying it sloughs from pilings and often removes organisms which were overgrown during the winter, thereby freeing patches of vacant space. Hence increases in the availability of vacant space during the summer months largely result from the life history of Botrylloides.

At the Inner Reef at Port Noarlunga the availability of vacant space was very low and changes during the year were small. Botrylloides was not as common at this site, colonies did not assume the same dimensions and nor was much space freed when they sloughed off in the late spring and early summer months.

These data were plotted but not analysed because the high variance observed between samples was likely to violate the assumption of homogeneity of variances, even after transformation of the data. Moreover, a small increase in the availability of vacant space may be biologically significant to the *Podoclavella* population but not statistically significant.

Figure 2.1 South Australian Gulf waters with study sites labelled. Upper circular inset depicts Port Noarlunga Jetty and reef while the lower circular inset shows Edithburgh Jetty.



Jetty
Outer Reef
Inner Reef
N
100 m
The Gap
SPENCER GULF
YORKE
PENINSULA
36°
GULF ST. VINCENT
ADELAIDE
Wool Bay
Port Giles
Edithburgh
35°
Pinnacle
Beach
Stenhouse
Bay
Port Noarlunga
N
Jetty
100 m
Rapid Bay
FLEURIEU
PENINSULA
137°
138°
139°

Figure 2.2 Relationship between zooid number and colony size (dry weight - g). Dotted lines are 95% confidence intervals around the regression line.

Zooid number = 24.15 + (69.5 x colony dry weight)

$r^2 = 0.89$

$t = 21.4$

$P < .001$

$df = 54$

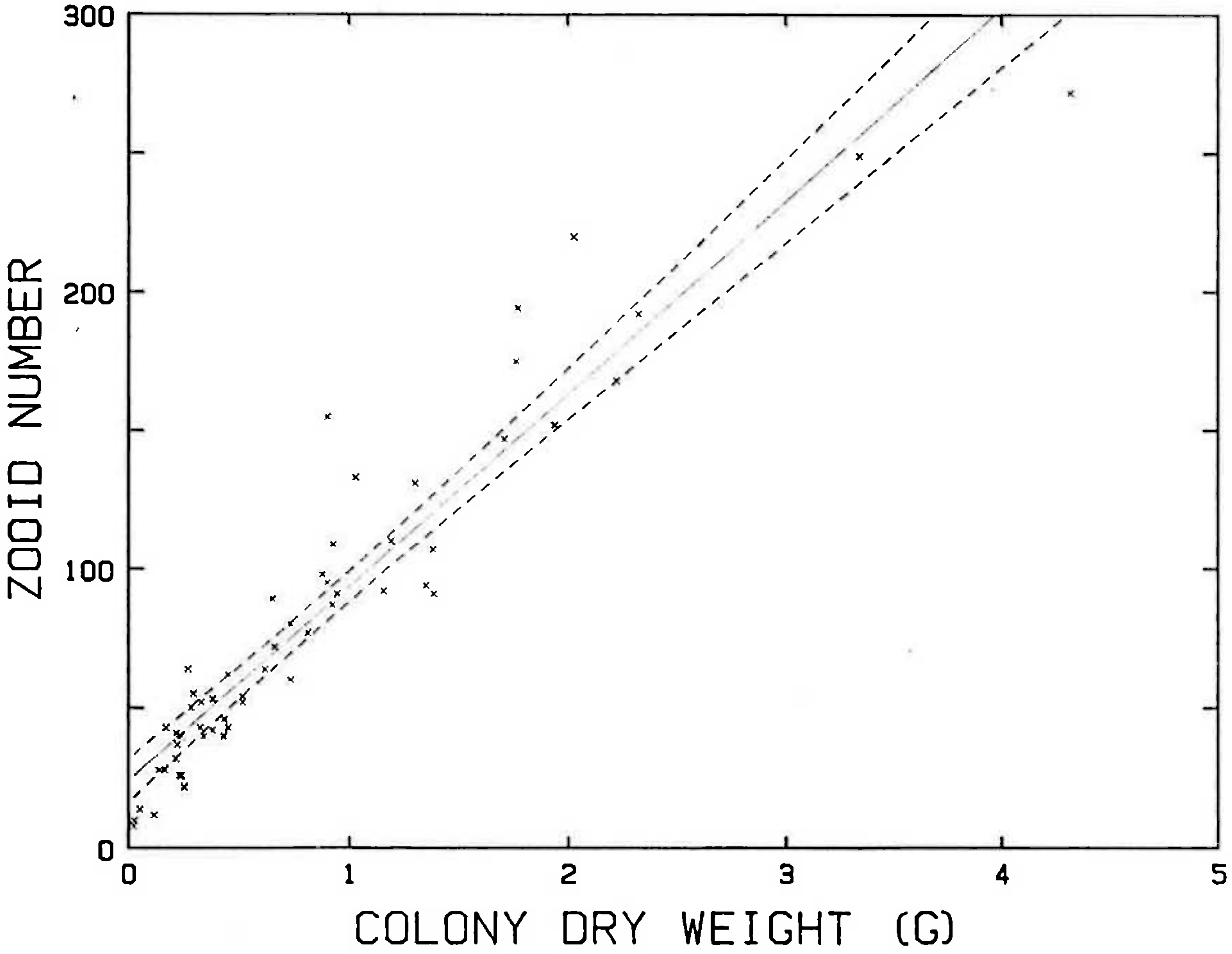

300
200
100
0
ZOOID NUMBER
0
1
2
3
4
5
COLONY DRY WEIGHT (G)

Figure 2.3 Relationship between zooid number and the area of colony attachment (mm^2). Dotted lines are 95% confidence intervals around the regression line.

Zooid number = 1.25 + (0.11 x area of attachment)

$r^2 = 0.75$

$t = 12.5$

$P < .001$

$df = 51$

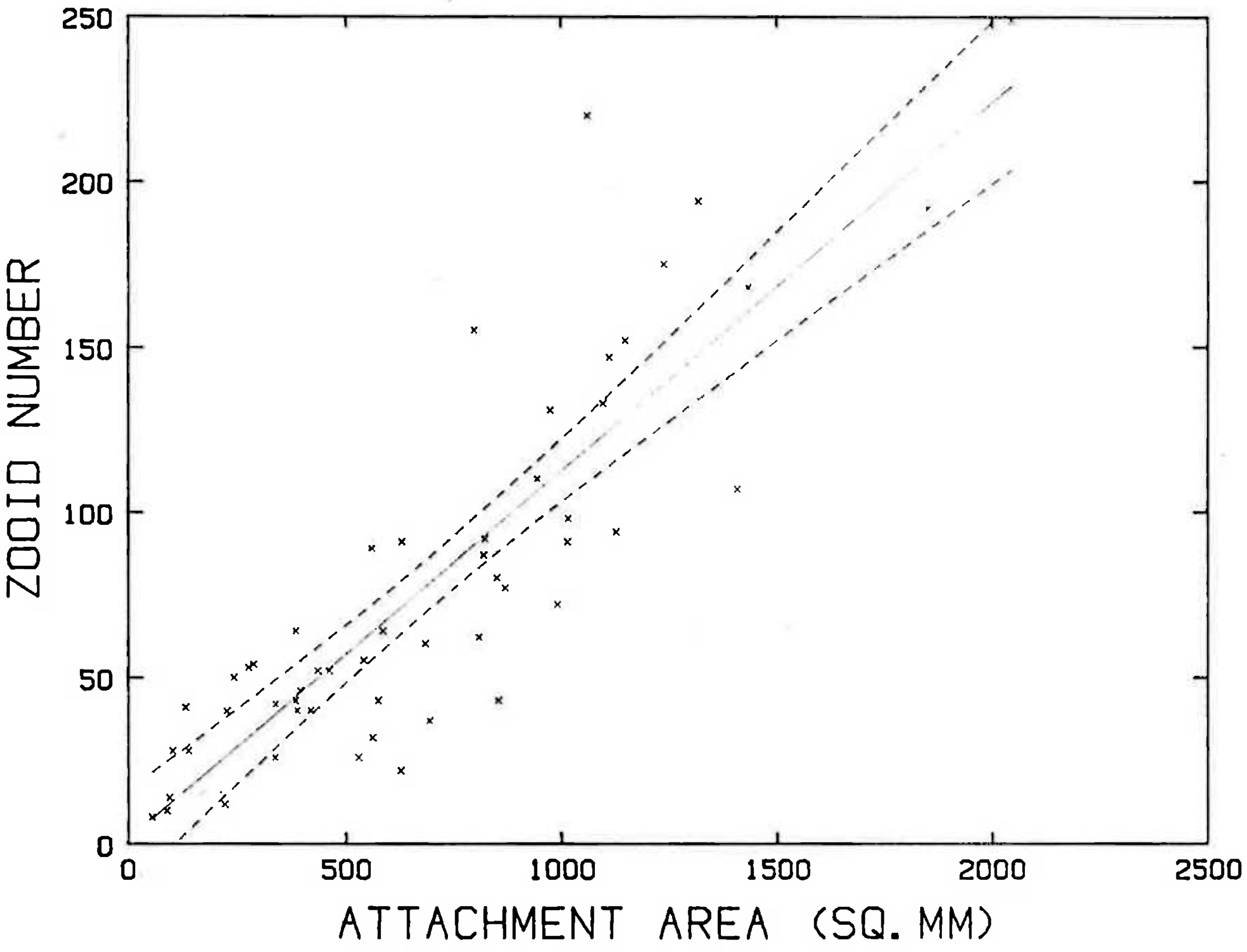

ZOOID NUMBER
ATTACHMENT AREA (SQ. MM)
0
50
100
150
200
250
0
500
1000
1500
2000
2500

Figure 2.4 Observed and expected frequencies of adult Podoclavella colonies on encrusting substrata and vacant space at Edithburgh Jetty. Counts were made with 97 quadrats each measuring 17.5x25cm.

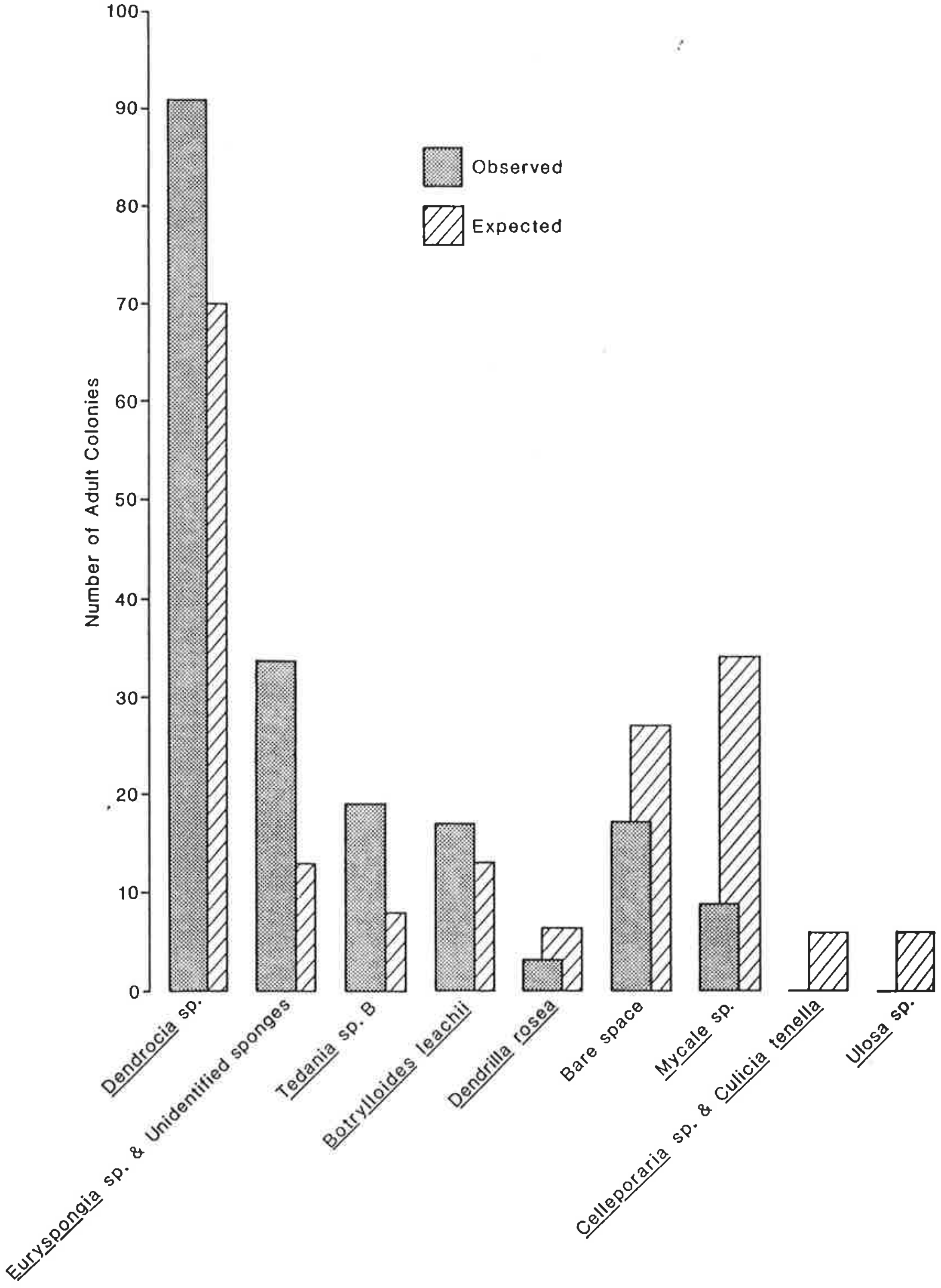

Number of Adult Colonies
100
90
80
70
60
50
40
30
20
10
0
Observed
Expected
Dendrocia sp.
Euryspongia sp. & Unidentified sponges
Tedania sp. B
Botrylloides leachii
Dendrilla rosea
Bare space
Mycale sp.
Celleporaria sp. & Culicia tenella
Ulosa sp.

Figure 2.5 Size frequency of daughter colonies, when first formed, at Port Noarlunga. Unshaded bars represent daughter colonies that disappeared within four months. Shaded bars represent daughter colonies that survived for at least this time (n = 33).

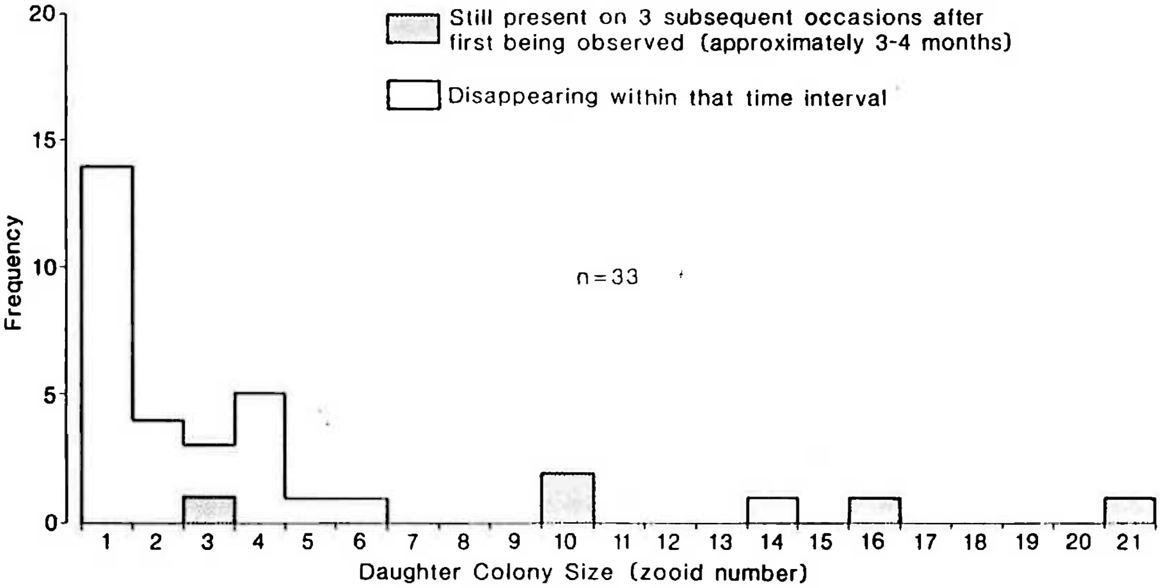

Still present on 3 subsequent occasions after first being observed (approximately 3-4 months)
Disappearing within that time interval
n=33
Frequency
0
5
10
15
20
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
Daughter Colony Size (zooid number)

Figure 2.6 Percentage of population that were degenerate at each site over time. The number of colonies on which each estimate was based are given on the graph.

○———○ Edithburgh

●-------● Port Noarlunga

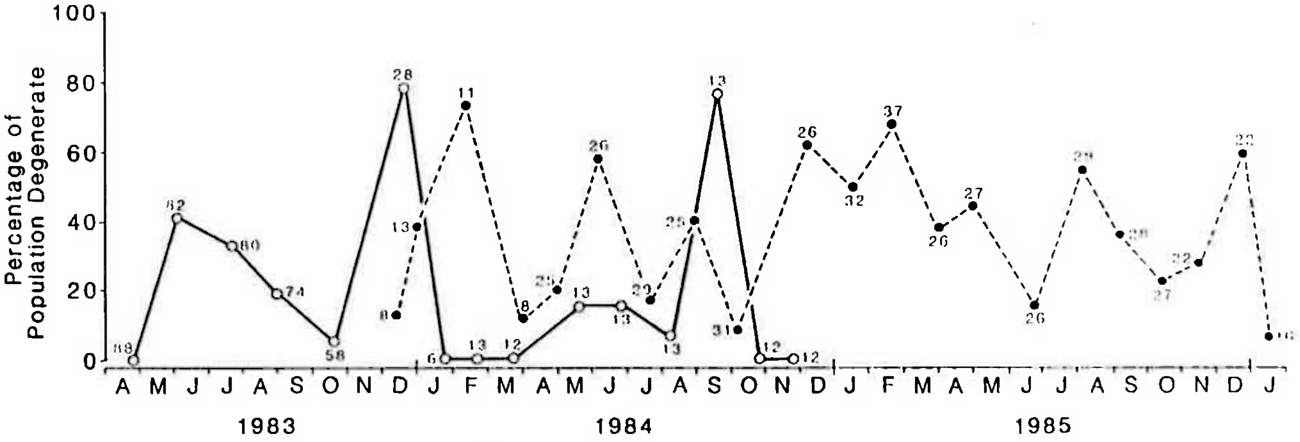

Percentage of Population Degenerate
100
80
60
40
20
0
88
82
80
74
58
28
8
13
6
11
13
12
8
25
13
26
13
29
13
25
13
31
12
12
26
32
37
26
27
26
29
28
27
22
22
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1983
1984
1985

Figure 2.7 Frequency distribution of the number of times colonies were observed to degenerate at each site. Frequency is represented as the percentage of the population undergoing degeneration. Frequencies are based on 76 observations at Edithburgh Jetty and 23 at Port Noarlunga. Colonies not followed for at least four months have been omitted.

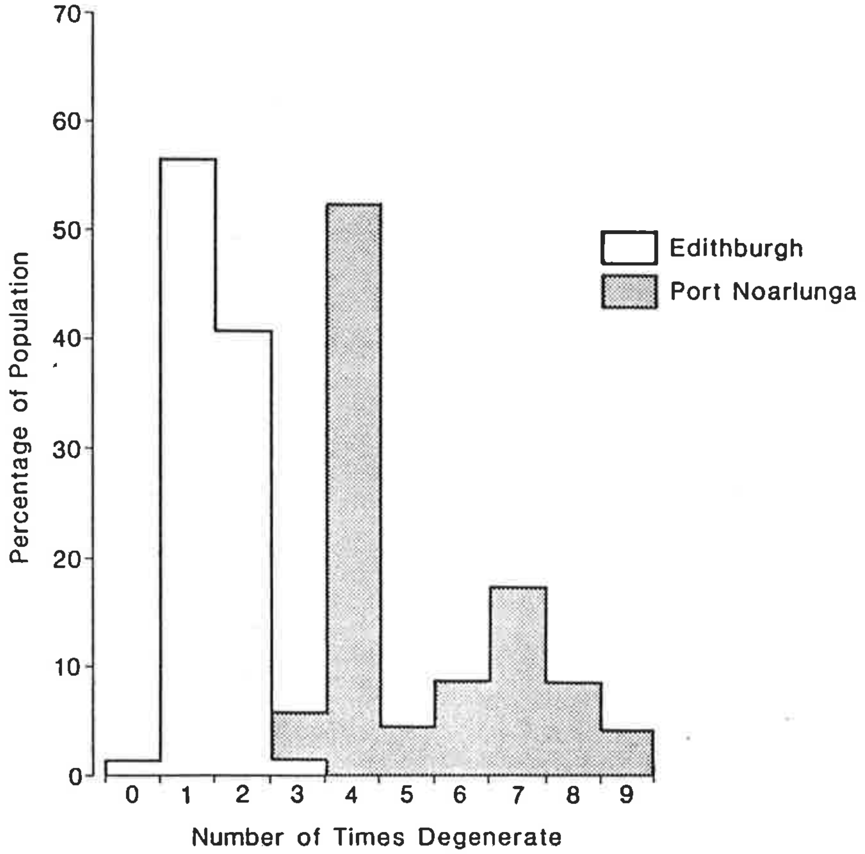

70
60
50
40
30
20
10
0
Percentage of Population
0
1
2
3
4
5
6
7
8
9
Number of Times Degenerate
Edithburgh
Port Noarlunga

Figure 2.8 Changes in density of Podoclavella with time at Edithburgh Jetty and the Inner Reef at Port Noarlunga. Means are number of colonies per $0.17m^2$, irrespective of whether they represent ramets or genets. Error bars are 95% confidence intervals. At each site the density of each new cohort is represented on a separate line. Note that recruitment was not quantified, although it did occur, at Edithburgh in November 1983, and Port Noarlunga in November, 1984. Also note the different scale on the Y axis.

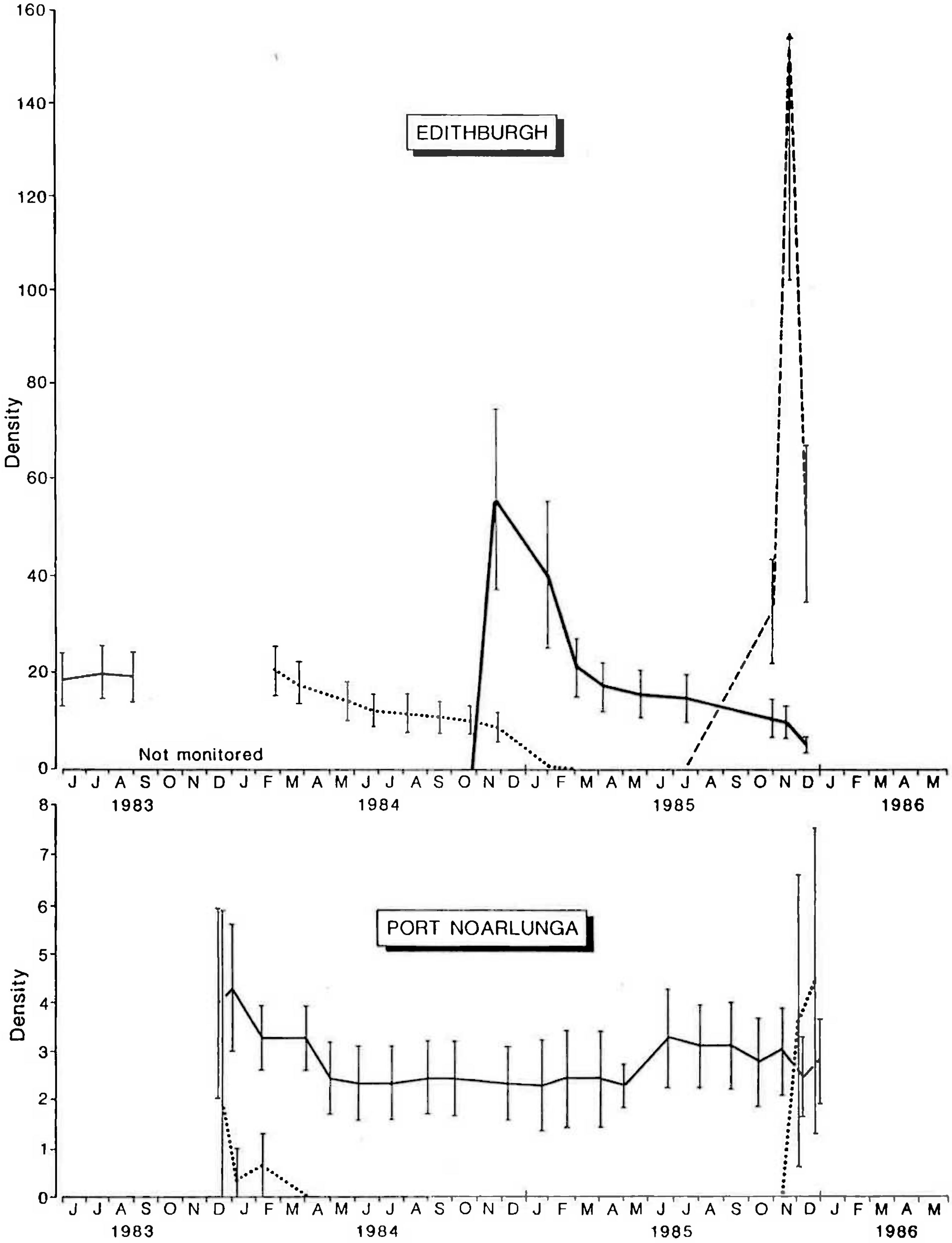

EDITHBURGH
Density
160
140
120
100
80
60
40
20
0
Not monitored
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1983
1984
1985
1986
PORT NOARLUNGA
Density
8
7
6
5
4
3
2
1
0
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1983
1984
1985
1986

Figure 2.9 Cumulative percentage mortality of colonies at each site. Only mortality of 'marked' colonies is considered, hence mortality of recruits has been omitted.

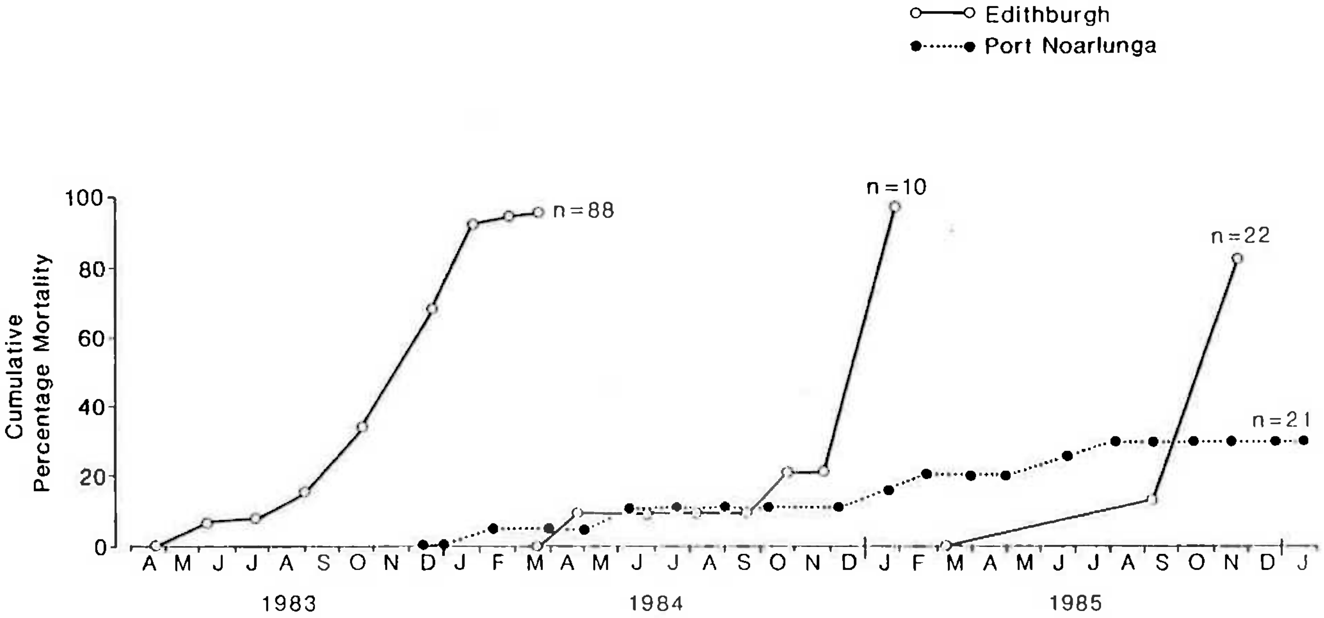

Edithburgh
Port Noarlunga
Cumulative Percentage Mortality
100
80
60
40
20
0
n=88
n=10
n=22
n=21
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J
1983
1984
1985

Figure 2.10a Size frequency distribution of colonies (zooid number) at Edithburgh Jetty. Arrows represent mean size.

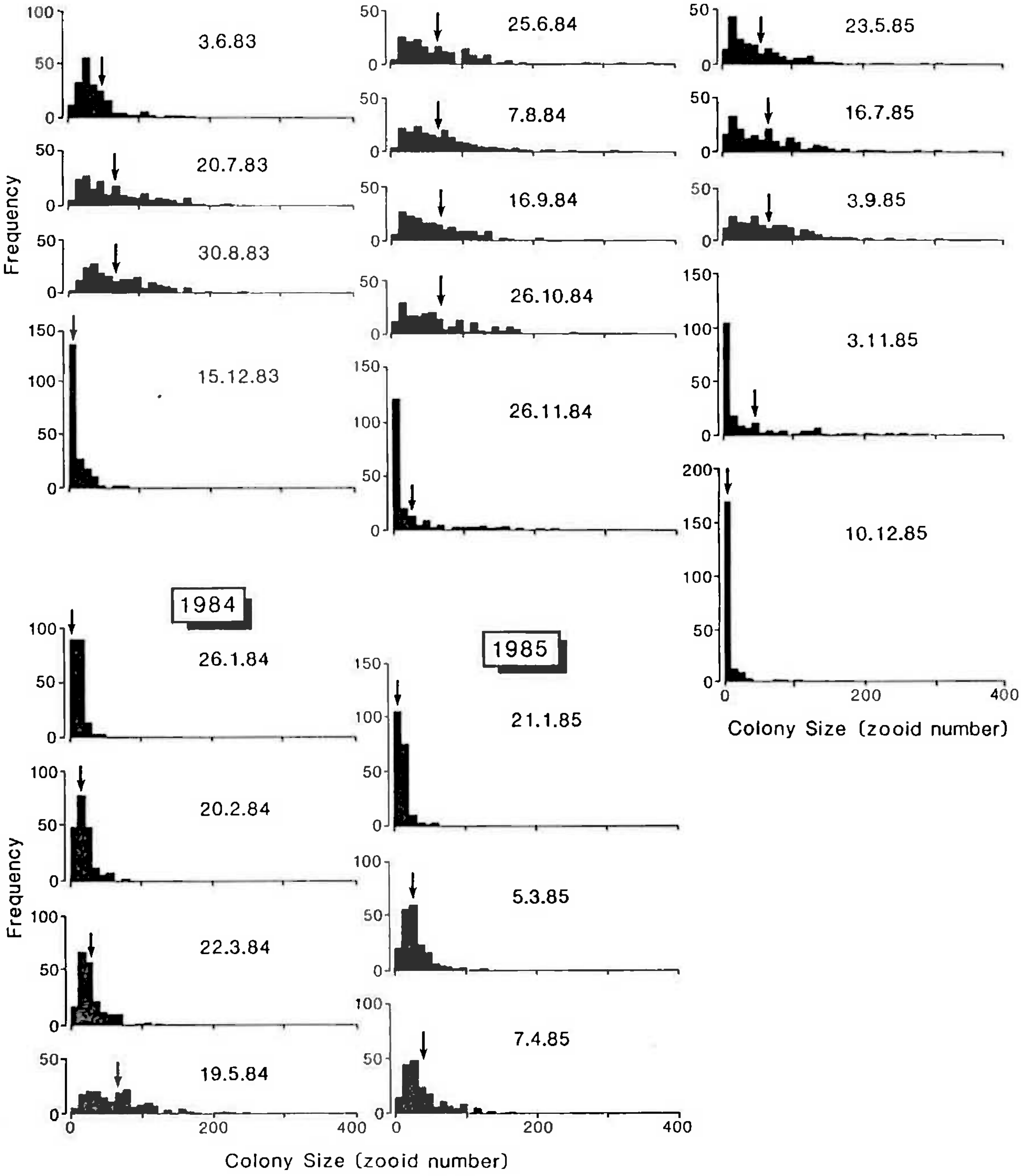

3.6.83
20.7.83
30.8.83
15.12.83
25.6.84
7.8.84
16.9.84
26.10.84
26.11.84
23.5.85
16.7.85
3.9.85
3.11.85
10.12.85
1984
26.1.84
20.2.84
22.3.84
19.5.84
1985
21.1.85
5.3.85
7.4.85
Frequency
Frequency
0
50
100
150
200
0
200
400
Colony Size (zooid number)
Colony Size (zooid number)

Figure 2.10b Size frequency distribution of colonies (zooid number) at the Inner Reef, Port Noarlunga. Arrows represent mean size. Two dates separated by a slash indicates that samples from these dates have been pooled.

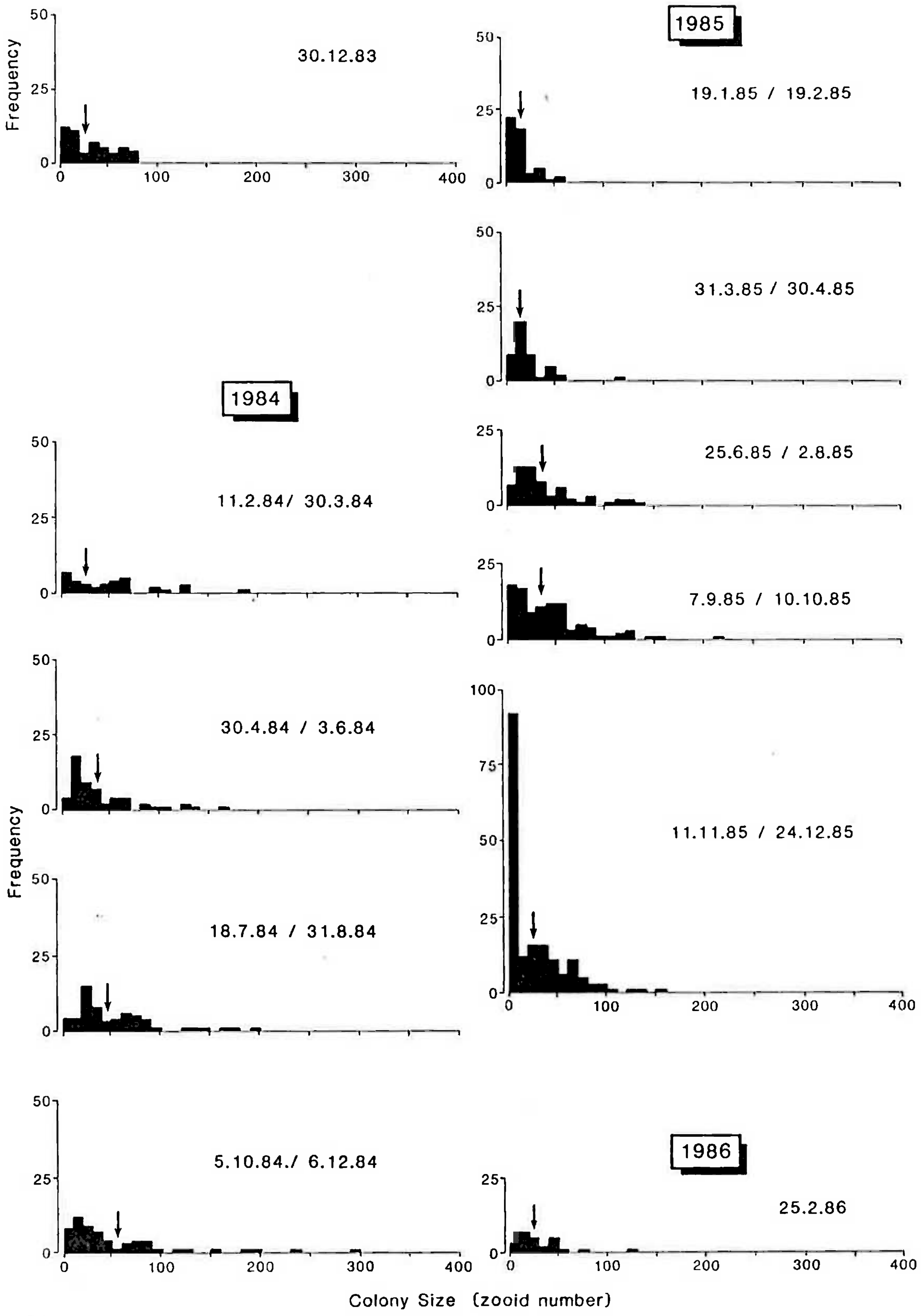
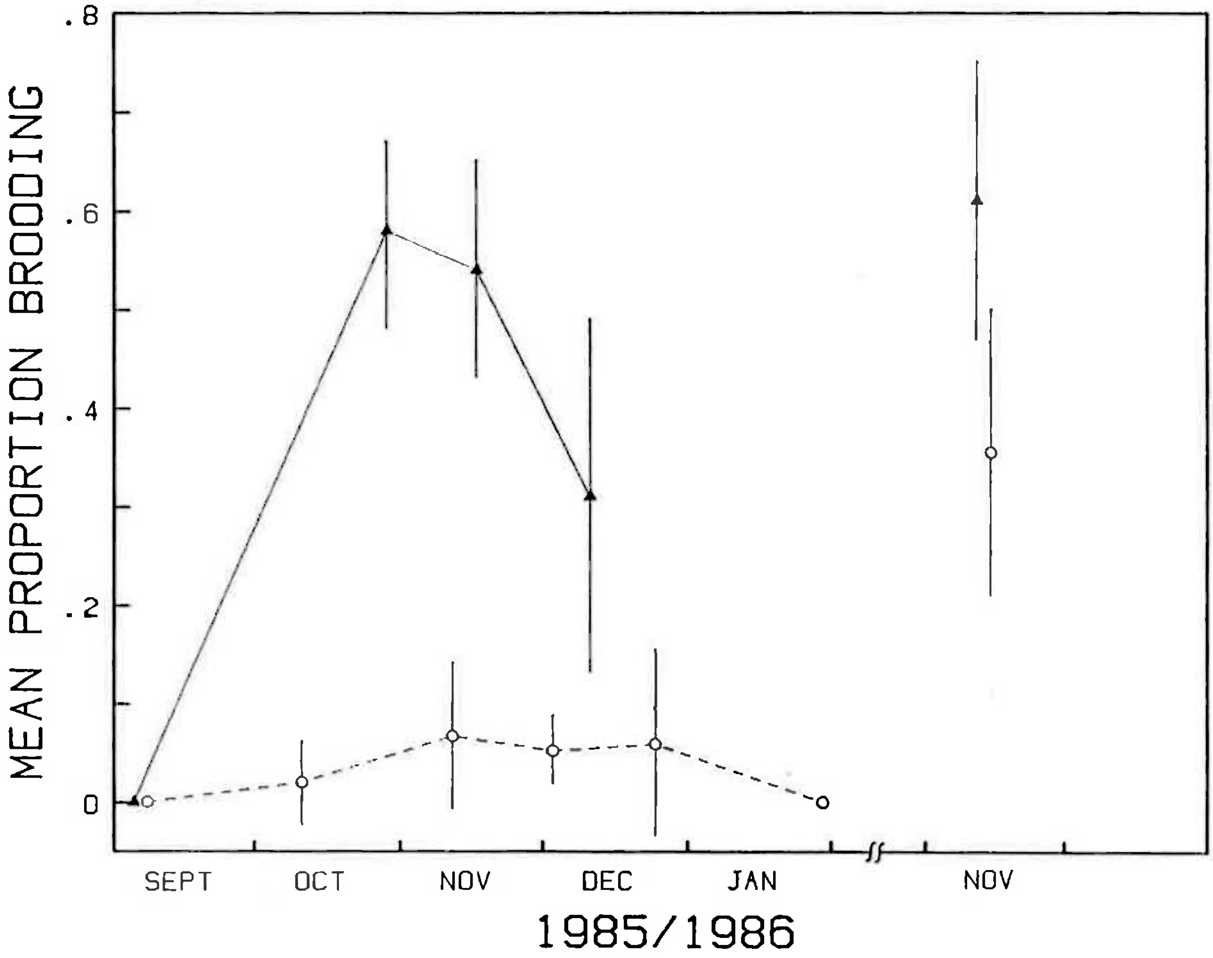

Frequency
30.12.83
1985
19.1.85 / 19.2.85
31.3.85 / 30.4.85
1984
11.2.84/ 30.3.84
25.6.85 / 2.8.85
7.9.85 / 10.10.85
30.4.84 / 3.6.84
11.11.85 / 24.12.85
18.7.84 / 31.8.84
5.10.84./ 6.12.84
1986
25.2.86
0
25
50
75
100
0
100
200
300
400
Colony Size (zooid number)

Figure 2.11 The mean proportion of a colony possessing brood pouches at the two sites. Means were calculated from counting all zooids within 10 - 14 colonies on each date. Error bars are 95% confidence intervals.

▲————▲ Edithburgh

o--------o Port Noarlunga



MEAN PROPORTION BROODING
.8
.6
.4
.2
0
SEPT
OCT
NOV
DEC
JAN
NOV
1985/1986

Figure 2.12 The frequency of brooding and non-brooding zooids versus zooid height (mm) at each site. Bars represent the mean percentage of each sample and were calculated from two years, 1985 and 1986. Lines are standard errors around the mean.

A. Edithburgh

B. Port Noarlunga

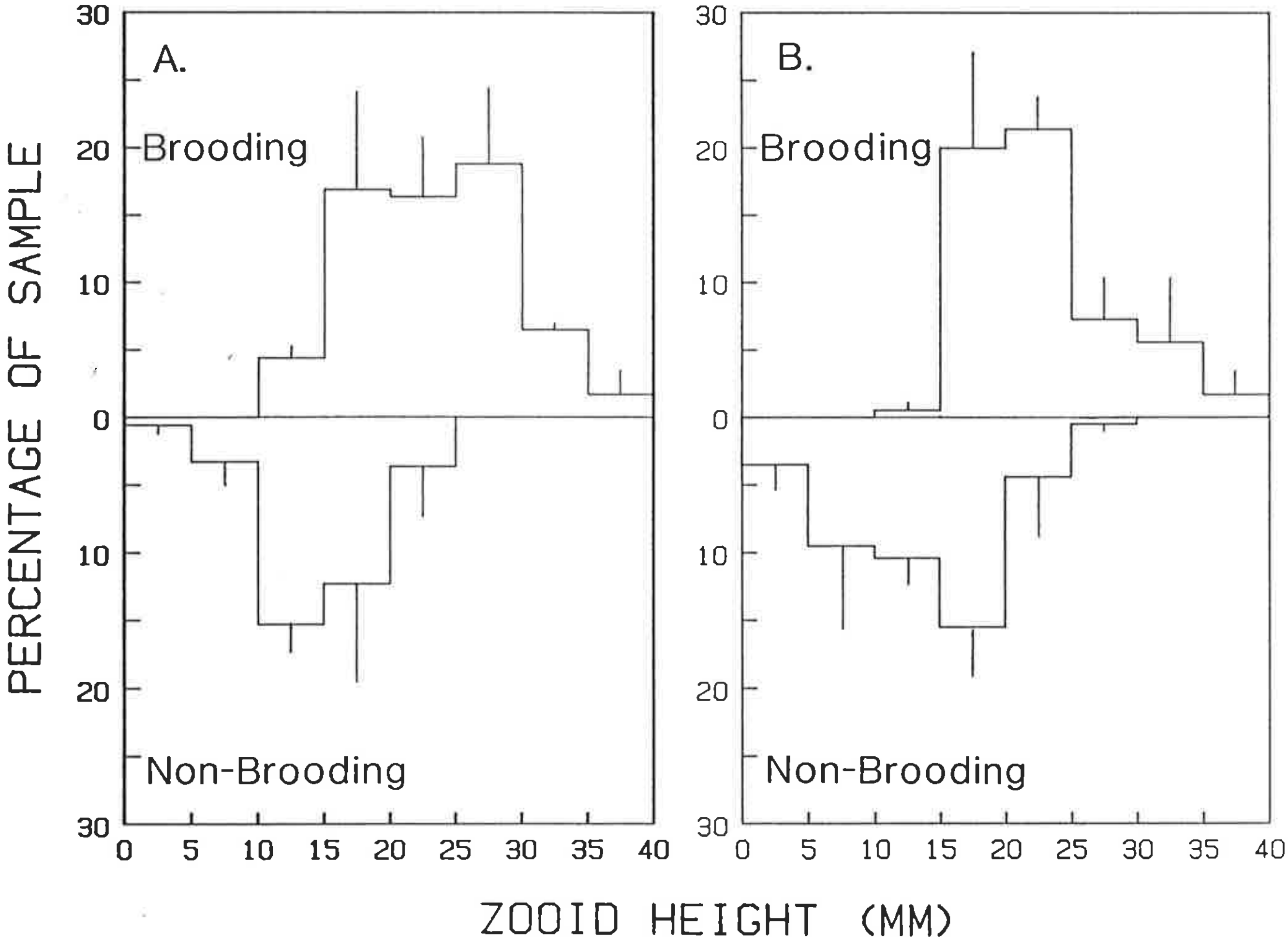

A.
B.
Brooding
Non-Brooding
PERCENTAGE OF SAMPLE
30
20
10
0
10
20
30
0
5
10
15
20
25
30
35
40
ZOOID HEIGHT (MM)

Figure 2.13 Availability of vacant space, expressed as a percentage of the total area, and the percent cover of the colonial ascidian *Botrylloides leachii* at the two sites. Vacant space at Edithburgh is considered to be bare areas of piling. At Port Noarlunga this category includes bare rock and encrusting coralline algae. Means were calculated from 12 samples at each site on each date and error bars are standard errors around the mean.

A. Edithburgh

B. Port Noarlunga

vacant space ●————●

Botrylloides leachii ▲---------▲

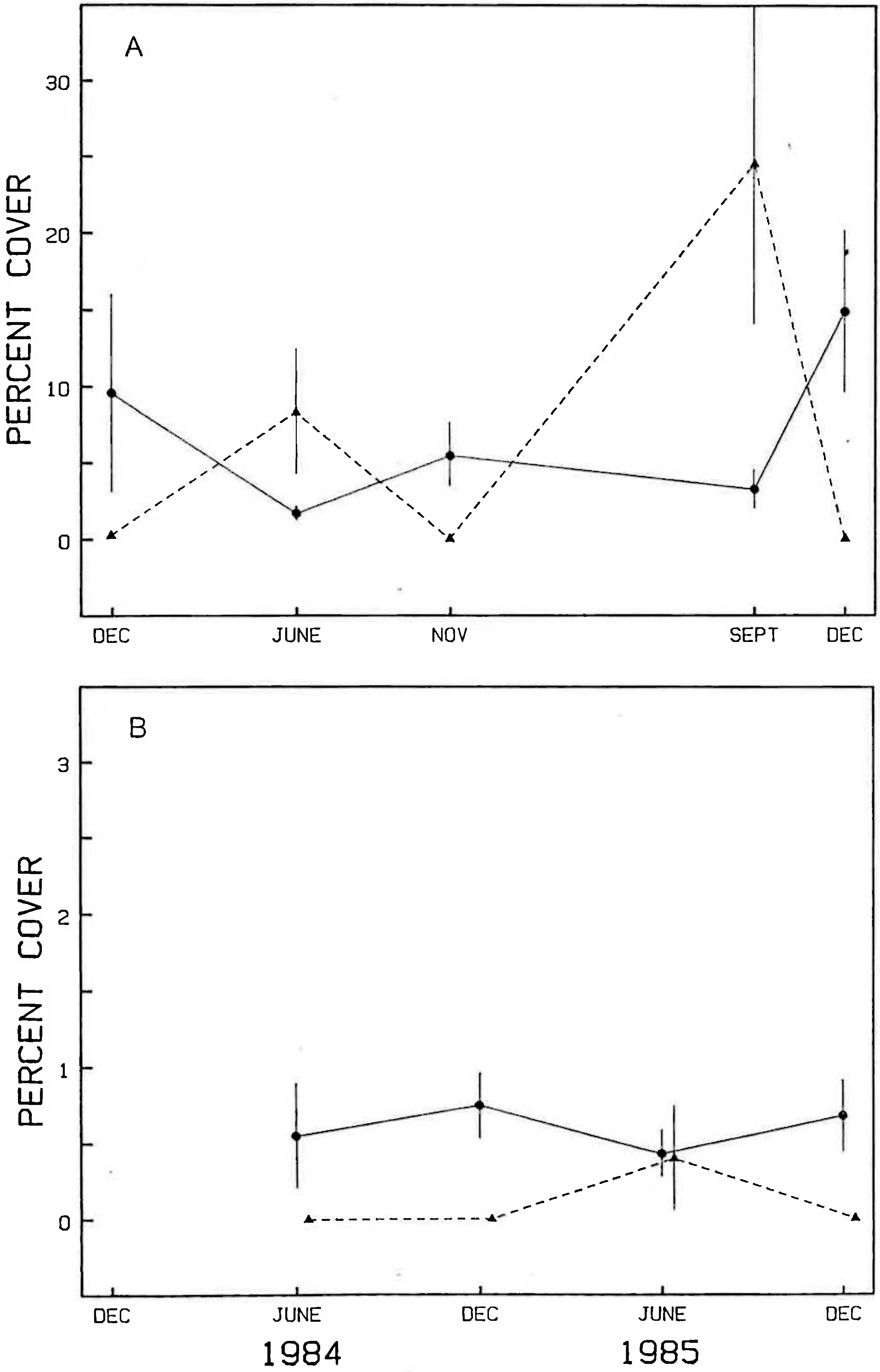

A
30
20
10
0
PERCENT COVER
DEC
JUNE
NOV
SEPT
DEC
B
3
2
1
0
PERCENT COVER
DEC
JUNE
DEC
JUNE
DEC
1984
1985

Table 2.1 Sites within St Vincent's Gulf in which colony number and size were determined. The nature and age of each substratum is listed, where appropriate, and each site is ranked by a subjective assessment of exposure (na = not applicable).

Site	Substratum	Year of erection	Most recent extension	Rank of exposure
Edithburgh Jetty	Wood	1873	1921	1
Wool Bay Jetty	Wood	1882	1912	2
Port Giles Jetty	Steel	1969	-	3
Port Noarlunga Jetty	Wood	1921	-	4
Rapid Bay Jetty	Steel	1941	-	8
Stenhouse Bay Jetty	Wood	1916	1932	9
Port Noarlunga Reef				
Inner	Aeolionite*	na	-	5
Outer	Aeolionite	na	-	6
The Gap	Aeolionite	na	-	7
Pinnacle Beach Reef	Granite gneiss	na	-	10

* Dune limestone

Table 2.2 Densities of *Podoclavella* within St Vincent's Gulf and Investigator Strait.

Site	Date	Quadrat size m^2	Density mean	SE	range	n	Density per $2.5m^2$
Jetties							
Port Noarlunga	13/8/1983	2.50	4.9	1.5	0- 25	20	5
Port Giles	16/8/1983	2.50	4.6	1.1	0- 17	20	5
Rapid Bay	4/8/1983	2.50	10.0	1.4	1- 29	20	10
Stenhouse Bay	15/8/1983	2.50	35.6	9.5	0-102	12	36
Edithburgh	20/7/1983	0.17	17.0	2.2	0- 33	20	236
Wool Bay	29/1/1984	2.50	0	-	-	20	0
Reefs							
Port Noarlunga							
Outer	16/9/1983	1.25	0.5	0.2	0- 2	20	1
Inner	16/9/1983	1.25	3.3	1.1	0- 19	20	7
The Gap	27/9/1983	1.25	1.8	1.2	0- 12	10	4
Pinnacle Beach	25/5/1985	1.25	3.85	1.4	0- 28	20	7

Table 2.3 Colony sizes within St Vincent's Gulf and Investigator Strait. Dates of sampling as for Table 2.2.

Site	Zooid number mean	SE	median	n
<u>Jetties</u>				
Stenhouse Bay	18.4	1.4	9	499
Rapid Bay	38.5	3.1	20	200
Port Noarlunga	57.0	6.2	40	88
Edithburgh	68.8	3.8	78	200*
Port Giles	90.8	12.0	70	92
<u>Reefs</u>				
Port Noarlunga				
Inner	49.6	5.9	37.5	56
Outer	51.0	16.4	34	10
The Gap	78.0	15.7	65	18
Pinnacle Beach	20.0	2.5	14	77

* Sizes obtained from a random sample of 200 colonies and not from permanent quadrats.

Table 2.4 Density of *Podoclavella* on vertical and horizontal faces in the presence and absence of large brown algae at two sites - Pinnacle Beach and Port Noarlunga Reefs. Quadrat size = 1.25m^2.

Site	Vertical Face				Horizontal face			
	+ Algae		- Algae		+ Algae		- Algae	
	$\bar{x}$ (SE)	n	$\bar{x}$ (SE)	n	$\bar{x}$ (SE)	n	$\bar{x}$ (SE)	n
Port Noarlunga Reef	0.6(0.3)	20	3.8(1.3)	20	0 (-)	20	0 (-)	20
Pinnacle Beach Reef	0 (-)	20	3.8(1.4)	20	0 (-)	20	0 (-)	20

Table 2.5 Percentage of colonies undergoing fission and the mean number of daughter colonies produced per fission event at Port Noarlunga reef and Edithburgh Jetty.

Site	Year	% of colonies undergoing fission		number of daughter colonies produced		
		%	n	mean	95%CI	n
Edithburgh Jetty	1983	4.5	66	2.3	0.4	9
	1984	7.6	79			
Port Noarlunga Reef	1984 +1985	39.0	33	4.7	1.5	13

Table 2.6 Analysis of the number of brood pouches per colony at Edithburgh Jetty and Port Noarlunga Reef in 1985 and 1986. Data were analysed with a two factor ANCOVA. The factors were site (fixed) and year (fixed), each with two levels. The means determined from the number of zooids with brood pouches divided by total colony size. Zero proportions were converted to 1/4n as recommended by Snedecor & Cochran (1980) and the data were arcsine transformed prior to analysis. Cochran's C on transformed data = .38 k=4 df=35 ns. The adjusted means and marginal adjusted means are from the raw data.

ANCOVA TABLE

Source	SS	df	MS	F	P	Reg. Coeff.
Site	1.14	1	1.14	27.3	<.001	
Year	0.95	1	0.95	22.6	<.001	
SxY	0.12	1	0.12	3.07	>.05	
Colony Size	0.52	1	0.52	12.4	<.001	.0009
Error	3.83	91	0.04			

ADJUSTED MEANS (RAW)

Site	Year		Adjusted marginal means
	1985	1986	
Edithburgh Jetty	0.44	0.55	0.50
Port Noarlunga reef	0.09	0.38	0.23
Adjusted Marginal means	0.25	0.47	

Table 2.7 The number of larvae per brood pouch in colonies from Edithburgh Jetty and Port Noarlunga Reef in 1985 and 1986. Data were analysed with a two factor ANCOVA. Factors were site (fixed) and year (fixed), both with two levels. Prior to analysis data were log transformed. Cochran's C on transformed data = .29 k=4 df=43 ns. The adjusted means and marginal adjusted means are from the raw data.

ANCOVA TABLE

Source	SS	df	MS	F	P	Reg. Coeff.
Site	1.23	1	1.23	13.4	<.001	
Year	1.81	1	1.81	19.6	<.001	
SxY	0.24	1	0.24	2.7	>.1	
Zooid Height	6.08	1	6.08	66.1	<.001	.036
Error	15.8	171	0.09			

ADJUSTED MEANS (RAW)

Site	Year		Adjusted marginal means
	1985	1986	
Edithburgh Jetty	10.2	20.6	15.4
Port Noarlunga reef	8.1	10.4	9.2
Adjusted Marginal means	9.1	10.4	

2.4 DISCUSSION

The density of colonies of Podoclavella showed considerable variation within St. Vincent's Gulf. Mean densities spanned more than two orders of magnitude. This degree of variation in density does not appear unusually high. Regional studies of ascidian populations in both temperate (Svane, 1983, 1984) and tropical waters (Bak et al., 1981) reveal variation in density of similar magnitude.

Usually density estimates are given as number per unit area. In their study of Trididemnum solidum in Curaçao, Bak et al. (1981) omitted to do this, thereby rendering their density estimates unreliable. They quantified the number of colonies along transects of variable length. Density per unit area could have been calculated from those data, but only density per transect was reported, so differences between transects may be attributable to transect length.

Many factors may act, independently or in concert with others, to alter the density of marine organisms. Field manipulations are time consuming and rarely can the effect of more than a small number of factors be assessed. Under these circumstances a sensible initial approach is to look for obvious correlations with density. For modular organisms density may be increased by settlement and fission, or decreased by the action of predators, competitors, physical factors and fusion. Amongst these, the only factor for which it is possible to make a confident subjective assessment is wave exposure, given information on the wave fetch and prevailing wind conditions.

The influences of water movement on benthic marine organisms are manifold; they depend on the adaptations organisms possess to withstand water movement and on the degree of water movement (reviewed by Hiscock, 1983). No consistent relationship between wave exposure and the density of Podoclavella was observed. Densities were high at Edithburgh Jetty, the most protected of all the sites, but they were not correspondingly low at sites subject to oceanic swell (Stenhouse Bay Jetty, Pinnacle Beach Reef and Rapid Bay Jetty).

The complete absence of Podoclavella from Wool Bay Jetty is noteworthy. There are two possible explanations for this absence; first, Podoclavella has not reached this jetty or second, larvae arrive but conditions are unfavourable for subsequent establishment. If the absence of colonies results from no larvae arriving at this site, then dispersal must be limited. Edithburgh and Port Giles Jetties, only a few kilometres to the south, both have large populations of adult colonies. These two jetties are, in terms of the general circulation pattern of the gulf, upstream of Wool Bay Jetty and therefore potential sources of larvae (Byte, 1976). Dispersal of Podoclavella will be discussed in the next chapter.

On the other hand, Wool Bay Jetty may not be conducive to the establishment of Podoclavella larvae. This site was the shallowest of any monitored: less than 2m deep at MLLW. At this depth even restricted wave motion may be detrimental to settled larvae , perhaps even adult colonies. I am not suggesting that water depth was the only factor interfering with the establishment of Podoclavella at this site. Without further work, however, it is not possible to distinguish between larvae not arriving, poor establishment, or both.

Colony size varied within St Vincent's Gulf. Unlike colony density, a strong correlation was observed between colony size and the ranking of wave exposure given to each site. The smallest colonies were found at Stenhouse Bay Jetty, Pinnacle Beach Reef and Rapid Bay Jetty. These three sites are the most exposed: all are subject to oceanic swells. Wave exposure may limit colony size in complex ways. Tissue may be removed directly by moving water, or indirectly by wave borne material. Alternatively, strong wave motion may impede growth by impairing feeding, or increasing competition with wave adapted species (Hiscock, 1983). The influence of wave motion on the size of Podoclavella colonies was not examined further.

It should be mentioned that an evaluation of colony density and size was hampered at Stenhouse Bay Jetty. At this site many pilings were heavily encrusted with a colonial ascidian, Amphicarpa dyptica (previously Stolonica dyptica). This ascidian formed an 'understorey' through which the stolonal mat of Podoclavella was not visible. Hence it was not possible to determine if a group of Podoclavella zooids were physiologically connected or separate. However, mis-identification of colony size, and therefore density, cannot account for the large number of diminutive colonies observed at Pinnacle Beach Reef and Rapid Bay Jetty.

The distribution and abundance of Podoclavella among encrusting substrata and naturally occurring bare space showed considerable variability. Colony densities were upto 3 times higher than expected on some substrata, yet on other substrata they were upto 4 times lower than expected. Podoclavella was absent from some substrata. These patterns may reflect several processes; larval settlement or survival may be poor on some substrata and high on others. It should be borne in mind also that the fauna at Edithburgh Jetty is dynamic (Kay & Keough, 1981; Kay & Butler, 1983), hence patterns observed several months after settlement may bear little resemblance to those immediately after settlement. I will consider patterns of distribution and abundance on encrusting substrata and naturally occurring bare space further in Chapter 4.

The distribution and abundance of Podoclavella within the reef sites showed clear, consistent patterns. This species is seldom encountered on upward facing surfaces, and is restricted to vertical rock walls, usually in the absence of large brown algae. Upward facing surfaces often support a lower diversity and density of sessile marine invertebrates (Buss, 1979, pers. obs.). This pattern of distribution has been attributed to the photo-negative responses of larvae at settlement (Thorson, 1964) and differential survival associated with microhabitats. The presence of grazing herbivores, macro-algae and high rates of sedimentation may all decrease the survival of new recruits (Young & Chia, 1984; Devinny and Volse, 1978), and some microhabitats are devoid of certain of these agents of mortality. The relative contribution of settlement and post-settlement mortality to the microhabitat distribution of Podoclavella will be examined in Chapter 4.

Early in this chapter I simplistically defined groups of physiologically connected zooids as individual colonies, irrespective of whether they represented ramets or genets. Having examined temporal changes at two sites it is now possible to examine the implications of this definition to this study. At Edithburgh individual colonies equate to genets. At Port Noarlunga, however, colonies may be either ramets or genets. Ramets usually can be easily distinguished by their small size and close proximity. In most instances I have considered the dynamics of colonies, but in comparisons with the population at Edithburgh I have also examined the dynamics of genets.

The population dynamics of colonies at Edithburgh Jetty and the inner reef at Port Noarlunga were markedly different. The Edithburgh population was characterized by large fluctuations in colony density and size, whereas the Port Noarlunga population was comparatively stable. These differences can be attributed to different life histories at the two sites, although some of the stability apparent at Port Noarlunga may result from an inability to distinguish small (1-5 zooid) ramets on the photographs.

The Edithburgh population was predominantly annual. Between 1-5% of colonies did survive into the second year, although none survived to reproduce a second time. This jetty population was semelparous and dependent upon large pulses of recruits to maintain population density.

In contrast, the Port Noarlunga inner reef population was perennial and relatively stable over time. Levels of genet mortality were low with a high percentage of the genets monitored still present after two years and longevity exceeding four years. This population was iteroparous, producing one brood per year. Levels of recruitment were an order of magnitude lower than those observed at Edithburgh Jetty and few recruits were observed to establish.

Fluctuations in the population densities of most benthic marine animals are determined by settlement, emigration, immigration and mortality. In sessile organisms, such as ascidians, emigration and immigration may be excluded except, perhaps, in those species which show considerable colony mobility (Ryland et al., 1984) and in those species that are commonly found on the backs of dromiid crabs (McLay, 1983). For animals constructed of modules, such as Podoclavella, an additional two processes are likely to influence population density; fission and fusion. These events may exert more influence on population density than the establishment of sexually produced larvae or mortality. For example, Bak et al. (1981) monitored a population of Trididemnum solidum in Curaçao that maintained a colony number of 38-50 during their 9 month study. Frequent examination of these colonies revealed that this population was far more dynamic than colony counts indicated; 85 novel colonies were produced (presumably through fission), 43 colonies disappeared through fusion and a further 33 colonies disappeared or were lost.

Fission and fusion were not significant life history attributes in Podoclavella. Fusion was not observed and fission occurred frequently only at one site, Port Noarlunga. Not only was fission relatively infrequent at Edithburgh, it was also inconsequential, usually occurring just prior to the death of colonies. At Port Noarlunga the products of fission were invariably small and short-lived. Very few survived to reproduce and the fecundity of these small colonies was low, as indicated by the significant covariate in the analysis of brood number (Table 2.6). High rates of mortality and low fecundity associated with the small size of daughter colonies has been observed in a range of invertebrate taxa (Highsmith, 1982; Hughes & Jackson, 1985; Karlson, pers. comm.). However, these 'drawbacks' may be compensated for by faster growth rates of these small fragments (Hughes & Jackson, 1985; Connell, pers. comm.; Karlson, pers. comm.) or enhanced feeding ability (McFadden, 1986). High rates of mortality were observed in small fragments of Podoclavella colonies; whether this was compensated for by faster rates of growth could not be adequately assessed because of a very small sample size.

The production of daughter colonies by fission may also spread the risk of genet mortality. Fragmentation reduces the chance of an entire genet being killed by a localized event. Hughes & Jackson (1985) documented highly localized mortality on a coral reef in which some coral genets had spread over five metres through fission. Genets of ramose corals may spread over even larger distances owing to their habit of dispersing by fragmentation and subsequent regrowth (Tunnicliffe, 1981; Highsmith, 1982). In Podoclavella colony fission spreads ramets over very small distances, seldom more than a few centimeters. So any event acting to remove a ramet and leave others intact would have to be extremely localized. But the spreading of risk need not be restricted to spatial scales, risks may also be spread through time (den Boer, 1968). For example, differences in the rate of maturation or the timing of birth may alter the probabilty of survival in a heterogeneous, fluctuating environment. The significance of colony fragmentation in *Podoclavella* to the spreading of risk in time was not assessed.

Colony fission in *Podoclavella* was almost always preceded by colony degeneration. Huxley (1926) documented shortening of the basal stolon by around one third, following stolon damage, in the clavelinid *Clavelina lepadiformis*. Perhaps shortening of the stolon during degeneration accounts for the colony fragmentation that is often observed in *Podoclavella* during this period.

Differences in the frequency and timing of colony degeneration at each site explained the differing rates of colony fission observed. Colony degeneration was frequent at Port Noarlunga, hence daughter colonies were produced year round. At Edithburgh, degeneration was restricted to the winter months and just after breeding in spring. Inexplicably daughter colonies did not form in winter at this site: they were only regularly observed just prior to colony death in early summer.

Colony regression followed by regeneration has been observed in other temperate (Stocker, 1984) and tropical (Bak *et al.*, 1981) species. Aside from *Podoclavella*, *Trididemnum solidum* appears to be the only other species documented as undergoing multiple phases of degeneration (Bak *et al.*, 1981). Yet Bak *et al.* did not speculate why this degeneration might occur. I postulate that degeneration may represent a cessation of feeding activity when it is no longer economic to feed in the unproductive winter months. Alternatively it may provide a means either to discard test material that has become so badly fouled as to inhibit feeding, or to facilitate the excretion of accumulated toxic by-products, analogous to leaf fall in deciduous trees, or both.

The degeneration and subsequent regeneration of colonies entails an energetic cost. Not only does regeneration require energy to be channeled into somatic growth, and therefore away from reproduction, it must also deplete the energy reserves of the colony as colonies cannot feed in their regressed state. Presumably there is a sound physiological reason for undergoing degeneration. For example, it may require less energy to break down and rebuild a zooid than to continue feeding with a fouled one.

Different life histories were apparent between populations at Edithburgh Jetty and Port Noarlunga. Semelparous and iteroparous life histories arise as a result of differences in age specific mortality (Charnov & Schaffer, 1973). If adult survival is high relative to the survival of offspring then selection will favour an iteroparous life history. Conversely, should the offspring stand a better chance of survival than their parents then semelparity should be favoured. As expected the semelparous population at Edithburgh has more broods and they are, on average, larger than those produced by the iteroparous Port Noarlunga population. These differences between semelparity and iteroparity raise two questions. First, is it differences in adult or juvenile survival which determine the life history tactics (sensu Stearns, 1976) adopted by Podoclavella and, second, are these life histories under genetic control or are they environmentally induced?

The first question is difficult to answer confidently but clear physical and biotic differences are apparent between Edithburgh Jetty and Port Noarlunga. Edithburgh Jetty is the more sheltered of the two, but biologically is highly dynamic. In their assessment of stability at Edithburgh Jetty, Kay and Butler (1983) found around 50% of the space changed hands at least once in the two or so years of monitoring. So, competition for space was intense at this site and the probability of overgrowth by neighbouring species was high. Even the most casual of glances through the photographs of permanent quadrats at Port Noarlunga Reef would reveal this community to be far less dynamic. Indeed, changes in the availability of vacant space and the annual colonial ascidian Botrylloides leachii demonstrate the differences in patch dynamics at these two sites (Fig. 2.13). The stasis observed at Port Noarlunga can be attributed to the large number of long-lived solitary animals, incapable of asexual reproduction, at this site.

An attempt was made to answer the second question, that is, to determine whether these life history differences were genetic or environmentally induced. Electrophoretic studies, although providing evidence of genetic differentiation among populations, cannot determine whether genetic differences are the basis for life history differences. Hence, an answer to this question requires a reciprocal transplant. In March 1985 a pilot transplant proved successful and so a reciprocal transplant was done later that year. Control colonies were moved an equivalent distance to those transported between sites and were replaced at their original site. Adult colonies were successfully transferred but within three months storms at both sites had reduced replication to a level which did not allow the experiment to be interpreted.

Hence the basis for these life history differences remains open to conjecture. Here I propose a possible environmental mechanism for the observed life history differences. I speculate that the availability of sperm, and in turn the number of ova fertilized, determines whether a colony is semelparous or iteroparous. If sperm are 'readily available', as at high population densities, then all ova produced by a colony will be fertilized and with insufficient energy remaining for somatic growth the colony will fail to regenerate after reproduction and die. If, however, the supply of sperm is 'limiting' any unfertilized eggs will be resorbed, as has been observed in Botryllus schlosseri (Goodbody, 1961), and energy redirected into somatic growth in the following year. As a result populations at low density will be perennial and iteroparous.

CHAPTER THREE

Dispersal and Larval Mortality

3.1 INTRODUCTION

Many marine invertebrates are sessile and rely upon the dispersal of propagules, usually larvae, to reach and colonize new habitat patches. The distances over which larvae may disperse span many orders of magnitude, from millimetres to thousands of kilometres. The distance moved by larvae is largely a function of the mode of larval development. Species which lack a pelagic larval stage move very small distances; for example the crawling planula larvae of cnidarians rarely venture more than a few centimeters from the parent (Gerrodette, 1981; Sebens, 1983a). Among species that possess a pelagic larval stage two modes of development may be distinguished: i) lecithotrophic or non-feeding larvae are nutritionally independent of their surroundings and disperse short to medium distances as they spend only a few minutes to hours in the plankton, and ii) planktotrophic larvae use the food resources available in the plankton and may drift for hours to months before settling (Thorson, 1950).

The longer a larva remains in the water column, the greater are the risks to which it is exposed. It has been estimated that mortality in the water column may be as high as 99%, reflecting the vulnerability of larvae to starvation, predators, and dispersal to inappropriate habitats (Thorson, 1950; Sastry, 1985).

The distance that a species disperses partly determines the rate at which populations recover from local disturbance and therefore the persistence and stability of these populations (Connell, 1985b; Sebens, 1985). Hence, the hazards of a long planktonic existence on one hand are balanced on the other by advantages of growth and dispersal. A long planktonic period may enhance dispersal but it may not reflect selection for enhanced dispersal (Strathmann, 1980).

A direct investigation of dispersal entails determining the distance moved during a time interval and usually requires some form of marking of the propagules. Seed and pollen dispersal in terrestrial plants has been successfully quantified by marking propagules with fluorescent dyes and even metal tags (Waser & Price, 1982; Sork, 1984). In marine environments tagging has so far been impossible and so the distances over which larvae disperse have only been inferred. Biochemical genetic studies or the range extensions of introduced organisms provide an indication of the distance moved by larvae (reviewed in Burton, 1983; Crisp, 1958; Quayle, 1964).

In this chapter I examine the larval dispersal and mortality of Podoclavella, which can be observed directly. The large size (4mm in length) and conspicuous pigmentation of Podoclavella larvae facilitated the continuous observation of larvae after their release from the adult colony and while settling. Two questions were examined;

i) What was the relationship between currents and the distance and direction of dispersal? and

ii) what proportion of larvae were killed by predators?

3.2 MATERIALS AND METHODS

The distances moved by *Podoclavella* larvae at Edithburgh Jetty were determined by continuous observations of individual larvae after their release from the adult colony. To ensure a ready supply of larvae, larval traps were fixed over five adult colonies. These traps were constructed of black shade cloth (15 threads per cm) and five 70ml clear plastic jars, supported on a steel frame (Fig. 3.1). The jars were removable and their bottoms were replaced with bronze mesh (0.25mm) to maintain water flow over the parent colony.

Larvae invariably swam into the uppermost jars after release. When a larva appeared, the jar was removed from the trap and the larva released into the water column. The larva was then followed, usually from a distance of 0.4-0.6m, until it was lost, consumed or observed to settle, taking care not to disrupt its swimming or the water flow impinging upon it. Settlement was easily distinguished as it was characterized by vigorous beating of the tail after the larva had attached. This beating was maintained for 3-5 minutes during which time it slowly decreased.

A number of variables were recorded whilst larvae were being followed, including;

i) the total swimming time in seconds,

ii) the total distance moved in metres,

iii) the net direction of movement in degrees, relative to the current direction (for example, a direction of 0° represents movement aligned with the current while moving perpendicular to the current equates to an angle of 90°),

iv) the number of times the substratum was encountered (touched), and

v) the taxa of the substrata encountered, identified to species if possible.

In addition, current speed was measured with a flow meter (General Oceanics Inc., model 2030) suspended 1.5m above the seabed, directly upstream of the point of release. Flow rate was determined from readings taken at 10-15 minute intervals.

Larval traps were checked as regularly as possible, but larvae spent variable amounts of time in traps. Some larvae were released as soon as they appeared, while others may have been swimming within traps for ten minutes or more before their release. The effect of this variation in the timing of release on the swimming and settling behaviour of larvae was examined in two groups of swimming larvae; 'just released' and 'previously attached'. These two groups span the range of time since release. The 'just released' group was obtained by gently shaking colonies to induce release of larvae. Often larvae acquired in this manner were not swimming properly. This did not result from damage, but from larvae being released early with incomplete unfurling of the larval tail. These larvae were retained in containers until they had assumed a normal swimming pattern, and then released. The second group of larvae, 'previously attached', were obtained by allowing larvae to attach to the plastic containers in the larval trap. Larvae usually attached to the plastic jars within 20-30 minutes of their appearance in the trap. A gentle shake dislodged these larvae and they could then be followed. For each group the distance dispersed, swimming time, and number of times the substratum was touched were recorded. Observations were made in 1984 and 1985, and the groups were compared with a two factor ANOVA, with the factors larval group and year.

3.3 RESULTS

A total of 270 larvae were followed in 1984 and 1985 and, of these, 100 were successfully tracked to settlement. Many of the remaining 170 larvae were lost, a small number were abandoned as they were not swimming normally, and several were consumed by predators (Table 3.1).

Larval mortality: The stony coral, Culicia tenella Dana, was the main predator, consuming a total of 12 larvae. This cnidarian ate 3% of the total larvae tracked in 1984 and 18% of all larvae followed in 1985. In addition, two larvae were ingested by juvenile clinid fishes, but were quickly rejected and went on to settle, apparently unharmed. The hydroid, Ophiodissa australis (Bale), was capable of catching Podoclavella larvae but did not appear to harm them. This hydroid was particularly common and caught large numbers of larvae but these larvae rarely remained captive for more than a minute. Larvae struggled violently, broke free and resumed swimming, apparently unharmed. On one occasion, however, a larva remained captive to an individual hydroid for 2 hours and 11 minutes. This larva eventually metamorphosed on the stem of the hydroid after failing to break free.

Larval dispersal: Larvae were competent to settle as soon as they were released from the parent colony. Consequently larvae did not disperse far; almost 80% of them settled within 2.5 metres of the adult colony. Larvae were observed to settle between 5 centimetres and 13.4 metres from their point of release. The average distance moved was 2.2m (SE = 0.3 n = 100), after swimming for 112 seconds (SE = 10 n = 98). A plot of the frequency with which larvae dispersed a given distance revealed a positively skewed distribution (Fig. 3.2). After smoothing (Tukey, 1977) these data conformed to a negative binomial distribution

(mean = 3.5, variance = 35.5, K-parameter = 0.51, Chi square test for goodness of fit to the negative binomial $\chi^2 = 21$, df = 24, ns, Fig. 3.3)

On their release larvae always swam vigorously into the current, but net movement was nearly always downstream. Larvae were rarely capable of maintaining their position relative to the seabed, so there was a strong positive relationship between swimming time and distance moved (Fig. 3.4). Larvae were only observed to swim upstream when they were close to the bottom or in the lee of an object, such as a jetty piling.

Current speed significantly influenced the distance that larvae dispersed. Larvae moved further as current speed increased ($P < .001$, $r^2 = .14$, Fig. 3.5). Current speed did not, however, influence the variation in the direction of movement ($P > .05$, $r^2 = .04$, Fig. 3.6). The flow meter was not calibrated for current speeds of less that 5cm per second. Consequently, all data obtained at flow rates lower than 5cm per second were arbitrarily placed at each of three rates of flow: 0, 2.5 and 4.5cm per second. Analysis of current speed with the distance and direction of dispersal was done three times, once for each of these arbitrary low rates of flow. The results of these analyses were the same for all three flow rates, so only the results obtained with the 2.5cm per second data set are reported here.

My ability to follow larvae after their release did not change over time. The time that larvae had been followed since their release was split into 60 second time intervals and the percentage of larvae lost of the total number entering each time interval was calculated. The percentage lost during each time interval was plotted and revealed a slope that was not significantly different from zero ($t=0.4$, $P > .05$, df=8, Fig. 3.7). Hence, the percentage of larvae lost did not change with time. The last time interval was omitted from the calculation of the slope as with only one larva present this interval had no degrees of freedom.

The length of time that larvae were held in the larval traps did not influence swimming or settling behaviour. Larvae which had already been attached swam longer, moved further and contacted the substratum more often, on average, than those that had just been released. None of these differences were significant between groups or years, however (Table 3.2, 3.3, 3.4). Where appropriate (Winer, 1971) the data were pooled across years and re-analysed but, again, no differences were found (Table 3.2, 3.3). The data for the number of times that the substrata was touched (Table 3.4) were not pooled across years as the probability of a type II error was unacceptably high (Winer, 1971).

Swimming and settlement behaviour: The vertical position of larvae in the water column was variable. On their release from traps larvae often maintained their height above the seabed and several immediately swam toward the seabed, despite larvae only swimming into the upward facing jars in the larval traps. One consistent pattern did emerge however. Larvae tended to be located closer to the seabed as distance from the larval source increased. Only once was a larva observed more than 2m above the seabed, after having moved more than 10m from the point of release.

A low percentage of the larvae observed ceased swimming occasionally and drifted for a few seconds. This behavioural change was only observed in larvae that had been swimming for more than approximately 6-8 minutes. Swimming activity was then resumed. All other larvae swam continuously.

Podoclavella larvae were capable of settling epizooically on a number of benthic invertebrates. Larvae attached to the substratum and either settled (accepted it) or dislodged themselves with a flick of the tail (rejected it). Almost 58% of larvae settled upon their first encounter with the substratum. Rejection of the substratum by a larva on more than 10 encounters was rare, but one larva rejected substrata 19 times before finally settling (Fig. 3.8). A plot of the number of encounters against time spent swimming revealed a significant positive relationship (Fig. 3.9).

A change in larval behaviour was often observed if a larva rejected the first substratum that was encountered. Larval movements then became more limited. The distance moved from the point of release to first encounter of a substratum was often large. The distance moved by several animals on this initial 'jump' was, on average, 5.2m (SE = 1.8 n = 7). Subsequent movements of these larvae were two orders of magnitude smaller - 0.03m (SE = 0.003 n = 28) after rejecting the first substratum encountered. This random sample of seven included the only larvae for which measurements were made of all movements to settlement.

Figure 3.1 Larval trap to be positioned over adult colony; note steel frame beneath black shade cloth and removable plastic containers.

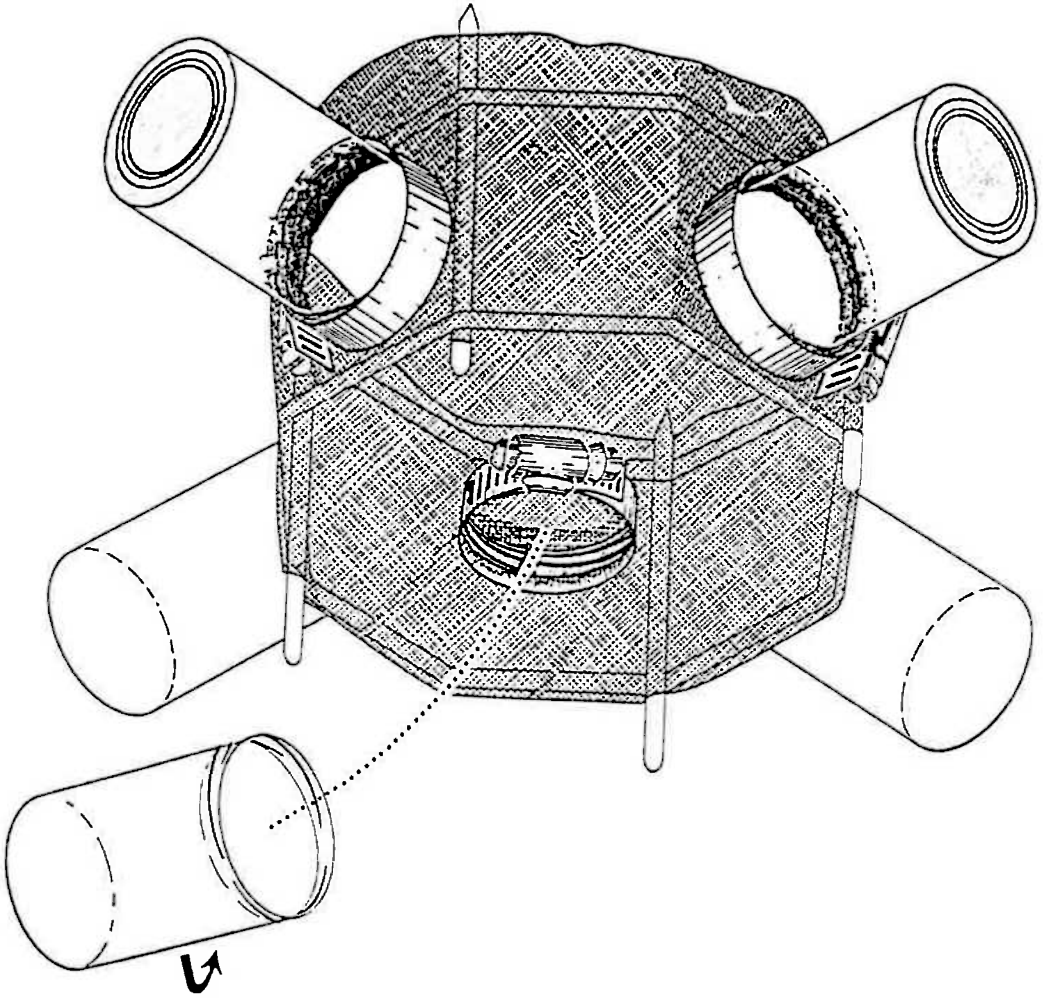


Figure 3.2 Frequency distribution of distance dispersed by larvae (metres). The distance was measured from the point of release to settlement.

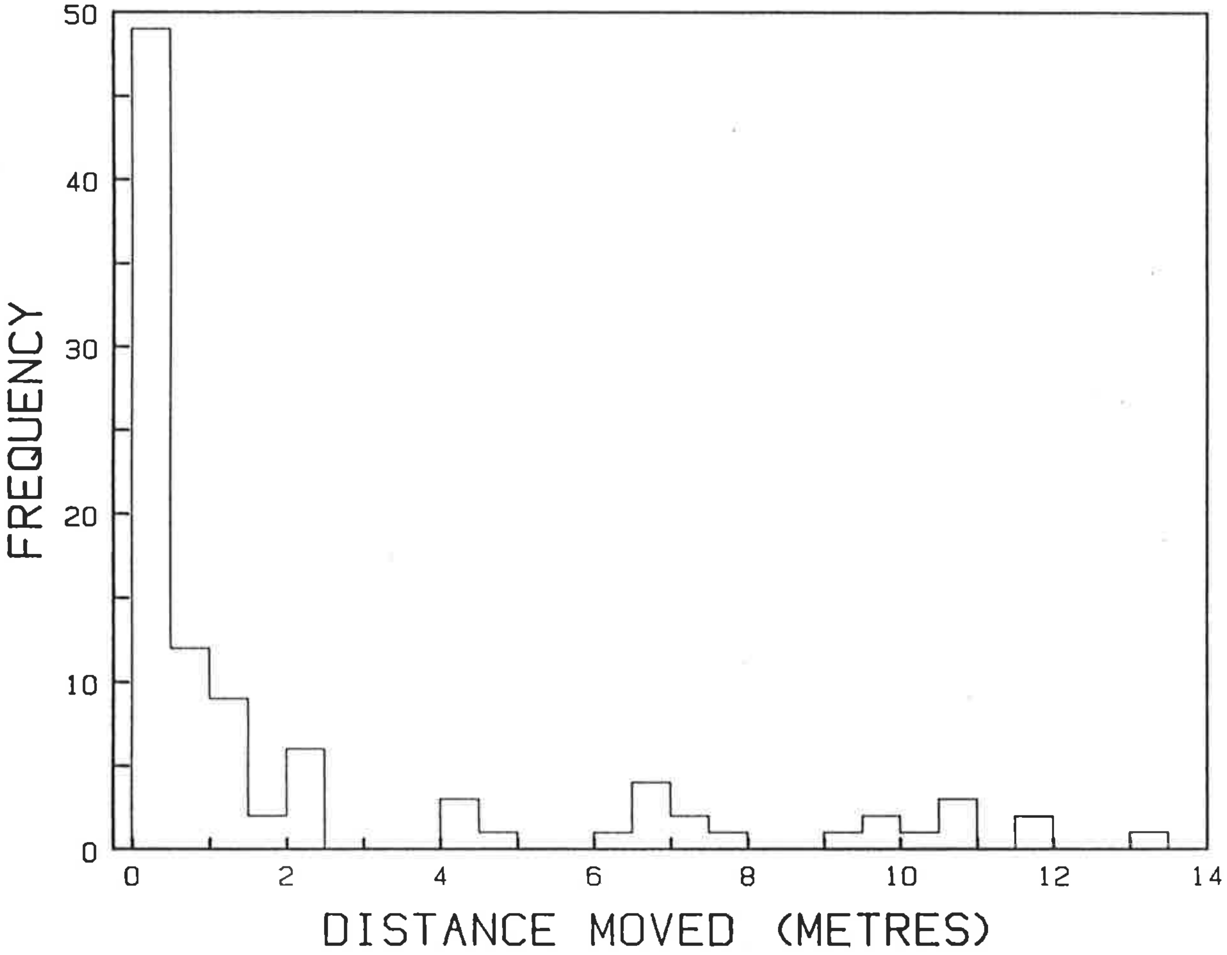

50
40
30
20
10
0
FREQUENCY
0
2
4
6
8
10
12
14
DISTANCE MOVED (METRES)

Figure 3.3 The observed and expected distribution of larvae from the parent colony. The 'observed' numbers have been smoothed using the method recommended by Tukey (1977). The 'expected' numbers were calculated from a negative binomial function fitted to the observed data. Parameters of the negative binomial were; mean = 3.5, variance = 35.5, K-parameter = .51.

Observed ————

Expected --------

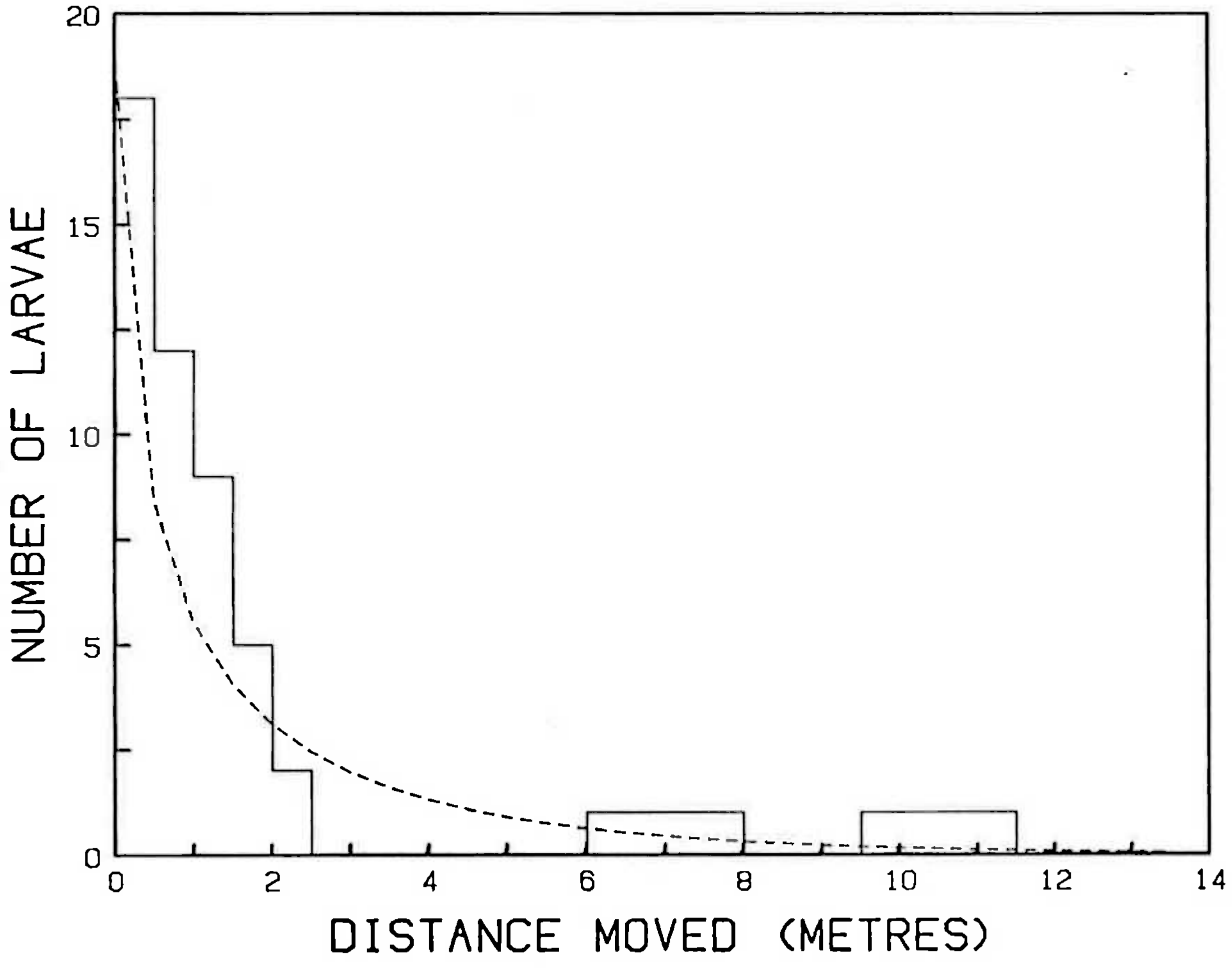

20
15
10
5
0
NUMBER OF LARVAE
0
2
4
6
8
10
12
14
DISTANCE MOVED (METRES)

Figure 3.4 Distance moved (metres) versus swimming time (seconds) of larvae.

$r^2 = .58$

$t = 0.58$

$P < .001$

$df = 86$

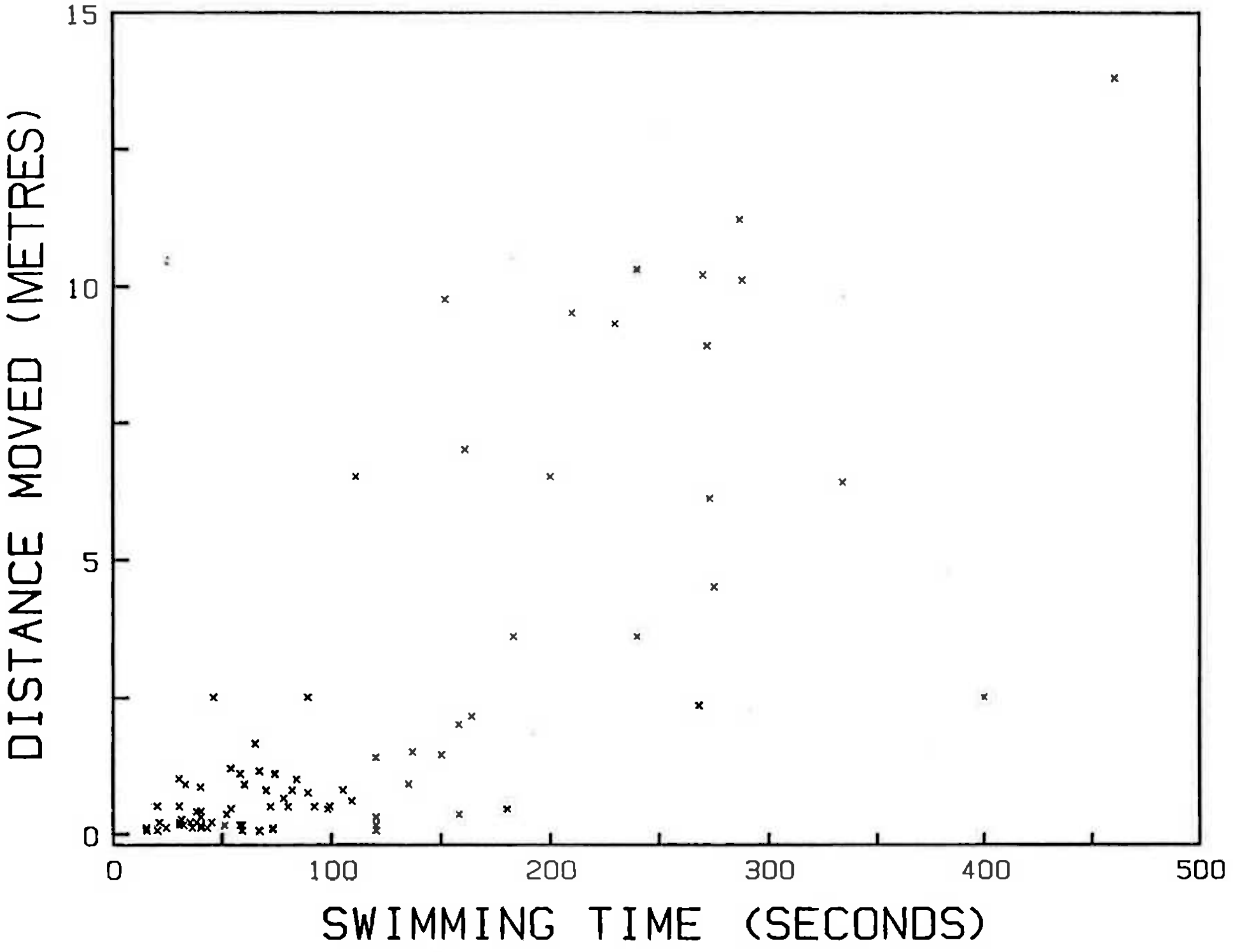

15
10
5
0
0
100
200
300
400
500
DISTANCE MOVED (METRES)
SWIMMING TIME (SECONDS)

Figure 3.5 Distance moved from parent colony (metres) versus current speed (cm per second).

$r^2 = .14$

$t = 3.9$

$P < .001$

$df = 87$

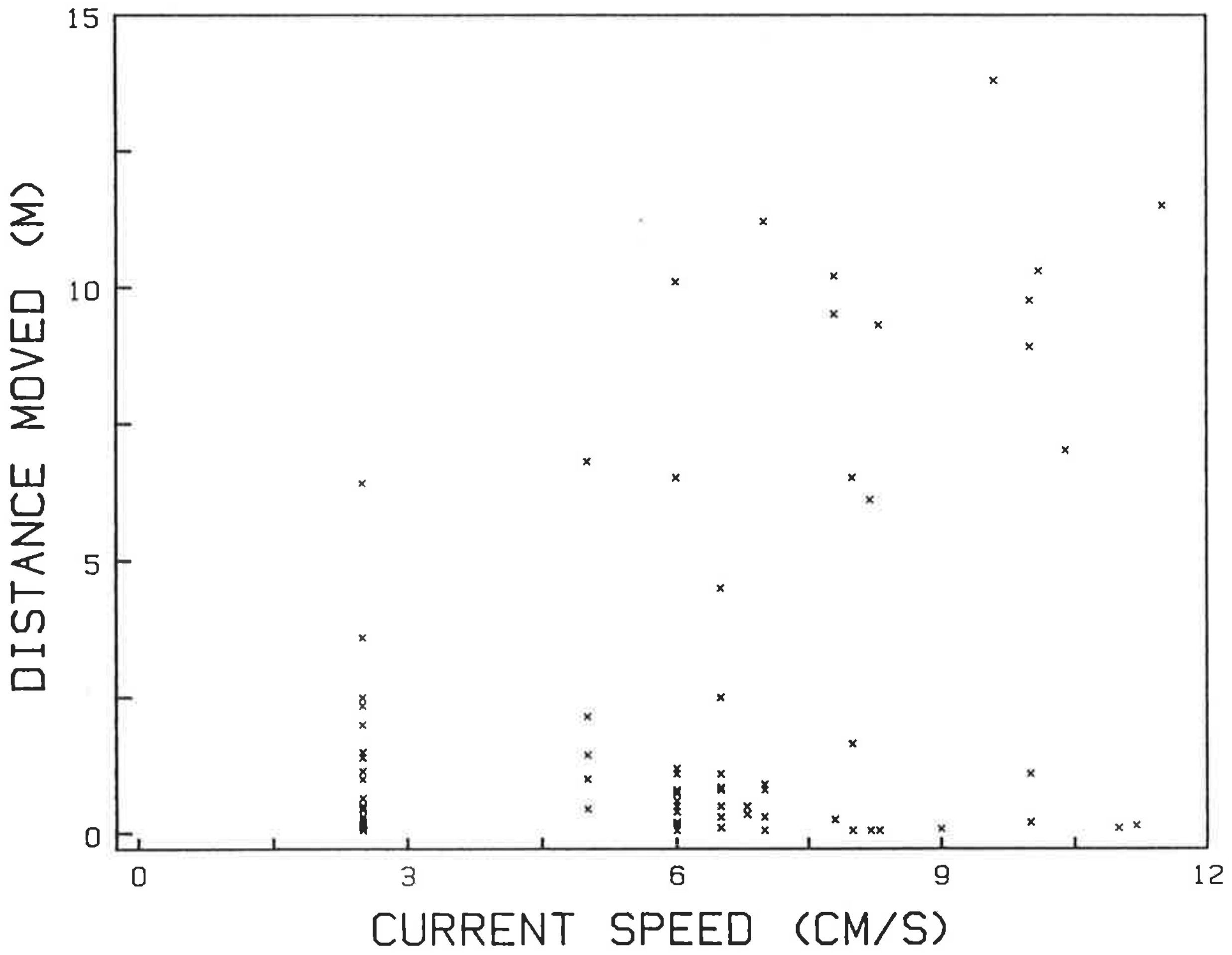

15
10
5
0
DISTANCE MOVED (M)
0
3
6
9
12
CURRENT SPEED (CM/S)

Figure 3.6 Net direction of dispersal versus current speed (cm per second). Direction of the larvae was measured in degrees relative to the direction of the current.

$r^2 = .04$

$t = 1.8$

$P > .05$

df= 88

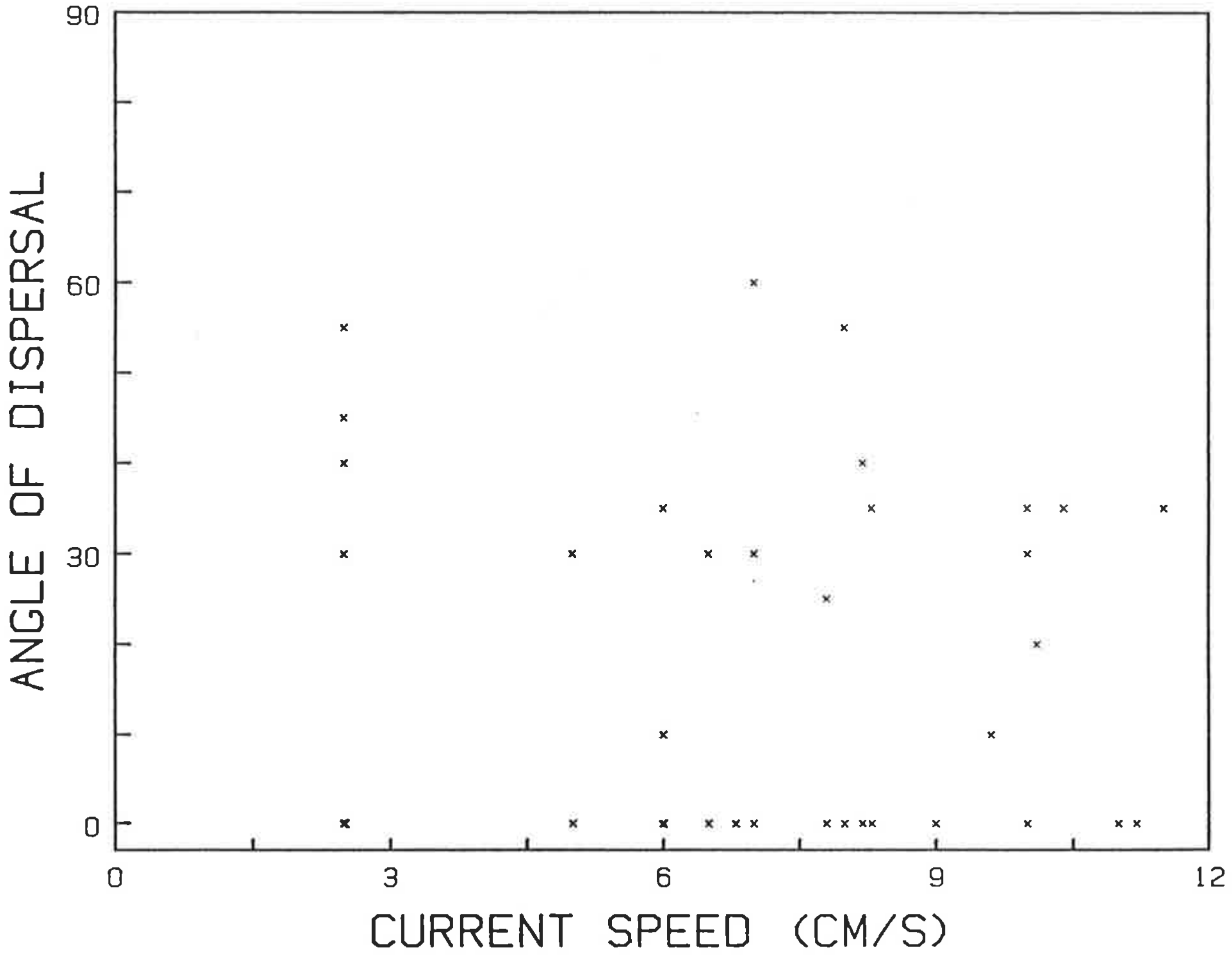

90
60
30
0
0
3
6
9
12
ANGLE OF DISPERSAL
CURRENT SPEED (CM/S)

Figure 3.7 The percentage of larvae lost during one minute time intervals after the release of larvae from adult colonies. The percentage lost was calculated from the number of larvae entering each time interval.

$t = 0.4$

$P > .05$

$df = 8$

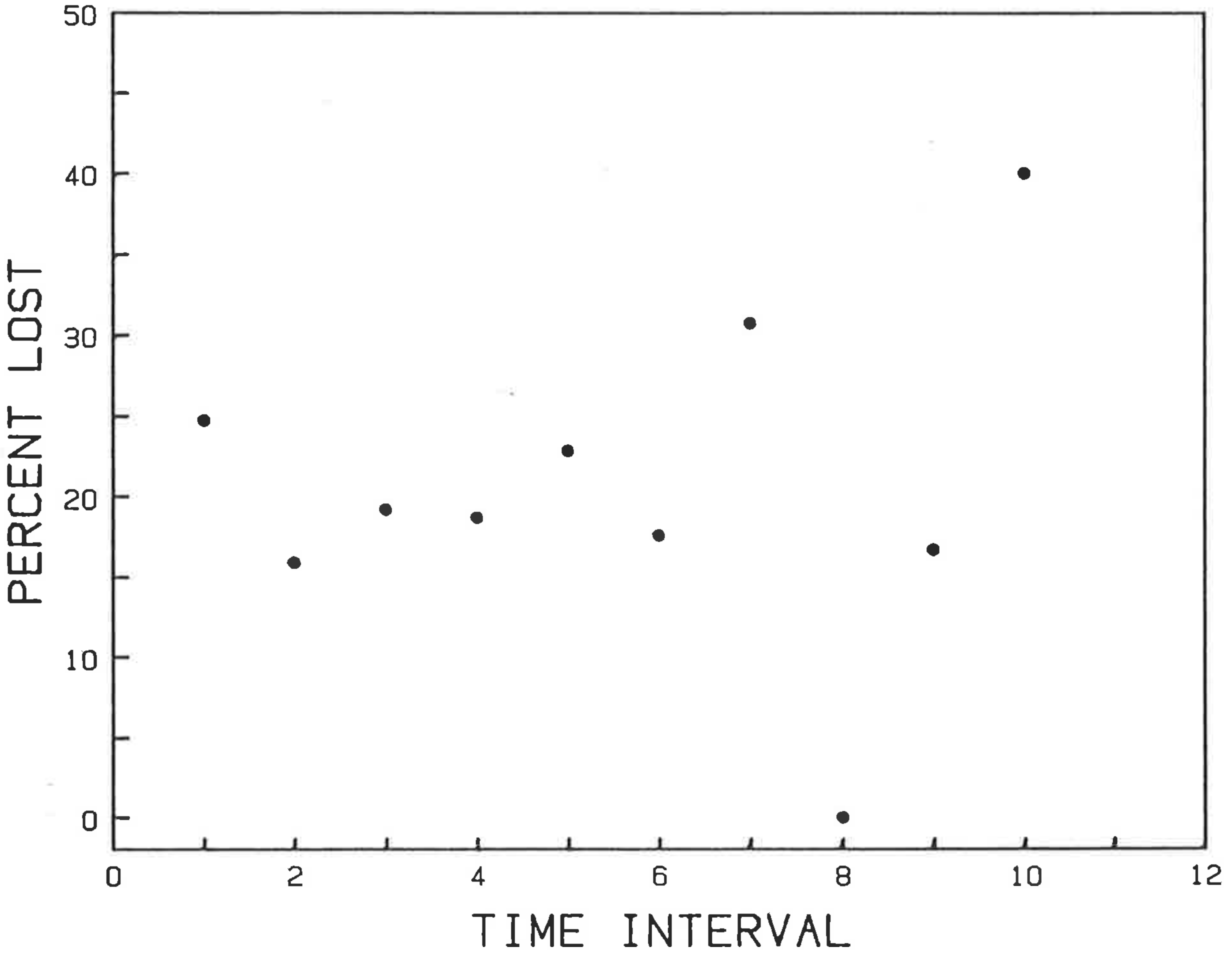

50
40
30
20
10
0
PERCENT LOST
0
2
4
6
8
10
12
TIME INTERVAL

Figure 3.8 Frequency distribution of the number of times larvae touched (encountered) the substratum.

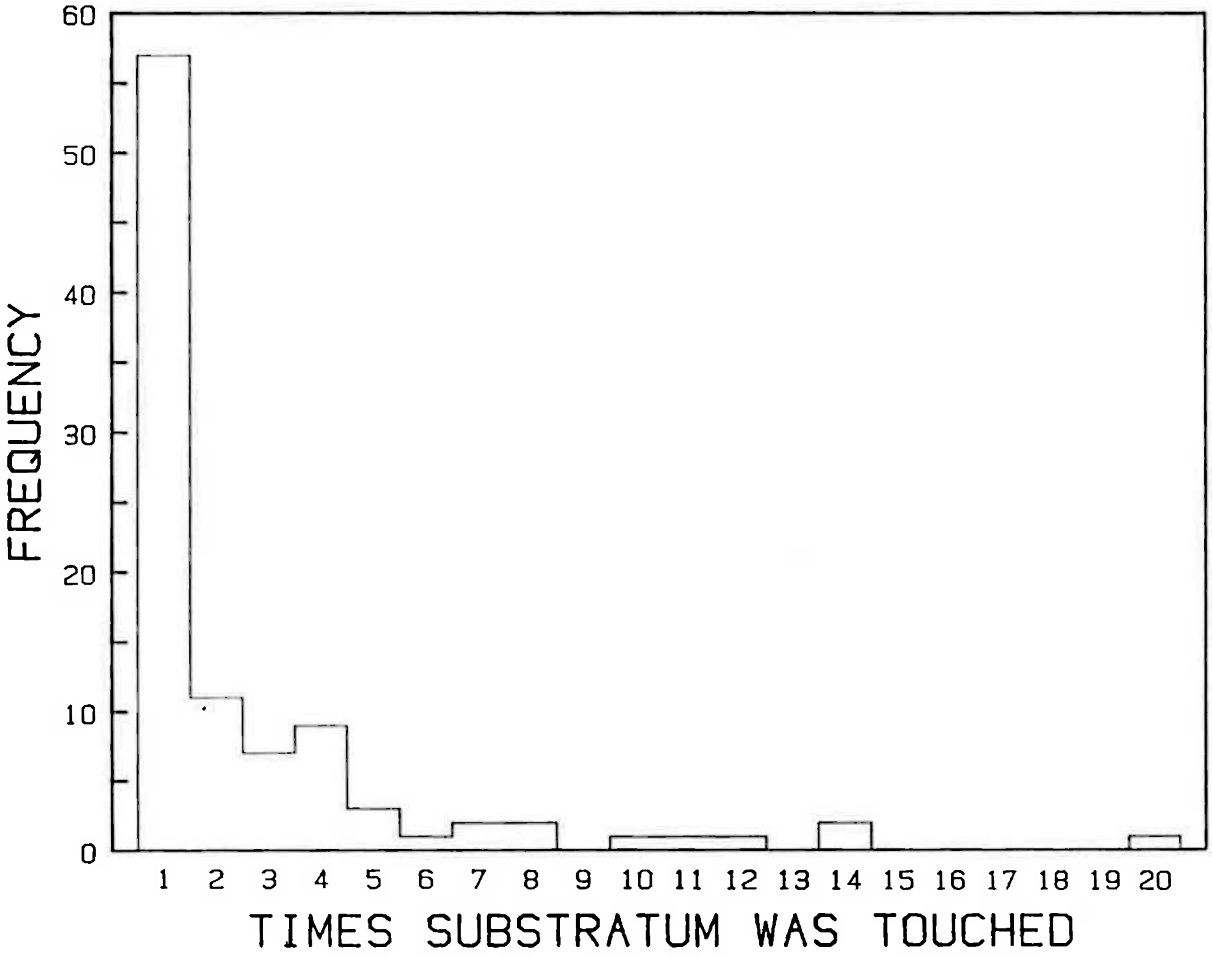

FREQUENCY
0
10
20
30
40
50
60
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
TIMES SUBSTRATUM WAS TOUCHED

Figure 3.9 The number of times larvae touched the substratum versus time spent swimming (seconds).

$r^2 = .09$

$t = 2.95$

$P < .01$

$df = 85$

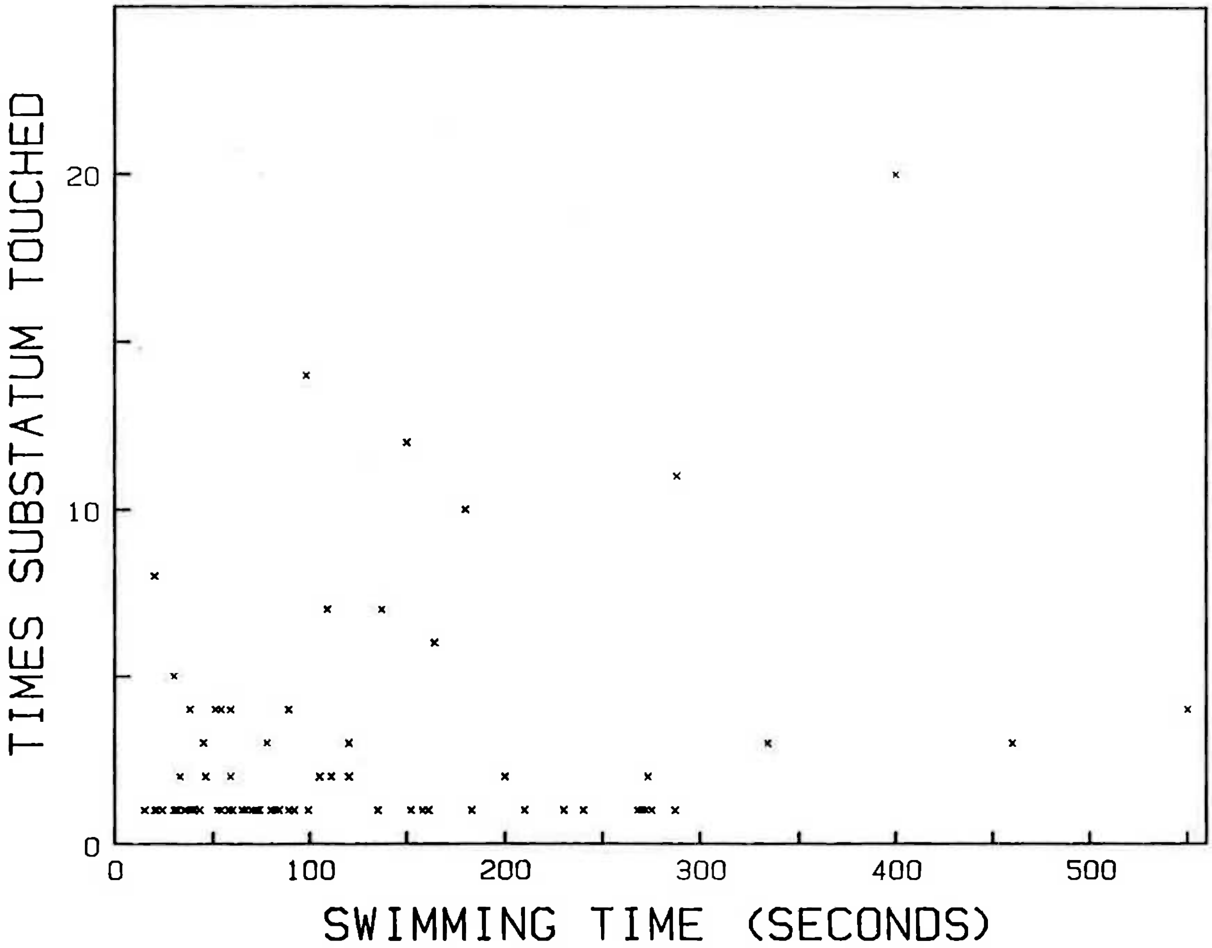

TIMES SUBSTATUM TOUCHED
0
10
20
0
100
200
300
400
500
SWIMMING TIME (SECONDS)

Table 3.1 Fate of larvae followed from their point of release in 1984 and 1985.

Fate of larvae	Year 1984	1985	Totals
Followed to Settlement	90 *	10	100
Lost	146	8	154
Abandoned	4	0	4
Eaten by <u>Culicia tenella</u>	8	4	12
Totals	248	22	270

* Two larvae ingested by clinid fishes, but rejected and went on to settle.

Table 3.2 Distance dispersed from the parent colony by larvae of two 'ages'. Means represent distance moved in metres. Data analysed with a two factor ANOVA. Factors were larval age (fixed) with two levels and year (fixed) with two levels. The factor year and the interaction term were then removed from the model by pooling. Cochran's C=.48 k=4 df=5 ns.

Age of larva	Distance moved (m) mean	SE
Just released	1.5	0.7
Previously attached to a substratum	2.8	1.1

ANOVA TABLE

Source	SS	df	MS	F	P
Treat.	9.03	1	9.03	.95	>.25
Year	0.75	1	0.75	.08	>.5
Treat.xYear	0.24	1	0.24	.03	>.5
Error	151.6	16	9.47		

AFTER POOLING

Source	SS	df	MS	F	P
Treatment	9.03	1	9.03	1.1	>.25
Pooled Residual	152.55	18	8.47		

Table 3.3 Time spent swimming by larvae of two 'ages'. Means represent swimming time in seconds. Data analysed with a two factor ANOVA. Factors were larval age (fixed) with two levels and year (fixed) with two levels. The factor year and the interaction term were then removed from the model by pooling. Cochran's C=.31 k=4 df=5 ns.

Age of larva	Swimming Time mean	 SE
Just released	111	32
Previously attached to a substratum	126	27

ANOVA TABLE

Source	SS	df	MS	F	P
Larval age	2881	1	2881	0.31	>.5
Year	11291	1	11291	1.23	>.25
L x Y	1428	1	1428	0.16	>.5
Error	146896	16	9181		

AFTER POOLING

Source	SS	df	MS	F	P
Larval age	2881	1	2881	0.32	>.5
Pooled residual	159616	18	159616		

Table 3.4 The number of times larvae of two 'ages' touched (encountered) the substratum. Data analysed with a two factor ANOVA. Factors were larval age (fixed) with two levels and year (fixed) with two levels. The factor year and the interaction term were not removed from the model as both had P values less than 0.25. Cochran's C=.51 k=4 df=5 ns.

Age of larva	Times Substratum was touched			
	1984		1985	
	mean	SE	mean	SE
Just released	1.5	0.2	4.2	1.5
Previously attached to a substratum	2.8	1.2	3.0	0.6

ANOVA TABLE

Source	SS	df	MS	F	P
Larval age	0.0	1	0.0	0.0	1.0
Year	10.8	1	10.8	3.0	>0.1
L x Y	7.5	1	7.5	2.1	>0.1
Error	57.0	16	3.6		

3.4 DISCUSSION

The larvae of Podoclavella are pelagic and appear competent to settle as soon as they are released from the parent colony. The average distance moved by a larva was roughly 2m. However, positive skewness was apparent in the frequency distribution of distance moved, indicating that a proportion of the population was moving much further (Fig. 3.2). Calculations from the negative binomial distribution revealed that the probability of a larva moving more than 7m was less than 0.05, yet 13% of the larvae observed dispersed further than this distance.

The maximum distance dispersed by larvae was difficult to determine. On three occassions larvae were followed for more than 20m beyond the parent colony. Rather than relying on direct observations of dispersal a better indicator of the maximum distance larvae were likely to move was their ability to delay metamorphosis. From observations of larvae that were caught by hydroids it appears that larvae were capable of delaying metamorphosis for at least two hours. Using the relationship between swimming time and the distance moved in Figure 3.4, and assuming that it is linear, two hours' swimming represents a dispersal distance of 165m. There are inherent dangers in extrapolating beyond the limits of a data set, particularly one in which the data show considerable scatter. However, this figure of 165m serves as a rough indication that the maximum distance moved by larvae at Edithburgh is in the order of several hundred metres and probably not kilometres.

My observations of swimming larvae indicate that dispersal over distances of even hundreds of metres will seldom be realized, however. The vertical position of sessile invertebrates in the water column may influence the probability of encountering a substratum and therefore the distance moved. Phototaxis has been suggested as a mechanism by which larval fish may alter their vertical position in the water column (Power, 1984) and many invertebrate larvae are photonegative just prior to settlement (Crisp, 1974). Negative phototaxis may ensure that larvae not only settle in favourable microhabitats (Young & Chia, 1984), but also that they do not disperse far. Podoclavella larvae were consistently observed to approach the seabed as distance from the adult colony increased.

Current speed and the availability of suitable substrata for settlement influenced the distance over which larvae were transported. Other ascidian larvae have been observed to prolong swimming activity in the absence of suitable substrata on which to settle (Olson, 1985). The significant relationship between current speed and the distance over which Podoclavella larvae were transported has been observed for other ascidian larvae (Olson, 1985) and is not unexpected, given that invertebrate larvae have rarely been documented as swimming faster than 2cm per second (Mileikovsky, 1973). Olson (1985) also reported that as current speed increased, the variance in the direction of dispersal of the tropical ascidian, Didemnum molle, was decreased. I detected no such decrease in variance despite current speeds exceeding 11cm per second at Edithburgh, while Olson's observations were made in currents that did not exceed 7cm per second. The discrepancy between my observations and those of Olson may be explained by the differences in the relative lengths of the two larvae. The swimming speed of ascidian larvae is directly proportional to their length (Berrill, 1931). As Podoclavella measures 4mm in length, whereas D. molle measures 2.5mm, it seemed that Podoclavella should be a more powerful swimmer and less influenced by currents. However, Olson recorded the swimming speed of D. molle as 2.5cm per second. This estimate, based on the observation of 14 larvae, is considerably faster than the swimming speed expected for an ascidian larva of this size (Berrill, 1931; Berrill's data was plotted by Chia et al., 1984). The measurements of swimming speed obtained by Berrill and Olson are probably underestimates. Their estimates were obtained in the laboratory, although this was not stated explicitly by Berrill, and viscous effects associated with the proximity of the walls of containers were likely to reduce swimming speed. These 'wall effects' may be present even when the walls of containers are upto several hundred body lengths from the larva (Vogel, 1981; Chia et al., 1984). Assuming that Berrill's relationship between length and swimming speed holds for Podoclavella, then a swimming speed of around 3cm per second would be expected for this species. This figure supports my contention that Podoclavella swims more strongly and is therefore less influenced by current speed than D. molle but, without direct measurements of swimming speed in Podoclavella, this figure is merely suggestive.

My ability to follow Podoclavella larvae did not change with time, indicating that my estimates of dispersal were unbiased and therefore representative of the actual distance dispersed, despite the loss of 63% of larvae (Fig. 3.7). Furthermore, these estimates were not influenced by the length of time that the larvae were held in the larval traps. No changes in behaviour were detected between larvae that were just released and those that had been attached previously (Table 3.2, 3.3, 3.4).

Can these estimates of dispersal distance, obtained beneath Edithburgh Jetty, be extrapolated to dispersal on natural substrata? Beneath a jetty the spatial distribution of settlement surfaces, jetty pilings, is very different from that observed on a rocky reef. Only beneath a jetty is a larva likely to encounter a settlement surface in mid-water. Under more natural circumstances a larva would continue to swim until encountering a substratum that was suitable for settlement. Hence the mean distance that a larva is transported would probably be higher on a rocky reef.* However, the range of distances a larva may travel, 5cm to more than 10m or perhaps several hundred metres, should be independent of whether the substrata are pilings beneath a jetty or vertical walls on a rocky reef.

Lecithotrophic larvae, such as those of ascidians, are provisioned with all their nutritional requirements for settlement and metamorphosis. Berrill (1975) considered ascidian larvae to function primarily in habitat selection rather than dispersal. Nevertheless, short distance dispersal has important ecological and evolutionary consequences for populations and species.

Larvae swimming short distances will have a lower probability of finding and therefore utilizing distant habitats which may be better for survival and reproduction (Roughgarden, 1974; Keough & Chernoff, in press). In the face of local environmental disturbance or change the recovery of these 'closed' populations may be slow, thereby increasing the chance of local extinction (Jablonski & Lutz, 1983). These populations may accumulate deleterious mutations associated with inbreeding (Scheltema, 1977). Such consequences are clearly disadvantageous to the establishment and maintenance of populations and ultimately the species. Yet, assuming that the individual derives some benefit from being transported short distances, this outcome is exactly what the theory of evolution would predict. Natural selection operates on the phenotypes expressed by individuals, hence adaptations increasing the fitness of individuals will be selected for even if they are ultimately disadvantageous to the population or the species. My suggestion that the fitness of individuals may be enhanced by short distance dispersal is supported by the theoretical treatment of Metz

*** See addendum on back cover**

et al. (1983). These workers found that fitness was improved by short distance dispersal relative to long distance dispersal in an unpredictable and heterogeneous environment.

Intuitively, short distance dispersal would be expected to decrease gene flow among populations; some population geneticists have however suggested, on the basis of computer simulations, that the exchange of one individual between subpopulations is sufficient to consider these populations panmictic (Frankel & Soulé, 1981; Chambers, 1983). More recently, Vavio et al. (1986) have argued that the equilibrium model used by these workers and their assumption of infinite sub-populations is rarely observed in real populations. With a more realistic model, assuming a finite number of small populations, Vavio et al. demonstrated that genetic differentiation among populations was dependent upon the size and number of these populations. Empirical support for their suggestion that the assumptions of other workers have been too restricted stems from the observations of marked phenotypic and genotypic differentiation among populations that possess larvae which swim only short distances (Sabbadin, 1981; Olson, 1985).

Restricted gene flow may also facilitate adaptation to local environments. Limited dispersal is not a prerequisite for local adaptation, however. Natural selection can result in the local adaptation of populations even in the face of significant gene flow (Struhsaker, 1968; Turkington & Harper, 1979; Ayer, 1985). Differential mortality of larvae or settlers possessing inappropriate genotypes may overcome high levels of gene flow (Burton, 1983; Johnson & Black, 1984; Koehn et al., 1984; Koehn, 1984).

The skewed distribution of dispersal-distances of Podoclavella (Figs 3.2, 3.3) may yield many of the benefits of short distance dispersal and yet reduce the longer term disadvantages. The release of larvae which are competent to settle immediately but are also capable of delaying matamorphosis, should inappropriate substrata be encountered, ensures that a small proportion of larvae are transported relatively large distances. Limited dispersal may account for the variation in colony density that I observed at sites within St Vincent's Gulf (Chapter 2). It is not possible to be confident that this is the case as many factors may act to produce spatial patterns of organisms; nevertheless, the patterns observed are consistent with this suggestion.

One of the major selective forces for short distance dispersal may be the reduction of mortality that results from reducing the length of the planktonic existence. Mortality is considered to be high during the pelagic phase of the life history of marine invertebrates (Thorson, 1950). However, few estimates of larval mortality are based on actual observations. This study and that of Stoner (1986 - abstract only) are, so far as I am aware, the only exceptions. Stoner was able to observe the larvae of the ascidian, Diplosoma similis, and estimated larval mortality at 32%. My observations of larval mortality for Podoclavella were lower and varied between years. Mortality was 3% in 1984 (n=248) and 18% in 1985 (n=22). This variation in mortality is partly explained by the different sample sizes in each year, but also reflects variation in the area of substrata occupied by the predatory coral Culicia tenella downstream of release sites.

Both my observations and those of Stoner are likely to underestimate larval mortality as neither of us could follow the dispersal of larvae to unfavourable sites, and our very presence close to the swimming larva probably scares off mobile predators such as fish. Nevertheless, our estimates of mortality for these lecithotrophic larvae reveal much lower rates of mortality than among planktotrophic larvae (Sastry, 1985). This is not unexpected as lecithotrophic larvae are exposed to risks of predators for much shorter periods of time than are planktotrophic larvae. Furthermore, lecithotrophic larvae represent a much higher energy investment per larva and might therefore be expected to be afforded some means of protection.

The defences of larvae may be structural or chemical. There is clear evidence that some ascidian larvae are chemically defended (Young & Bingham, pers comm) and possess aposematic pigmentation. The conspicous pigmentation of Podoclavella larvae and their rejection by fish indicates that this species may be similarly protected. In a series of elegant experiments Young & Bingham reduced predation on larvae by pigmenting the palatable larvae of one ascidian species with the aposematic coloration of an unpalatable species. Why then do not all ascidian larvae possess chemical defences? Presumably it is energetically expensive to defend larvae with chemicals, hence the degree of protection would be expected to reflect the relative risks to which the larvae of each species are exposed. An alternative explanation is that unprotected species have not (yet?) developed the genetic machinery to produce chemical defenses. I do not favor this latter hypothesis as the palatable species with which Young & Bingham experimented was a Clavelinid, a member of the same family as Podoclavella.

Ascidian tadpole larvae may also possess a structural defense, their tail. Muscular contractions, although primarily for locomotion, also allow larvae to break free from substrata. For example, a larva may, upon contacting a cnidarian, be held by the nematocysts but not harmed. This is regularly observed when Podoclavella contacts the hydroid Ophiodissa australis. Podoclavella larvae break away from this cnidarian by vigorous beating of their tails, whilst larvae which move by the beating of cilia would have no such means of escape.

At settlement Podoclavella larvae were capable of discriminating among substrata, rejecting substrata up to 19 times prior to settling. However, more than half of the larvae observed settled on their first encounter with the substratum. The length of time that larvae had been swimming appeared to influence how discerning they were at settlement; larvae showed a significant positive relationship between swimming time and the number of times the substratum was encountered. However, on closer scrutiny the plot of swimming time and the number of times Podoclavella encountered the substratum (Fig. 3.9) revealed that the significant relationship hinged on a single outlying data point. After removal of this data point no relationship was detected. It would be unwise to draw inferences about changes in the settlement behaviour of larvae with time, from this data set. The effect of substratum type on the settlement behaviour of larvae will be considered further in Chapter 4.

Limited dispersal imposes definite evolutionary and ecological constraints on populations. Such populations may be regarded as effectively closed. Hence, spatial and temporal patterns in recruitment to these populations are highly predictable and directly proportional to the size of the resident adult population. Consequently local factors, such as disturbance, predation and competition would be expected to have a profound influence on the size and persistence of local populations.

CHAPTER FOUR

Patterns of Recruitment: settlement and post-settlement mortality

4.1 INTRODUCTION

The settlement of planktonic larvae is dependent upon two variables: the number of larvae encountering a substratum (Gaines *et al.*, 1985; Olson, 1985) and the behaviour of those larvae upon encountering that substratum (Grosberg, 1981; Young and Chia, 1981). After larvae have metamorphosed, post-settlement mortality will determine the level of recruitment. In this thesis settlement will be defined as the attachment and metamorphosis of a larva on a substratum whereas recruitment will be considered the survival of that larva until censused by an observer (as done, for example, by Keough & Downes, 1982).

The discriminatory behaviour of planktonic larvae at settlement is well documented (Wilson, 1952; Crisp & Barnes, 1954; Meadows & Campbell, 1972) and may ensure improved survival of settlers (But see Harriot, 1983). Settlement may be influenced by the physical or biological nature of the substratum (Scheltema, 1974; Crisp, 1976). The physical nature of the substratum can also influence post-settlement mortality; survival for some species is highest in concavities (Connell, 1961; Keough & Downes, 1982). Post-settlement mortality on biological substrata has rarely been examined but may influence the preference of larvae for some substrata (Doyle, 1975).

The number of larvae settling can be an important determinant of adult distribution and abundance (Connell, 1985a) and even community structure (Gaines & Roughgarden, 1985). These studies indicate that ignoring the input of propagules from the plankton, as do many models of community structure and dynamics (Connell,1975; Menge & Sutherland, 1976; Paine, 1980, 1984; but see Roughgarden et al., 1985), may be inappropriate in some cases. This chapter is split into three sections and examines the relative importance of initial settlement and subsequent survival of settlers in influencing patterns of adult distribution and abundance.

Each of the following sections is self contained, with an introduction, methods, results and finally an interpretation subsection. Most of the work reported in this chapter was performed at one site, Edithburgh Jetty. Where appropriate and feasible, additional work was conducted on the inner reef at Port Noarlunga.

4.2 PATTERNS OF RECRUITMENT

Introduction

It is often extremely difficult to estimate the initial settlement of planktonic propagules. Larvae are invariably small and are often difficult to see and confidently identify with the unaided eye. Measuring patterns of recruitment represents a more convenient means of assessing the input of sexually derived products into the population, but fails to distinguish between settlement and pre-recruitment mortality. Estimates of recruitment do however provide an indication whether the patterns of adult distribution and abundance are produced by processes occurring before or after recruitment.

In this section I ask: do patterns of recruitment correspond to the distribution and abundance of adult colonies? Patterns of adult distribution and abundance were established in Chapter 2; adult colonies were observed on some substrata, particularly some sponge species, more often than expected given a random allocation of colonies (Fig. 2.4) and were seldom seen on horizontal faces (Table 2.4). Recruitment was therefore estimated on naturally occurring substrata (that is, sponges, ascidians and vacant space) and on vertical and upward-facing horizontal surfaces.

The relationship between the number of recruits in permanent quadrats and the number of adult colonies in the same quadrats 11 months later was also examined.

In the remaining sections of this chapter the questions addressed were: what are the relative contributions of settlement and post-settlement mortality to the patterns of recruitment that I observe on i) naturally occurring substrata (Section 4.3) and ii) vertical and horizontal faces (Section 4.4).

Materials and Methods

Podoclavella larvae were released for roughly six weeks, beginning in November, during each year of this study. Approximately three weeks after settlement had begun, patterns of recruitment were examined on vertical and horizontal surfaces and on a range of naturally occurring substrata.

Recruitment of *Podoclavella* onto encrusting animals and naturally occurring bare space was estimated with 149 quadrats each measuring 12.5x17.5cm and placed haphazardly on 30 pilings. This quadrat size was small enough to be occupied by one substratum type (e.g. an ascidian colony) yet large enough to yield an adequate number of recruits. To simplify the analysis, recruits were not counted unless an estimated 95% of the quadrat was covered by one type of substratum. To facilitate the satisfaction of this criterion, the quadrat was rotated around one of its corners, after the initial placement, until the dominant substratum covered more than 95% of the quadrat. If this criterion could not be met after rotating the quadrat through a maximum of 45°, then the quadrat was placed elsewhere. Following placement the number of recruits in the quadrat was counted and the type of substratum recorded.

Expected frequencies of recruits for a substratum were calculated by multiplying the mean number of recruits within all quadrats by the number of quadrats falling on that substratum. Observed and expected frequencies were then compared for goodness of fit.

Recruitment on vertical and horizontal rock surfaces and wooden surfaces was examined at Edithburgh Jetty with quadrats measuring $81cm^2$. Recruitment on vertical and horizontal rock surfaces was also investigated at Port Noarlunga, but owing to the lower numbers of recruits observed at this site, quadrat size was increased to $324cm^2$. At both sites, quadrats were placed haphazardly onto these surfaces and the number of recruits counted within each quadrat.

The relationship between recruit density and the number of adult colonies in permanent quadrats was examined at Edithburgh Jetty. If recruit mortality is independent of their density then a positive relationship would be expected between the number of recruits in a quadrat and the number of adults in that same quadrat some time later. Counts of the number of recruits in permanently marked $0.17m^2$ quadrats were made within a month of the appearance of recruits at Edithburgh Jetty in 1984 (n=35) and 1985 (n=36). Counts of the number of adult colonies were made 11 months later in these same quadrats. The percentage mortality of recruits per quadrat was calculated and plotted against recruit density for each year. In addition, the number of recruits were plotted against the number of adult colonies in the same quadrats 11 months later.

Results

Recuitment patterns on naturally occurring substrata differed significantly from that expected if the recruits had been positioned randomly (X^2=2329.2 df=7 P<.001, Fig. 4.2-1). Of the 149 quadrats monitored, 148 were dominated by sponges or bare space. Four sponge species, *Tedania* sp.B (SP51), *Dendrilla rosea* Lendenfeld (SP1), *Dendrocia* sp. (SP30) and particularly *Mycale* sp. (SP20), received lower numbers of recruits than expected. The recruitment observed upon *Tedania* sp.A (SP50) and *Ulosa* sp. (SP48) was close to that expected. Much higher recruitment was observed than expected on bare space and

Euryspongia sp.(SP46). On bare space recruitment was close to three times that expected and on Euryspongia sp. almost twice that expected.

The rank correlation between recruit and adult densities on these substrata was low (Kendall's tau= .24, N= 10, n= 7, $P > .05$, N is the numerator of Kendall's tau and tabulated values for this stastistic are given by Sokal & Rohlf, 1969 p.537, Table 4.2-1). Hence the patterns of recruitment and the distribution and abundance of adults were significantly different.

Recruitment was substantially higher on vertical than on horizontal faces (Table 4.2-2). This recruitment pattern was consistent at both sites and on rock and wooden substrata at Edithburgh. Futhermore, comparison of this pattern with the distribution and abundance of adult colonies on vertical and horizontal surfaces revealed a perfect rank correlation (c.f. Table 4.2-2 with Table 2.4).

The mortality of recruits was not independent of density (Fig. 4.2-2). Mortality was 100% at densities of below 0.2 recruits per dm^2 in 1984-1985 and 0.8 recruits per dm^2 in 1985-1986. The percent mortality then fell, sometimes to as low as 20%, as density increased to around 1 recruit per dm^2 and subsequently increased to almost 100% as recruit density approached 10 or more per dm^2. This pattern was particularly clear in the 1984-1985 data set and was consistent over the two time periods, although mortality was markedly higher in 1985-1986. Despite the dependence of recruit mortality on their density a significant positive relationship between recruit and adult number was apparent in both time intervals (1984-1985, t= 8.9 df= 33 $P < .001$ $r^2 = .70$; 1985-1986, t=2.6 df= 28 $P < .05$ $r^2 = .20$, Fig. 4.2-3).

Peripheral to this chapter, but noteworthy nevertheless, was the two-fold difference in recruitment between rock and wooden substrata.

Figure 4.2-1 Observed and expected recruit densities of Podoclavella for bare wood and several sponge species. Unidentified sponges include Aplysilla sulphurea and four unidentified species. (148 of the 149 quadrats were dominated by sponges or bare space). Note the log scale on the Y axis.

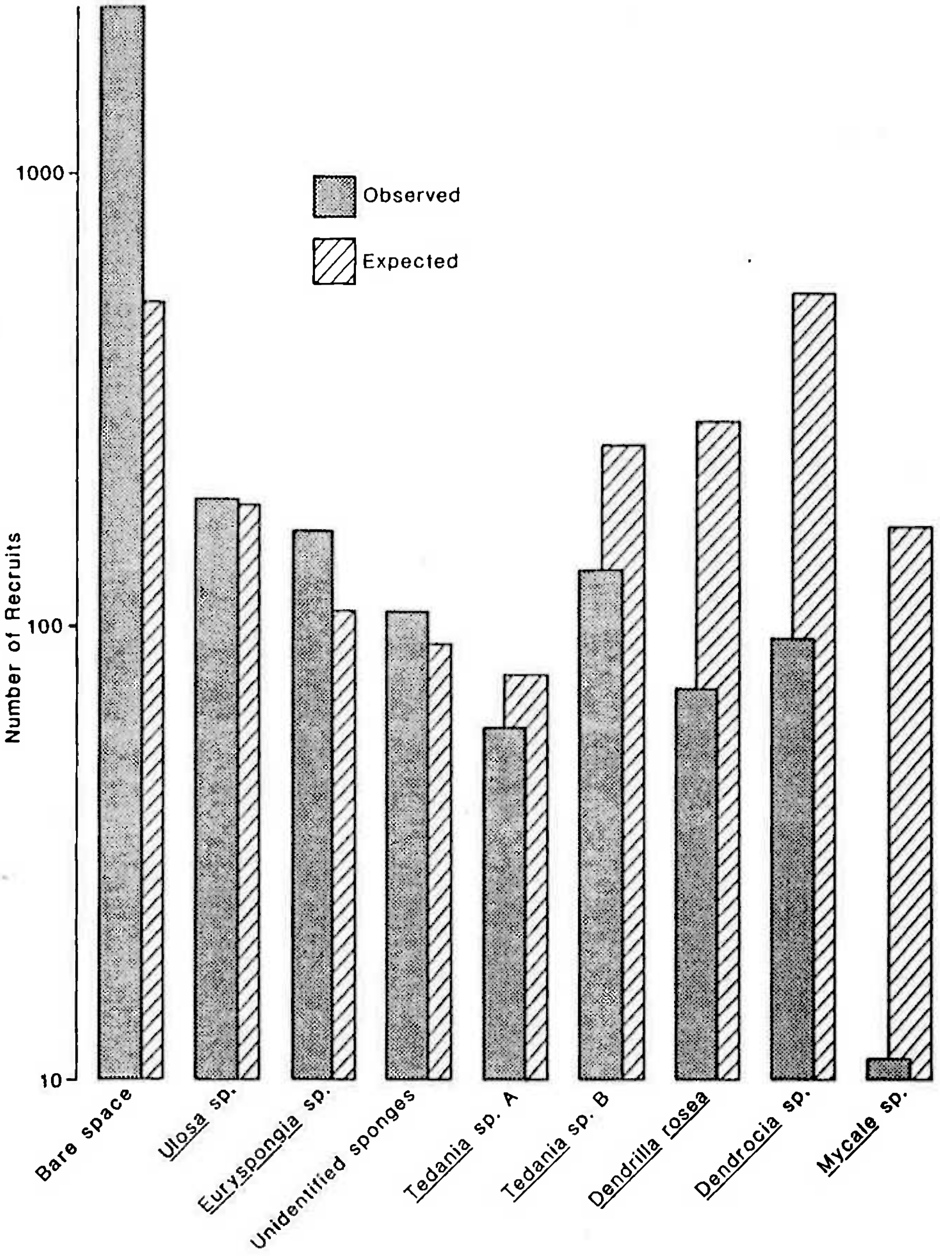
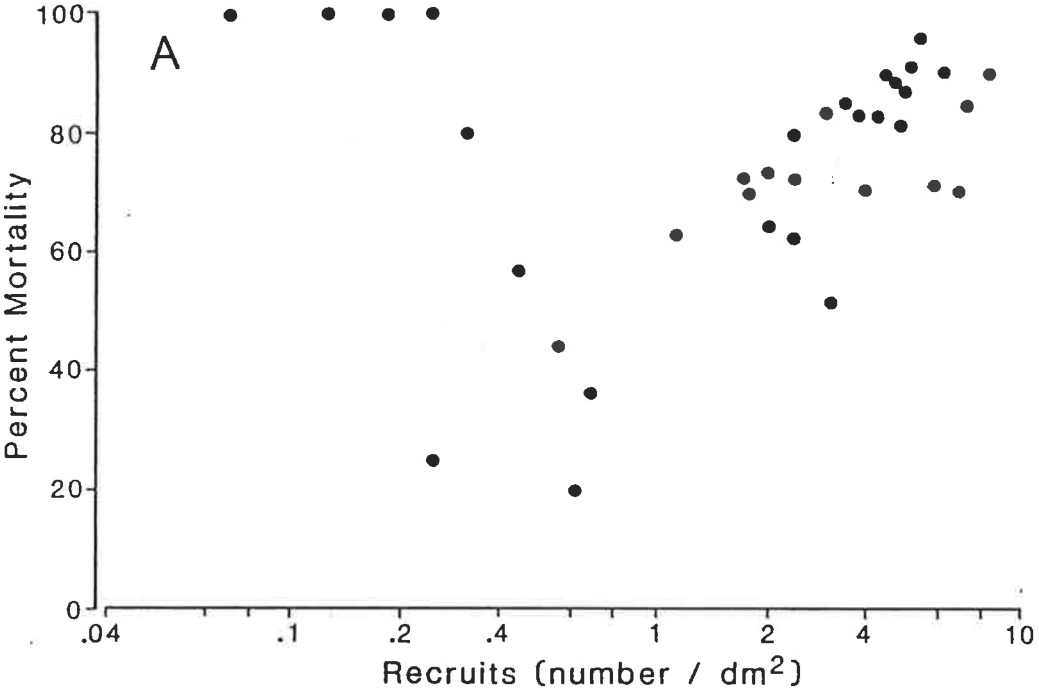

Number of Recruits
1000
100
10
Observed
Expected
Bare space
Ulosa sp.
Euryspongia sp.
Unidentified sponges
Tedania sp. A
Tedania sp. B
Dendrilla rosea
Dendrocia sp.
Mycale sp.

Figure 4.2-2 Percent mortality in the first 11 months following recruitment versus recruit density. Counts were done in permanently marked 0.18m^2 quadrats at Edithburgh. Each point represents one quadrat.

A 1984 recruits

B 1985 recruits


A
Percent Mortality
100
80
60
40
20
0
.04
.1
.2
.4
1
2
4
10
Recruits (number / dm2)

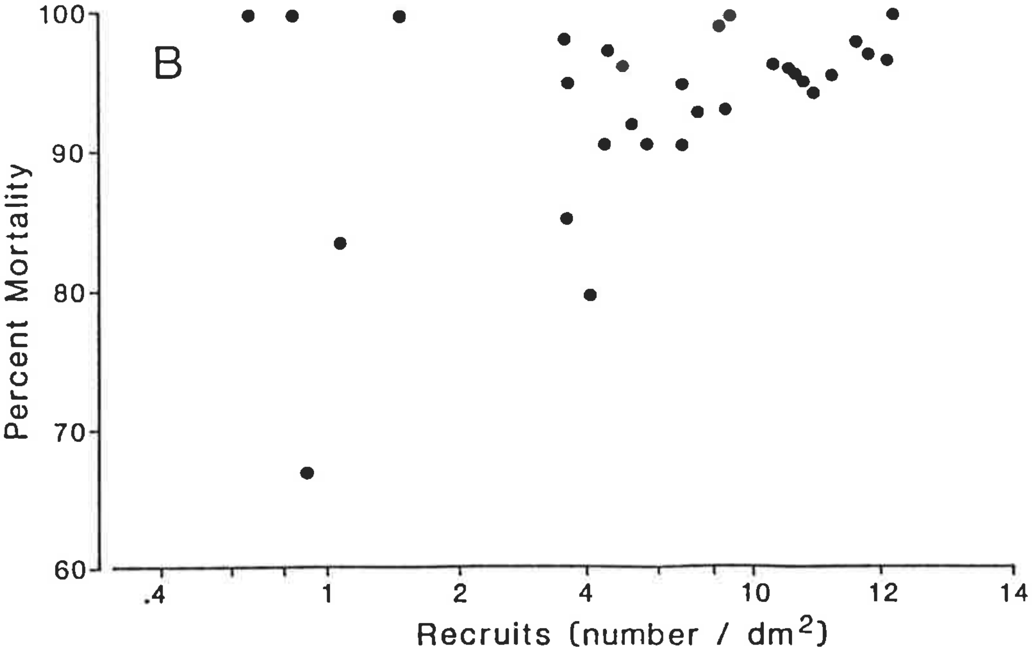
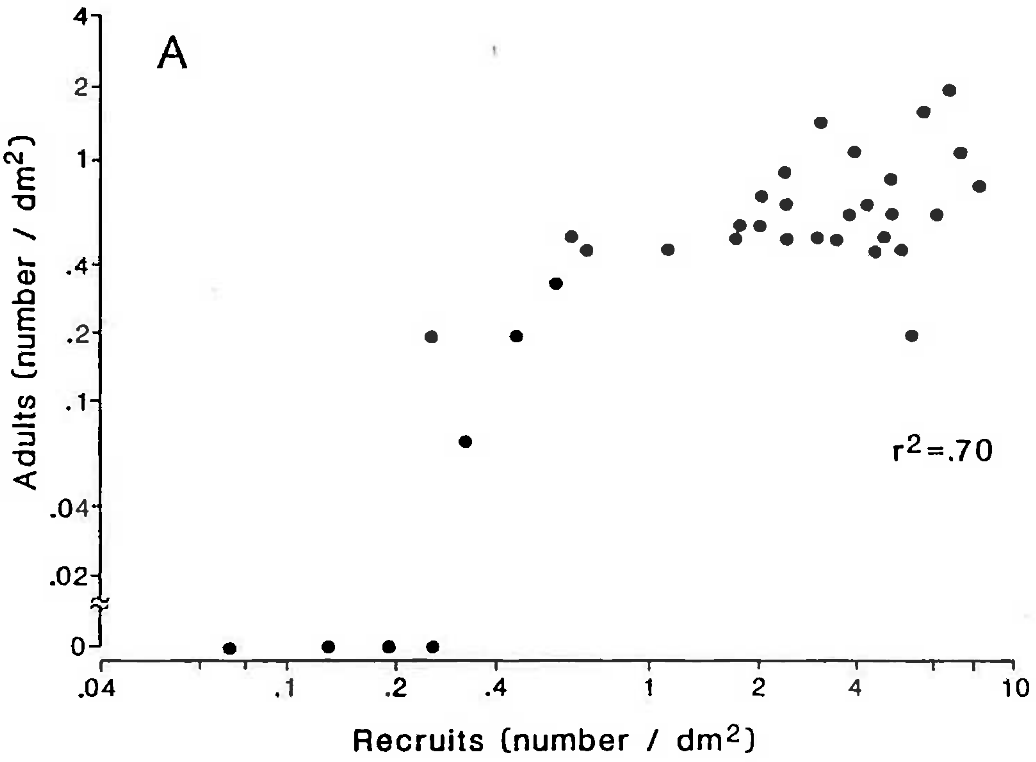

B
Percent Mortality
100
90
80
70
60
.4
1
2
4
10
12
14
Recruits (number / dm2)

Figure 4.2-3 Density of adult colonies (11 months after recruitment) versus the density of recruits in the same quadrats at Edithburgh Jetty. Each point represents one quadrat.

A 1984 recruits

B 1985 recruits


A
r^2=.70
Adults (number / dm^2)
4
2
1
.4
.2
.1
.04
.02
0
.04
.1
.2
.4
1
2
4
10
Recruits (number / dm^2)

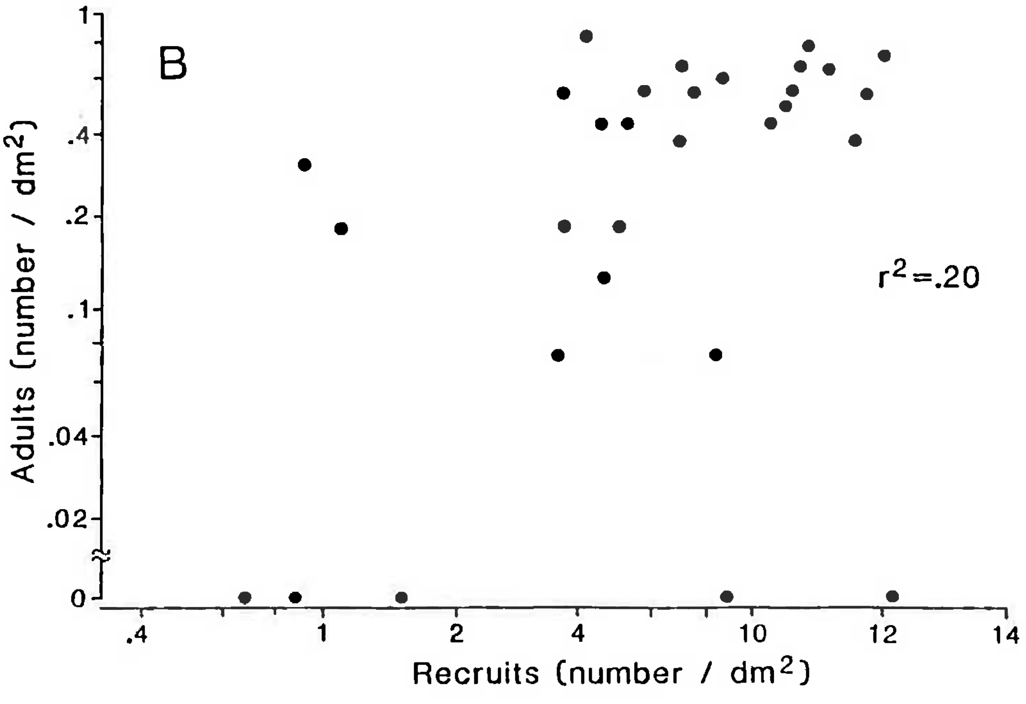

B
r^2=.20
Adults (number / dm^2)
1
.4
.2
.1
.04
.02
0
.4
1
2
4
10
12
14
Recruits (number / dm^2)

Table 4.2-1 Rank correlation of recruitment and adult density on naturally occurring substrata at Edithburgh Jetty. Note quadrat sizes are different, $0.022cm^2$ for recruits and $0.044cm^2$ for adult colonies.

SUBSTRATUM	RECRUITS		ADULTS	
	Mean No. per Quadrat	Rank	Mean No. per Quadrat	Rank
Bare Space	42.3	1	1.2	4
Euryspongia sp.	23.1	2	6.5	1
Ulosa sp.	15.8	3	0	7
Tedania sp A	11.8	*	-	*
Tedania sp B	8	4	4.5	2
Dendrilla rosea	3.8	5	0.7	5
Dendrocia sp.	2.5	6	2.5	3
Mycale sp.	0.9	7	0.5	6

Kendalls Tau = .24 N = 10 n = 7 ns

* not ranked as no quadrats fell on this species during estimates of adult colony density

Table 4.2-2 Recruitment of Podoclavella onto vertical and horizontal surfaces measured approximately three weeks after settlement began. Quadrat size was 81cm^2 at Edithburgh (n=10) and 324cm^2 at Port Noarlunga (n=15). 95% C.I. represents the 95% confidence interval around the mean.

Site	Substratum	Horizontal Surface		Vertical Surface	
		$\bar{x}$	95% C.I.	$\bar{x}$	95% C.I.
Edithburgh Jetty	Jarrah	0.2	0.3	61.6	37.3
	Limestone	0	0	12.4	5.1
Port Noarlunga Reef	Aeolionite	0	0	0.2	0.2

Interpretation

Patterns of recruitment of Podoclavella were not random, but were dependent on the substratum type and the orientation of surfaces. Recruitment onto vertical and horizontal surfaces corresponded closely with the distribution and abundance of adult colonies observed in Chapter 2. Recruits and adult colonies were only rarely observed on horizontal upward facing surfaces. No such correspondence was observed between recruit and adult patterns of distribution and abundance on encrusting substrata and naturally occurring vacant space. For example, bare space had almost three fold the number of recruits expected, but less than two thirds of the adult colonies expected (Fig. 2.4). Similarly, Dendrocia sp. received less than one fifth of the number of recruits expected but more adult colonies than expected.

The lack of congruence between recruits and adult distribution and abundance on these substrata does not necessarily indicate that processes occurring after recruitment are more important in determining these patterns than pre-recruitment processes. The community at Edithburgh is dynamic, with up to 20% of the substratum changing hands, that is vacated or grown over, every three months (Kay & Butler, 1983). Hence, the significance of pre-recruitment processes may be masked by interactions among the encrusting substrata. For example, should Podoclavella recruit heavily on bare space which subsequently becomes overgrown by neighbouring sponge species, then Podoclavella colonies will appear to have established on a sponge and not vacant space. In this hypothetical scenario the patterns of distribution and abundance of adult Podoclavella colonies would reflect the ability of the sponge species to encroach upon vacant space and the significance of this space to the recruitment of Podoclavella would be obscured.

The patterns of recruitment observed in this section may stem from differences in the rate of encounter of the substrata or faces, active choice by larvae, or the modification of patterns of settlement by post-settlement mortality. In the remainder of this chapter I examine the relative contributions of these factors to the patterns of recruitment observed.

A significant positive relationship existed between the number of recruits in a quadrat at Edithburgh and the number of adult colonies present in the same quadrat 11 months later. This finding was consistent in 1984-1985 and 1985-1986. Hence, the density of adult colonies may be inferred from the number of recruits that are present in the previous year. This inference could be made confidently in 1984-1985 as the variability in the relationship was low (r^2= .70). However, in 1985-1986 variability was much higher (r^2= .20).

A non-linear relationship was apparent between recruit density and the percentage mortality. Positive density dependence was apparent at low to medium densities (less than 1 recruit per dm^2), while at medium to high densities of recruits mortality showed a negative density dependence. A similar pattern was observed between the density of settlers and their mortality in the intertidal barnacle Tesseropora rosea (Connell, 1985a, Figs 1,2). Connell also noted that among low shore populations of the intertidal barnacle Balanus balanoides, mortality was high at both low and high densities of recruits. Adults were only produced at moderate recruit densities in these low shore populations. Connell suggested that predators were responsible for high mortality among low densities of recruits, while the formation of unstable, 'hummocked' sheets which subsequently fell off produced high mortality among high densities of recruits. Gaines & Roughgarden (1985) also reported high levels of mortality associated with predation by the starfish Pisaster ochraceus on high densities of recruits of the barnacle Balanus glandula. The agents of mortality on high and low densities of Podoclavella were not identified.

It was noteworthy that recruitment onto wood was five fold higher than on rock surfaces at Edithburgh. However, the purpose of these estimates of recruitment was to assess the generality of patterns of recruitment on surfaces of different orientation. There was no intention of examining the effect of substratum type on the total level of recruitment. Without experimental evidence it was not possible to determine whether the differences in settlement on rock and wood surfaces stemmed from different rates of encounter, active choice by the larvae, or differential mortality.

*

*** See addendum on back cover**

4.3 SETTLEMENT PREFERENCES AND POST-SETTLEMENT SURVIVAL ON NATURALLY OCCURRING SUBSTRATA

Introduction

Podoclavella is a facultative epibiont, often settling on living organisms as well as non-living substrata. In a diverse, subtidal, epifaunal community, these larvae can potentially encounter a large number of suitable substrata. Larval preferences for these substrata and the subsequent mortality of newly settled juveniles will determine the level of recruitment, but it cannot be assumed from the outset that either is estimable from recruitment.

Workers have distinguished the contribution of active larval choice and post-settlement mortality by sampling substrata over short time intervals (Strathmann *et al.*, 1981; Luckenbach, 1984; Caffey, 1985; Woodin, 1985). However, the interval between settlement and monitoring must be very short if this approach is to be used with confidence (Keough & Downes, 1982).

Larval settlement and the fate of newly settled juveniles were determined on several encrusting substrata (sponges) and naturally occurring bare space. The aim was to distinguish between the contribution of active larval choice and post-settlement mortality to patterns of recruitment observed in the field. In addition, the basis for the selection of substrata by larvae was examined by conducting settlement trials with extracts of sponge substrata. The large size and conspicuous pigmentation of *Podoclavella* larvae facilitated these observations.

Materials and Methods

i) Settlement Preferences

Selected substrata: Following the collection of the recruitment data, five substrata were selected for more detailed investigation of settlement preferences and survival. Their selection was based upon the level of recruitment they received; they spanned a wide range of recruitment levels, from much higher than expected to considerably lower than expected. The substrata chosen were naturally occurring bare space and four species of sponge; Dendrocia sp. (SP30), Euryspongia sp. (SP46), Mycale sp. (SP20), and Ulosa sp. (SP48).

The preferences of larvae to settle on different substrata were investigated by following larvae underwater and observing settlement. To ensure a ready supply of larvae, the traps described in Chapter 3 were fixed over five adult colonies. Larvae invariably swam into the uppermost jars after release. When a larva appeared, the jar was removed from the trap and the larva released into the water column. The larva was then followed, taking care not to disrupt its swimming or the water flow impinging upon it, and the outcome (settlement or rejection) of its first encounter with a substratum was recorded. Where possible the time spent swimming by the larva from release to this initial encounter was also noted.

Settlement was readily distinguished from rejection in Podoclavella, see p.50.

To assess the relationship between the number of settlers and the amount of bare space and epifauna associated with each species of sponge, the availability of bare space was determined from tracings of nine, 81cm^2 quadrats on each sponge species. Two species of epifauna were common on these sponges, the hydroid Ophiodissa australis (Bale) and a spionid polychaete Pseudopolydora sp. The numbers of epifauna (counts of hydroid stems and spionid polychaete tubes were pooled) were counted in 100 haphazardly placed 2x2cm quadrats on each of the four sponge species.

Chemical basis for settlement preferences: Settlement trials were conducted with extracts of one of the sponges, Mycale sp. Two sets of trials were performed in 70ml containers in the field. In the first set, larval settlement was examined with sponge extract of an unknown concentration. The second set of trials exposed larvae to four concentrations of extract; none (control), half natural (see below), natural, and twice natural.

Sponge extract for the first set of trials was prepared from 1.12kg of frozen Mycale sp. The sponge was broken into pieces, blended (Waring blender) with distilled acetone (6 litres) and filtered under vacuum through a celite pad. Most of the acetone was evaporated in vacuo to provide an aqueous residue (800ml). The aqueous solution was extracted with distilled diethyl ether (400ml, three times) and dryed over anhydrous $MgSO_4$. The ether was removed in vacuo to provide a deeply coloured viscous oil (2.99g). The resulting extract was then diluted with ether and pipetted onto filter paper and left to dry. On the controls only ether was pipetted onto the filter paper. Within one hour of pipetting the extracts were used in settlement trials.

The appropriate concentration of extract for use in the second set of trials was calculated from sponge samples of known area. Concentrations were based on area measurements rather than sponge volume as chemical substances used as inhibitors of fouling are likely to be concentrated at the sponge surface and Mycale sp. possesses a thin encrusting growth form. Three pieces of sponge measuring 9.5x9.5cm were removed from pilings and extracted as above. These fragments yielded, on average, 136mg of extract (SE= 4.0). Hence, in trials a concentration of about 1.5 mg per cm^2 was considered a 'natural' concentration.

Extract and controls (ether but no extract) were exposed to larvae in 70ml screw top plastic containers. Filter paper with sponge extract pipetted onto it was pressed into the lid of the container. The control for all trials was filter paper with ether pipetted onto it. Larvae were introduced into the plastic containers underwater, a single larva per trial, and the filter paper top screwed on. The container was then turned so that the filter paper was facing down. The time to settlement and the substratum settled upon (i.e. filter paper or plastic) were recorded. Trials were terminated after ten minutes even if larvae had not settled. The data were analysed with contingency tables.

ii) Post-settlement Survival

Post-settlement survival was examined on the same five substrata on which settlement was observed. For each of these substrata three pilings were selected and on each piling three areas were delineated, measuring $81cm^2$. The criteria for placing these areas on a piling were that areas were between 0.5 and 4m above the sea bed and were as close to 100% cover of the substratum assigned to that piling as possible. A small galvanized iron nail marked the top left hand corner of each area. Two sets of three pilings were selected for the bare space substratum, one on the upcurrent side of the jetty and the other on the downcurrent side (despite the bidirectional tidal currents referred to in Chapter 2, high tide was usually in the afternoon and so the current was flowing north during the release of larvae). Settlement was expected to be higher on the downcurrent bare quadrats, thereby representing a potentially important source of variation that required quantification. The distinction between upcurrent and downcurrent sides of the jetty was not made for the sponge substrata. The four sponge substrata were each represented by nine areas, and bare space by 18, giving a total of 54 areas.

Survival was monitored in these areas daily for 30 consecutive days. Observations commenced on November 1, 1984, just as adult colonies were beginning to release larvae. Prior to this date no larvae had settled on the delineated areas. Each afternoon the positions of settling larvae were mapped onto acetate sheets supported just above the substratum by a small perspex 'table'. Disappearance of previously settled animals was also recorded.

Areas were monitored in the late afternoon because most Podoclavella were released and settled around midday. This reduced the time in which mortality, prior to my monitoring, could occur. Resorption of the larval tail after settlement allowed me to distinguish recent settlers from older settlers. In Podoclavella, tail resorption takes five to six hours and so an incompletely resorbed tail indicated that a recruit had just settled. Settlement of other species was rare during this experiment and was not recorded.

Survivorship curves were compared by fitting a Cox proportional hazards regression model to the curves (Hopkins, 1983). All survival analyses were performed with BMDP survival packages 1L and 2L.

As the 54 areas in this experiment were monitored daily, it was possible to investigate the relationship between settlement and the number of survivors (recruits) remaining at the end of the 30 day period of monitoring. Regression analysis was used to examine this relationship.

The number of larvae that disappeared in the first few hours following settlement could not be determined by the survival experiment. Survival in these few hours of potentially great vulnerability was examined more closely on three of the five substrata, namely, bare space, Dendrocia sp. and Mycale sp. Two areas measuring 21x30cm were marked on each of these substrata. Just after midday the positions of new settlers were mapped onto acetate sheets. Between 2.25 and 4 hours later the mapping procedure was repeated and the number of animals remaining was determined.

Results

i) Settlement Preferences

Selected Substrata: There were significant differences in settlement preferences between substrata for the 84 encounters recorded (X^2=34.2 df=4 P<.001, Fig. 4.3-1). An a posteriori test by Simultaneous Test Procedure (STP - Sokal and Rohlf, 1969 p.582) revealed that significantly more larvae settled upon bare space and Euryspongia sp., at first encounter, than upon Dendrocia sp. and Mycale sp. Settlement on Ulosa sp. was not significantly different from either of these groups. Preferences for Euryspongia sp. must be interpreted cautiously, owing to the low number of settlement observations.

Larvae usually rejected the unfouled surface of sponges, settling instead on patches of bare space or epifauna associated with the sponges. Few sponges have a uniform surface; they are usually pock marked with patches of bare space or some form of epifauna. There were consistent differences in the amount of bare space and epifauna between species of sponge (Table 4.3-1). For example, the presence of bare space is dependent upon the growth form of the sponge. Thin encrusting sponges e.g. Ulosa sp. and Mycale sp., are more likely to have patches of bare space than a sponge with a massive growth form, e.g. Euryspongia sp. These bare patches may result from damage, as is the case with Dendrocia sp. and Mycale sp., or fragmentary growth, as in Euryspongia sp.

Differences, significant at the 5% level, in the amount of epifauna on each sponge species were also detected (One Way ANOVA, F=155.3 df=3,396 $P < .001$; Tukeys HSD= 1.9; variances heterogeneous, Cochrans C = 0.45). Epifauna were sparse on Mycale sp. and Dendrocia sp., on average, with 5.5 or less spionid tubes and hydroid stems per $4cm^2$. Epifauna were three to four times more common on Euryspongia sp. and Ulosa sp. Settlement was greater on sponges that had a high cover of bare space or epifauna associated with them (Table 4.3-1).

Chemical basis for settlement preferences: The first set of settlement trials with extracts of Mycale sp. indicated that chemical substances within this sponge significantly inhibited settlement onto filter paper (G=13.1 df=1 $P < .01$, Table 4.3-2). However, total settlement in the 48 trials, irrespective of the surface settled upon (plastic or filter paper), was independent of the presence or absence of sponge extract (G=3.1 df=1 $P > .05$, Table 4.3-3).

The second set of trials indicated that the inhibition of settlement on the filter paper was dependent on the concentration of the extract (G=11.1 df=3 $P < .05$, Table 4.3-4). A-posteriori comparisons using STP revealed that settlement was significantly inhibited by the twice 'natural' concentration of extract relative to the control. Interpretation of further comparisons was hampered by illogical results (see Underwood (1981) p.530 for a discussion of these).

ii) Post-settlement Survival

Survival was recorded for over 1250 Podoclavella settlers arriving on the five substrata; more than half of these animals (772) were still alive after 30 days (Table 4.3-5). Survivorship curves and median survival estimates, generated for the 30 day period of monitoring, differed between the five substrata (Fig. 4.3-2, Table 4.3-5). Survival showed a very similar pattern to that of settlement. It was very high on bare wood, with over 85% survival in the first four days following settlement on the southern pilings, ranging to low on the sponges Dendrocia sp. and Mycale sp.

The effect of substratum, piling and depth on survival was tested using the Cox proportional hazards regression model. These effects were included in the model as dummy variables. Terms in the model that did not explain a significant amount of variation in survival at the 0.05 level of significance were removed. The elimination of the five substrata from this truncated model revealed that substrata explained a significant amount of the variation in recruit survival (X^2=93.5, d.f.=5, P<.001). In addition to this main effect, several other terms remained in the truncated model indicating that they too accounted for a significant amount of the variation in survival. These terms included depth on bare space (south) and depth and piling terms on bare space (north) and Ulosa sp. These effects show the variability inherent in this dynamic system. Survival varied within some substrata.

In this experiment, post-settlement mortality (within 30 days of settlement) showed a significant negative relationship with settlement density; considerable scatter was apparent in this relationship (r^2= .05, Fig. 4.3-3). The density of settlers showed a strong positive relationship with the density of recruits; 86% of the variation in recruitment was explained by settlement (Fig 4.3-4, Table 4.3-6).

Losses in the first few hours following settlement were very low, indicating that the survival estimates obtained from the longer term experiment were reliable. Of the 93 new recruits observed only 2 disappeared. No losses were recorded from bare space (Table 4.3-7).

Figure 4.3-1 Number of larvae accepting (settling) and rejecting bare space and four species of sponge on first encounter. An *a posteriori* test by simultaneous test procedure (Sokal & Rohlf, 1969 p.582) revealed that *Euryspongia* sp., bare space and *Ulosa* sp. formed a homogenous group at the 5% level of significance. Similarly *Ulosa* sp., *Dendrocia* sp. and *Mycale* sp. formed a homogenous group at this level of significance.

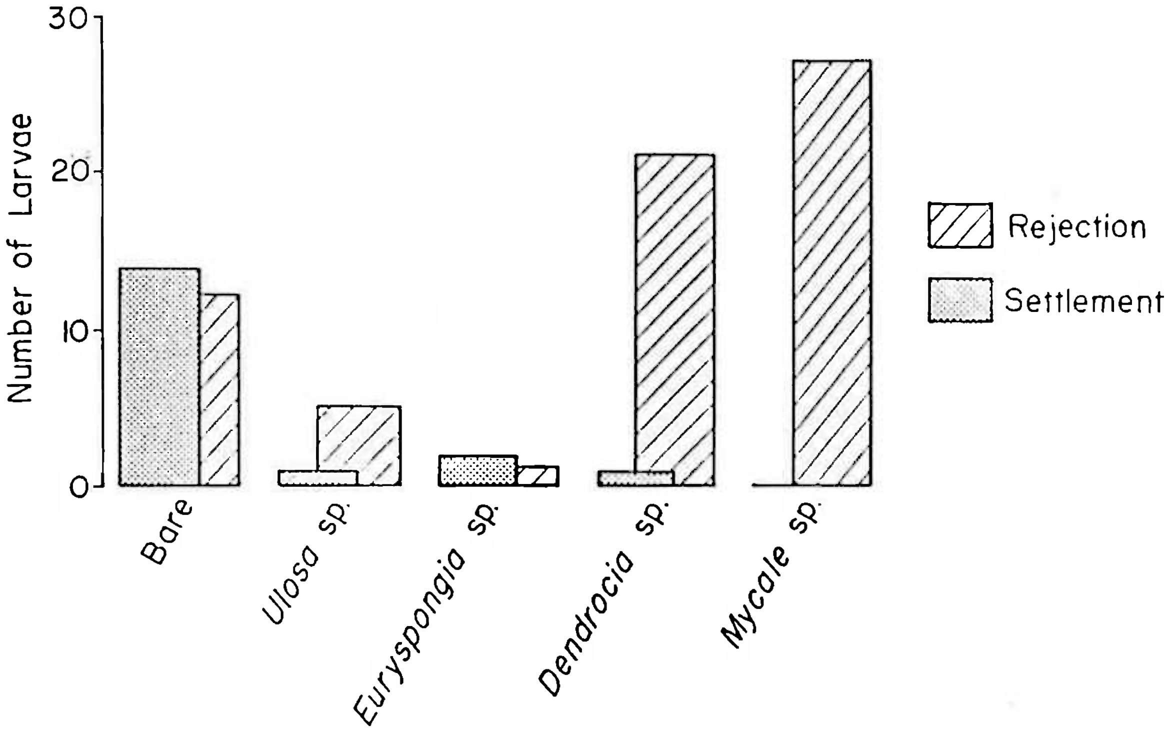

Number of Larvae
30
20
10
0
Rejection
Settlement
Bare
Ulosa sp.
Euryspongia sp.
Dendrocia sp.
Mycale sp.

Figure 4.3-2 Survivorship curves of settled Podoclavella larvae for the five substrata. Note survivorship for bare space on the northern and southern sides of jetty are plotted. Plots were generated by the actuarial life table method (Cutler & Ederer, 1958) BMDP survival package 1L.

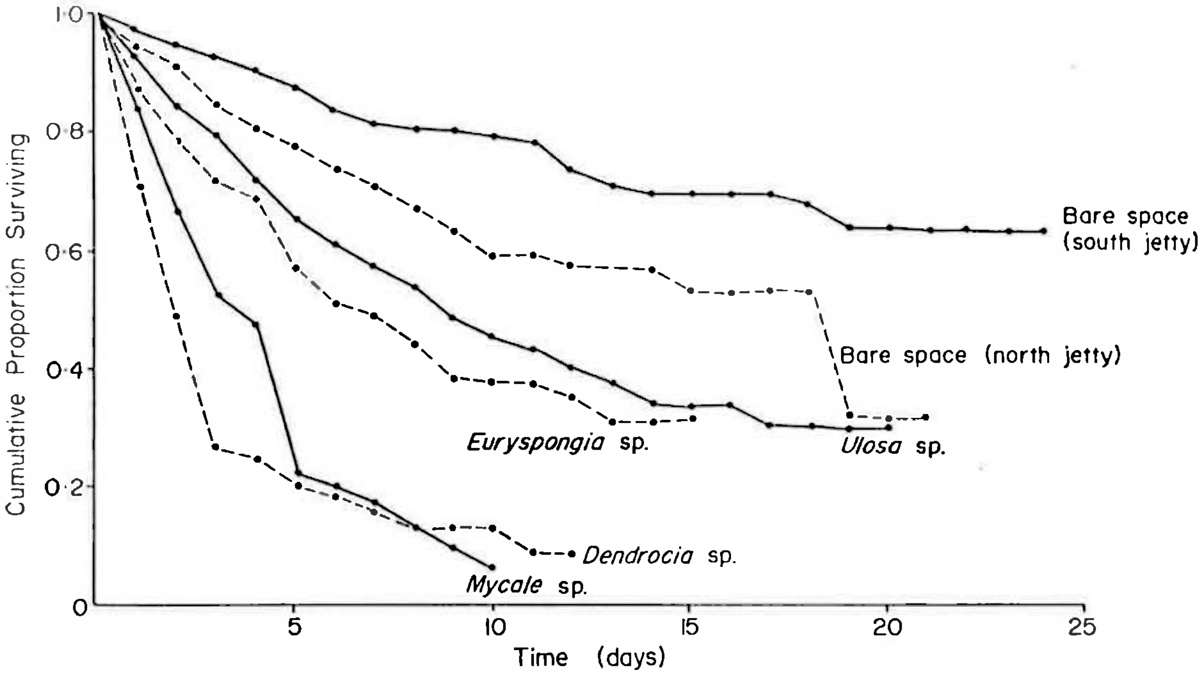
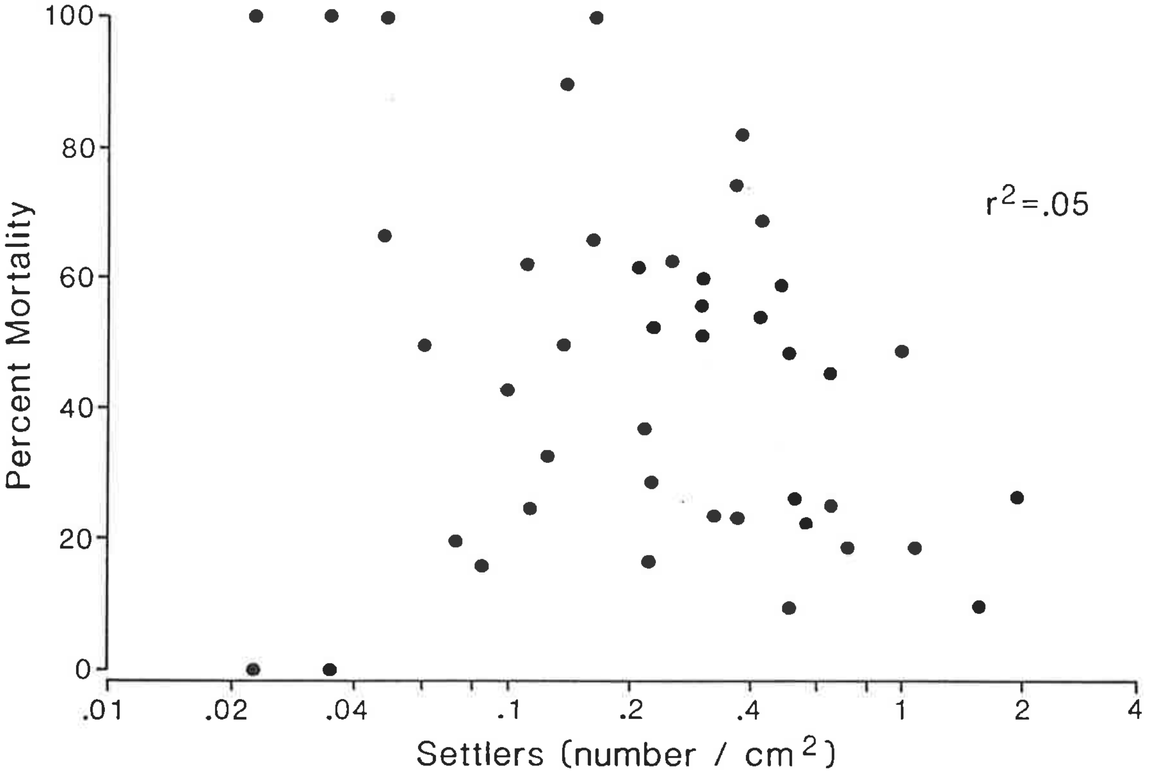

1·0
0·8
0·6
0·4
0·2
0
Cumulative Proportion Surviving
5
10
15
20
25
Time (days)
Bare space
(south jetty)
Bare space (north jetty)
Euryspongia sp.
Ulosa sp.
Dendrocia sp.
Mycale sp.

Figure 4.3-3 Percentage mortality in the first 30 days after settlement versus settlement density. Counts were done in permanently marked 0.81cm^2 quadrats at Edithburgh. Each point represents data from one quadrat.



Percent Mortality
100
80
60
40
20
0
r^2=.05
.01
.02
.04
.1
.2
.4
1
2
4
Settlers (number / cm^2)

Figure 4.3-4 The density of recruits (30 days after settlement began) versus the density of settlers in the same quadrat at Edithburgh Jetty. Each point represents data from one quadrat.

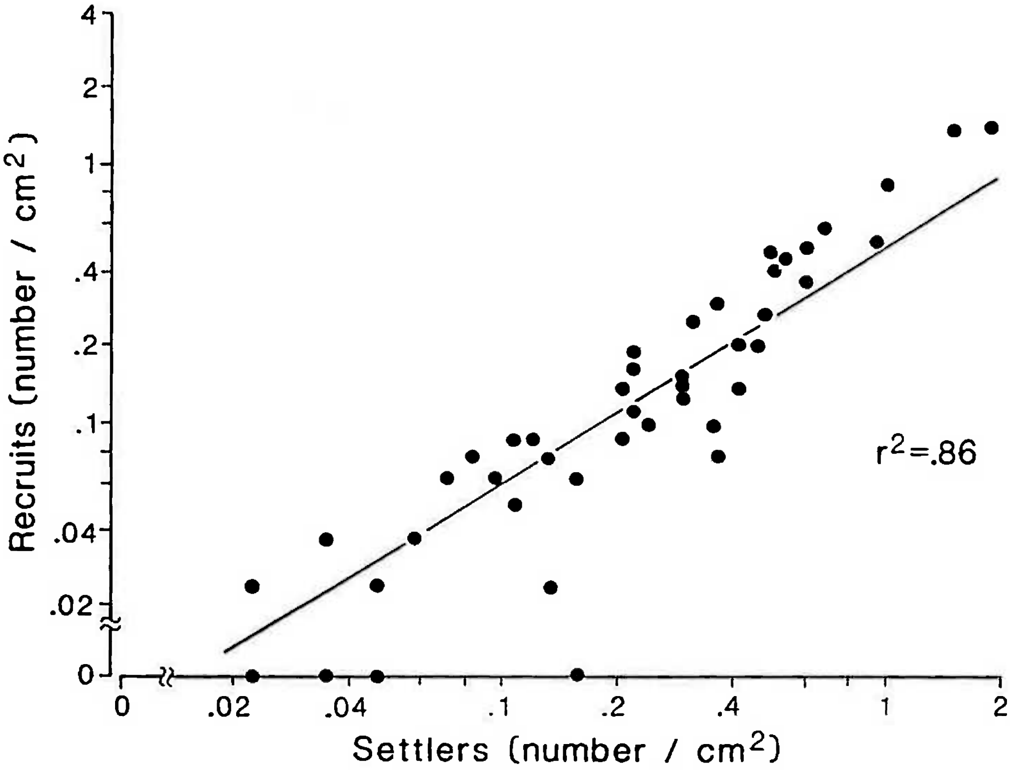

Recruits (number / cm^2)
4
2
1
.4
.2
.1
.04
.02
0
r^2=.86
0
.02
.04
.1
.2
.4
1
2
Settlers (number / cm^2)

Table 4.3-1 Comparison of Podoclavella settlement with the availability of bare space and number of epifauna associated with the four sponge substrata.

Sponge species	Total number[a] settling	Percent[b] cover of bare space			number of[c] epifauna		
		$\bar{x}$	(SE)	n	$\bar{x}^{d}$	(SE)	n
Ulosa sp.	312	36	(5.2)	8[e]	16.4	(0.5)	100
Euryspongia sp.	121	0		9	12.4	(0.3)	100
Dendrocia sp.	89	0.5[f]		9	5.5	(0.7)	100
Mycale sp.	37	0.5	(0.3)	9	2.4	(0.5)	100

a From Table 4.3-6

b Quadrat size 81cm^2

c Quadrat size 4cm^2 Hydroids and Polychaete tubes pooled.

d All means significantly different at the 5% level (One Way ANOVA and Tukeys HSD - variances heterogenous, Cochrans C = 0.448)

e Quadrat that had availability of bare space increased by fungal attack was not included

f Estimated without a tracing

Table 4.3-2 Settlement on filter paper in the presence of Mycale sp. extract. Controls had ether pipetted onto them but no sponge extract. Numbers represent trials, each with one larva. The G-statistic for homogeneity was calculated after Yates correction had been applied.

Treatment	Settled on paper within 10 minutes	Did not settle on on paper within 10 minutes
Control	7	0
Treatment	9	32

G (Yates) = 13.1 df = 1 P <.01

Table 4.3-3 Total settlement (on filter paper and the plastic container) in the presence of Mycale sp. extract. Controls had ether pipetted onto them but no sponge extract. Numbers represent trials, each with one larva. The G-statistic was calculated after Yates correction had been applied.

Treatment	Settled within 10 minutes	Did not settle within 10 minutes
Control	7	0
Treatment	25	16

G (Yates) = 3.1 df = 1 ns

Table 4.3-4 Settlement on filter paper with four concentrations of *Mycale* sp. extract; none (control), half natural, natural, and twice natural. Calculation of dilution is described in text. In the STP analysis concentrations joined by lines are not significantly different at the 5% level.

Treatment	Settled on paper within 10 minutes	Did not settle on paper within 10 minutes
None (control)	13	1
Half Normal	5	3
Normal	4	2
Twice Normal	7	11

G = 11.1 df = 3 $P < .05$

Results of STP *a posteriori* analysis

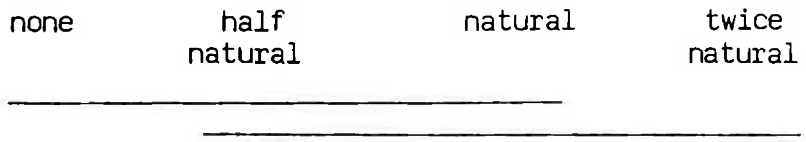


Table 4.3-5 Sample sizes in survival experiment, including median survival estimates (in days) and standard errors (SE).

Substratum	Total	Dead	Alive at end	Percent Alive at end	Median Survival	SE
Bare Space (south)	552	120	432	78.3	⩾11.5[a]	0.6
Bare Space (north)	151	56	95	62.9	18.1	0.5
Ulosa sp.	312	143	169	54.2	8.7	0.7
Euryspongia sp.	121	75	46	38.0	6.3	1.4
Dendrocia sp.	89	63	26	29.2	3.3	1.1
Mycale sp.	37	33	4	10.8	1.9	0.3
TOTALS	1262	490	772			

[a] 75th Quartile, survival was too high to calculate median

Table 4.3-6 Relationship between the density of larval settlers and i) the density of recruits and ii) mortality to the end of the settlement period. Data are not transformed for comparison to log transformations shown in figures 4.3-3, 4.3-4. Quadrats with no settlers were excluded from the percent mortality data set. The levels of significance are * $P < .05$, *** $P < .001$.

Independent variable		Dependent variables					
Larval settlement (No./cm^2)		Density at end of period (No./cm^2)			Percent mortality to end of period		
median	range	slope	signif. of slope	n	slope	signif. of slope	n
0.21	0 - 1.9	0.76	***	54	-21.6	*	48

Table 4.3-7 Short term survival; the number of settlers remaining a few hours after settlement on three substrata.

	SUBSTRATA			
	Bare space	*Dendrocia* sp.	*Mycale* sp.	Total
Initial No. Present.	64	28	1	93
No. present 2.25 - 4 hrs later.	64	26	1	91
n[a]	6	8	5	19

[a] Represents number of occasions a total of two patches of each substratum were monitored

Interpretation

Podoclavella larvae discriminate between substrata at settlement, thereby significantly influencing patterns of recruitment. Over 50% of initial encounters with bare space resulted in settlement whereas some sponges, particularly Mycale sp., were consistently rejected. Larval preference for Euryspongia sp. must be regarded with caution, owing to the low number of encounters observed with this sponge.

I have suggested that Podoclavella larvae choose a substratum at settlement. An alternative explanation is that larvae may accept a substratum and settle upon it not because of preference but in response to the time they have been swimming. There is evidence from laboratory studies that swimming larvae become less discerning in their choice of settlement sites over time (Knight-Jones, 1953; Crisp, 1974). 'Preference', then, would be determined by the distance of the substrata from the larval release point, those substrata furthest away being 'preferred'. However, a one-way ANOVA failed to detect any differences in swimming time between larvae that settled on a substratum at first encounter and those rejecting it (F=1.03 df=(1,28)). The aversion of Podoclavella larvae to settle on certain sponge species was maintained over time. It is possible that the reduction in larval selectivity associated with some laboratory experiments is determined not by time but by the number of times a larva has tested substrata.

The preferences of Podoclavella at settlement are determined by the amount of unfouled sponge surface on each species of sponge. Settlement was greater on sponges that had a high availability of patches of bare space or large numbers of epifauna associated with them. This is shown by the total number of larvae settling on each sponge species (Table 4.3-1) and explains the high settlement on Ulosa sp. and Euryspongia sp., relative to that seen on Dendrocia sp. and Mycale sp.; the latter two having only small areas of bare space and a limited epifauna associated with them. All Podoclavella larvae settling 'on' Mycale sp. in the survival experiment settled on patches of vacant space (wood) within this sponge.

The rejection of the unfouled exterior of at least one sponge, Mycale sp., appeared to be in response to chemical substances. A low frequency of fouling on some sponges may result from avoidance of these sponge species by invertebrate larvae. A low cover of fouling organisms on sponges has been correlated with the possession of toxic metabolites (Thompson et al., 1985; McCaffrey & Endean, 1985). Rejection of the extract (or sponge surface) was preceded by a period of contact, but the presence of sponge extract in the settlement trials did not totally inhibit settlement; larvae often settled on the plastic in close proximity to the filter paper coated with extract.

Surface contact was an important component in the rejection of this sponge and testing of the substratum was almost certainly occurring. Sensory receptors are found on the attachment organs of ascidian tadpoles; the adhesive papillae (summarized in Burke, 1983). The restriction of searching activity in this species simply to contact, allowed larvae to assess the suitability of a substratum for settlement, but would not allow Podoclavella larvae to determine the proximity or taxonomic affinity of their neighbours. As a result Podoclavella regularly settle next to competent spatial competitors such as the fast growing sponge Mycale sp. or the encrusting colonial ascidian Botrylloides leachii. The most likely outcome of this interaction is overgrowth, resulting in death of the Podoclavella recruit (pers. obs.).

Post-settlement mortality also exerted a significant influence on the patterns of recruitment observed in Podoclavella. Median survival estimates on the five substrata monitored showed a near perfect rank correlation with the settlement preferences of larvae for these substrata (Kendall's tau = .80). It should be emphasized, however, that the a posteriori (STP) analysis revealed only two significantly different groups of substrata based upon larval preferences. Nevertheless these findings indicate that cues eliciting settlement in Podoclavella were used in concentrating larvae on substrata where survival was enhanced. Larval settlement in response to cues has been shown to reduce mortality in other marine invertebrates (Connell, 1961; Grosberg, 1981; Young and Chia, 1981, 1984). The rejection of the sponge, Mycale sp., in apparent response to chemicals, suggested that Podoclavella larvae were avoiding a negative chemical cue.

In the first 30 days following settlement, survival was high on bare space. This high survival may be attributed to decreased significance of the sources of recruit mortality identified for other invertebrate species. For example, 'sweeping' by algae (Hawkins, 1983) is not important as macro-algae were not present on the pilings monitored. Grazing by urchins (Sammarco, 1980; Ayling, 1981; Sebens, 1983b) can be excluded as urchins do not occur on the pilings. 'Bulldozing' by grazers (Dayton, 1971; Denley and Underwood, 1979) is unlikely to be an important source of mortality as the herbivorous gastropods present, Astraea squamifera (Koch) and small Clanculus spp., occur at very low densities on pilings. Both species were absent more than two metres above the seabed (20x20cm quadrats n=27) and densities were very low (20x20cm quadrats x=0.15 SE=0.05 n=46) below this level on pilings. Monacanthid fishes are regarded as significant ascidian predators (Ayling, 1981) , particularly of juveniles (Russ, 1980; Keough, 1984a). Schools of monacanthid fishes were regularly observed at Edithburgh and the impact of predators will be considered in the following chapter.

It should be stressed that the absence, or decreased significance, of these sources of mortality is not merely because this study was conducted on a wooden jetty. They appear to be either absent or of little significance on many vertical rock walls in South Australian gulf waters.

Two important sources of recruit mortality were identified; patch overgrowth and the dislodgement of substrata that had been settled upon. Rates of patch overgrowth in this community are influenced by a number of factors (Kay and Keough, 1981). In this study, patch size and the growth rate of neighbouring sponges were important determinants of patch closure and therefore mortality in *Podoclavella*. The low survival observed on the fast growing sponge *Mycale* sp. is attributable to such overgrowth. The second source of mortality was the dislodgement of epifauna associated with sponges on which *Podoclavella* settles. Hydroids remain firmly attached but the tubes of *Pseudopolydora* sp. are easily dislodged. The probability of dislodgement of spionid polychaete tubes was presumably increased as the metamorphosed ascidian grew. Polychaete tubes are more common on *Dendrocia* sp. than the other three sponge species and dislodgement of these tubes probably accounts for the low survival observed on this sponge species.

The strong positive relationship between the density of settlers and recruits indicates that it is possible, for this subtidal species, to infer patterns of settlement from the density of recruits at Edithburgh Jetty. It also underscores the importance of settlement in determining recruitment patterns of *Podoclavella*.

4.4 SETTLEMENT PREFERENCES AND POST-SETTLEMENT SURVIVAL ON VERTICAL AND HORIZONTAL SURFACES

Introduction

The near absence of colonial benthic animals on upward facing surfaces, and their prevalence on vertical faces and underhangs has been well documented (Kitching et al., 1934; Forster, 1958, 1961; Hiscock, 1979). The explanation for these patterns is considered to be larval settlement preferences, associated with the strong correlation of incident light with changes in surface angle, or a decrease in post-settlement mortality relating to the reduction in sediment flux and light with an increase in surface angle. Larvae of many invertebrates are photonegative at settlement and therefore show a preference for vertical or downward-facing substrata (Thorson, 1964; Crisp, 1974). High light levels on upward-facing surfaces encourage algal growth which may preempt space or physically damage larvae that settle (Hartnoll, 1983). Grazers, associated with the algae, may also damage or dislodge animals (Sammarco, 1980; Young & Chia, 1984).

Sediment may also kill animals, particularly recruits, by abrasion (Shelbourne, 1957), burial (Marshal & Orr, 1931; Hiscock & Hoare, 1975), or the clogging of feeding apparatus (Johnson, 1972; Bricelj et al., 1984).

No study, so far as I am aware, has examined the relative contributions of settlement and post-settlement mortality to patterns of recruitment on vertical and upward facing horizontal surfaces. Distinguishing the contribution of each of these factors to the patterns of recruitment observed in Podoclavella was the objective of this section.

First, I determined if the responses of larvae to light and gravity cues influenced how they oriented at settlement. Their responses to these cues were then compared with settlement observations in situ. Second, the impacts of potential sources of mortality were examined, where feasible, with manipulative experiments. The sources of mortality investigated were: sediment, algae, and 'bulldozing' by grazers.

Materials and Methods

i) Settlement Preferences

The influence of light and gravity on the orientation of larvae at settlement was tested in submerged polyvinyl chloride (PVC) boxes. The null hypothesis examined was that the orientation of larvae at settlement was random with respect to vertical surfaces, horizontal upward-facing surfaces and horizontal downward-facing surfaces. This hypothesis was tested in response to two stimuli; i) gravity and ii) gravity and a light gradient. In testing this hypothesis two asssumptions were made. First, in the absence of light, gravity is the only other orientational cue available to larvae. Second, larvae were in the centre of the box when trials began, and should larvae not react to any stimuli, then there is an equal probability of a larva encountering any face. This assumption was made in calculating the expected frequencies and these were compared to the observed frequencies with goodness of fit tests.

To test this hypotheses two boxes were constructed, one of 2.5mm clear PVC sheet and the other of 2.5mm opaque grey PVC sheet. Boxes were cubic and measured 15x15x15cm. The base and four sides of each box were heat welded while the tops were fixed to the boxes with eight small wingnuts. All welds were on the outside of the boxes, hence the inside of each box consisted of uncontoured 90° corners. The outside of one half of the clear plastic box was masked with black tape (Fig. 4.4-1).

Larvae were obtained from the larval traps discussed in Chapter 3 and transferred to the settlement boxes in the removable plastic jars. Larvae were introduced to each trap through a 4.6cm diameter hole in the top of the box. Once a larva swam into the box a snugly fitting PVC plug was placed into the hole and the box was spun quickly through at least 360°. Upon assuming a previously determined orientation the box was placed on the seabed (both boxes were negatively bouyant) and the larva left to settle.

Only one larva was introduced to a box at any time and the marking of where that larva had settled in the box represented the completion of a successful trial. After each trial the inside of each box was wiped with a neoprene glove and after every five to ten trials each box was removed from the water, washed in hot soapy water, rinsed and left to dry.

Twenty trials were done in the opaque box and the box was turned through 90° or 180° on four occasions between trials to ensure that results were not biased by where larvae had settled in previous trials.

The light and dark box was oriented in three ways, summarized in Figure 4.4-2:

a) Dark half facing downwards, one set of twenty trials.

b) Dark half facing upwards, two sets of twenty trials. In the second set of trials the dark half of the box was taped on the inside as well as the outside, to reduce the possibility of reflections interfering with the results. Unfortunately, the taping unavoidably altered the surface properties for settlement.

c) Dark half facing to the side, two sets of twenty trials. The dark half of the box was facing west for the first set of trials and east for the second set.

As with the opaque box, every three to five trials the light and dark box was rotated through 90° or 180°, while maintaining the orientation of the dark half, to ensure that results were not biased by the settlement positions of larvae in earlier trials. Settlement on the dark and light halves of the settlement box were initially compared for the five orientations outlined above in a 5x2 contingency table. Then the number of larvae settling on horizontal upward and downward-facing surfaces and on vertical surfaces were examined with contingency tables.

The distribution of settlers was examined <u>in situ</u> by observing larval encounter and settlement on vertical and horizontal surfaces. Observations were made on two wooden blocks that had been submerged for at least three years and probably considerably longer. One block measured 30x30x25cm and the other 35x35x30cm. Areas measuring 20x20cm were delineated on three faces of these blocks with small galvanized iron nails. The faces were: i) horizontal ii) vertical and parallel to the current iii) vertical and perpendicular to the current. Observations were made of the horizontal face and one of the vertical faces simultaneously. Within a fifteen minute period the number of larvae touching the surface of each area and those settling were recorded.

ii) Post-settlement survival

The correlation of potential sources of mortality with vertical and horizontal faces:

Three potential sources of mortality associated with upward-facing surfaces were examined: i) burial, abrasion or interference with feeding by sediment; ii) disruption of settlement or physical damage as a result of sweeping by algae; and iii) 'bulldozing' by grazers. The likely effects of these potential agents of mortality were assessed by measuring their relative occurrence on vertical and horizontal surfaces.

The horizontal and vertical distributions of algae and grazing gastropods were quantified at Port Noarlunga reef using quadrats. Counts of grazers were made within $0.25m^2$ quadrats on large boulders at The Gap (n=12) and on rock walls on the Inner Reef (n=11). Quadrats were placed haphazardly on vertical and horizontal faces and the grazers were identified to species level and counted.

The density of macroalgae and coverage of turfing and crustose algae on vertical and horizontal faces was quantified at the inner reef. The density of laminarian and fucoid algae, Ecklonia radiata and Sargassum spp., was estimated by counting the number of stipes in a $0.17m^2$ quadrat. Quadrats in which macroalgae were not common were photographed with the equipment described in Chapter 2. The positions of quadrats corresponded to random numbers on a tape laid across the tops of rock walls. Slides were projected to half their actual size and the percent cover of turfing algae was determined from point counts with 464 regularly arranged points per quadrat.

The accumulation of sediment on horizontal surfaces at the inner reef was examined using 25ml syringes with the fronts cut off. A syringe was placed against the substratum, the plunger was pulled back rapidly and the open end quickly corked. The corked syringes were returned to the laboratory, vacuum-filtered onto Whatman Grade GF/C preweighed paper filters and oven dried for 24 hours at 60°C before weighing.

The effect of sediment:

The null hypothesis examined under this heading was that different rates of sedimentation have no effect on the survival of Podoclavella recruits. The influence of settling particulate material on the survival of newly settled recruits was investigated by manipulating rates of sedimentation and examining the influence on recruit mortality. Close to a source of sediment, for example the sea bed, resuspended material may have a large particle size and considerable abrasive power. So as not to confound the effect of settling particulate material with scouring effects the experiment and earlier pilot studies were positioned 1.5m above the seabed.

Rates of sedimentation are difficult to manipulate but may be increased over organisms in two ways; first, sediment may be applied manually. This material must be of a realistic size and flux if its impact on animals is to be adequately assessed. The second method entails transplanting animals to areas with higher incident sediment flux. This may be conveniently achieved by reorienting animals from the vertical to the horizontal (upward-facing) plane. The transplantation of animals to an upward facing surface will increase the incident flux of sediment on those animals, but confounds the increase in sedimentation with a change in orientation of the animals. In my attempts to alter the rate of sedimentation the orientation of treatment colonies was not altered relative to that of controls, both were placed on the horizontal plane and the flux of sediment onto the treatment colonies was reduced using apparatus described below.

Incident sediment flux was measured with sediment traps. There are a number of criteria with which traps should comply if they are to minimize biases in estimates of sedimentation rates. Traps should i) be tubular (Gardner 1980a,b); ii) have an internal diameter of 45mm or more

(Blomqvist and Kofoed, 1981); and iii) have a height to width ratio of 2.3 (for currents up to 9cm/sec) (Gardner 1980a). Traps must also be held in a steady vertical position if they are to yield realistic estimates of vertical flux (Gardner 1985).

In this study cylindrical traps with a height to width ratio of 1.84 (Height 12.5cm, mouth width 7cm) were used to judge the performance of apparatus designed to increase and decrease sediment flux, and compare experimental treatments with controls. These traps may have overestimated the actual sediment flux (Gardner, 1980a), but are nevertheless adequate for these comparisons.

Two to fourteen days after deployment sediment traps were capped and returned to the laboratory. The contents of each trap were first seived though 350 micron plankton mesh to separate sediments from material dropping from the jetties. The resulting filtrate was then vacuum filtered onto pre-tared Whatman Grade GF/C filter paper and dry weights were obtained by oven-drying for 24 to 36 hours at 60°C. The dry weight of sediment was then converted to a weight per cm^2 per day (sediment flux).

Apparatus was constructed to either increase or decrease the incident flux of particulate matter. The ability of this apparatus to perform the task for which it was designed was tested at Port Noarlunga Jetty. An attempt was made to reduce the quantity of sediment by erecting clear PVC plates horizontally above the sediment traps. Two sizes of plate were used: $400cm^2$ and $1600cm^2$, with sediment traps positioned 5cm below each plate. Control 'plates' were constructed of trellis wire (1 mesh per 25.4cm, wire size = 1.6mm) cut to the same area as the PVC plates. These plates excluded animals such as fish (as do the PVC plates) but allowed sediment to 'rain down' (Fig. 4.4-3A,B).

Two pieces of apparatus were tested for their ability to increase the flux of sediment. The first was a sieve constructed of 16cm diameter plastic tubing and 350 micron plankton mesh. The sieve was filled with sediment and placed 5cm above a sediment trap. The sediment ran through the plankton mesh and the quantity of sediment in the sieve was replenished regularly (Fig. 4.4-3c). The second piece of apparatus mimicked the come-like trap which Gardner (1980a) demonstrated was particularly efficient at overtrapping sediment. For my purposes a trap with an open bottom and top was more appropriate than Gardner's dome-like trap with only an open top - so a plastic salad bowl was inverted and modified. The bowl measured 27.5cm in diameter at its widest point and 13cm in height. A 9cm diameter hole was cut in the original base of the bowl. This base measured 13cm in diameter (Fig. 4.4-3d). The lower rim of the inverted bowl was set 5cm above a sediment trap. Initially, apparatus tested at Port Noarlunga jetty was unreplicated, although trials were performed on a number of occasions. Later trials were done with two replicates.

Survival of Podoclavella recruits following the manipulation of incident sediment flux was examined at Edithburgh Jetty. Twenty $100cm^2$ wooden (jarrah) plates were nailed to pilings and left to gather Podoclavella recruits. After two weeks of submergence I reduced the number of recruits on each plate to ten. Recruits were not removed at random, but were spread over as wide an area of the plate as possible. This ensured a wide separation of recruits and reduced the likelihood of colonies becoming indistinguishable as they grew. Plates with less than ten recruits were discarded. The positions of the remaining recruits were marked onto acetate sheets.

Ten plates were positioned horizontally 1.75m above the seabed. These plates were fixed to an aluminium bracket with cable-ties and the bracket was, in turn, nailed to a piling. The bracket was also designed to accommodate a sediment trap, held in position with two strong rubber bands (see Fig. 4.4-4). The five even numbered plates then had inverted plastic bowls (described above) erected over them.

The survival of recruits was examined each week for the first two weeks, and then monthly for 4 months. Measurements of sediment flux were obtained during the first month of the experiment. Following initiation of the experiment on November 15, 1985 the sediment traps were removed and replaced four times prior to their final removal on December 22, 1985. The measurements of sediment flux permitted me to establish the effectiveness of my sediment manipulation and allowed me to calculate the regression of recruit survival on sedimentation during the first few weeks of the experiment.

The effect of grazers:

The null hypothesis to be investigated was that grazers do not dislodge Podoclavella recruits during the course of their grazing. Pilot caging experiments, in the laboratory and field, revealed that the behaviour of the most common gastropod, Turbo (Subninella) undulatus Solanger, was so modified by fences or cages that the hypothesis could not be examined. A test of the hypothesis with other gastropod species would have required unrealistically high gastropod densities within enclosures and so an investigation of the effect of grazers was abandoned.

The effect of algae:

Two aspects of the influence of algae on recruits were examined. The first was pre-emption of space by turfing algae. The second was the potential for mechanical damage, even dislodgement, in the presence of algae.

The influence of turfing algae on the daily recruitment of Podoclavella and subsequent survival of the recruits was assessed in twelve 81cm^2 quadrats at the bases of two pilings at Edithburgh. Each quadrat was delineated by two small galvanized iron nails and had a luxuriant growth of turfing algae. Algae were scraped from half of these quadrats with a diving knife. Over the next fourteen days the positions of recruits were marked onto acetate sheets, supported above the substratum on a small perspex 'table'.

Piling and treatment effects on total settlement, over the fourteen day period of monitoring, were analysed with a two factor analysis of variance. Survival was examined by generating survivorship curves and assessing differences between treatments with a log-likelihood ratio test using BMDP survival packages 1L and 2L respectively (Dixon, 1983).

A manipulative investigation of physical damage and the dislodgement of recruits by algae was hampered by low numbers of Podoclavella recruits. A correlative approach was adopted instead. The density and size of Podoclavella colonies were compared on large wooden (jarrah) settlement plates (2500cm^2), submerged five months earlier, which had developed a growth of long algal strands or shorter turfing algae. Two plates with long algae and two plates with short algae were each subsampled with three 81cm^2 quadrats. Colony density, size (zooid number), and the heights of zooids were recorded. Zooid height was measured by placing a graduated rod next to a zooid and reading off the height in millimetres. The height of algal strands was relatively consistent within a quadrat and only the longest algal strand in each quadrat was measured. The reason for the development of long algae on some plates and short algae on others was not known, but fortuitously plates with long and short algae were interspersed. The short turfing algae included *Ceramium* spp. while the long algal strands were predominantly *Polysiphonia daryae* (UDA A57359) and *Thaumatella disticha* (UDA A57360) (numbers and letters in parentheses refer to voucher specimens held in the herbarium, Department of Botany, University of Adelaide.) Recruitment of *Podoclavella* larvae had been counted in one central 81cm^2 quadrat two weeks after the plates were initially submerged and provided a rough indication of the initial density of recruits.

Results

i) Settlement preferences

In the absence of light the settlement of larvae differed significantly from a random distribution; they displayed a strong geonegative response ($G=17.6$ $df=2$ $P < .001$, Table 4.4-1). More larvae settled on the box top (downward facing surface) than expected and no larvae settled on the bottom of the box. Settlement was so concentrated at the top of the box that only two larvae settled more than 2cm from the upper surface.

In the presence of a light gradient the settlement of larvae on dark and light surfaces was dependent on the orientation of the light and dark box ($G= 42.7$ $df= 4$ $P < .001$, Table 4.4-2). Hence, the geonegative behaviour of larvae was modified by a photonegative response. The degree of modification was dependent upon the orientation of the dark half of the box. With the dark half overhead the gravity and light stimuli coincided and the geonegative response was not modified (Fig. 4.4-2a, Table 4.4-3). In all trials at this orientation, larvae settled in the dark top half of the box and settlement on the top (downward facing) surface was much higher than expected ($G=42.2$ $df=3$ $P < .001$).

Upon turning the dark half of the box onto the side (Fig. 4.4-2b,c) the geonegative response was slightly modified by photonegative behaviour. In each set of trials 75%, or more, of the larvae settled in the dark half of the box. Over both sets of trials 95% of the larvae settled in the upper half of the box and no larvae settled on the bottom surface. Where settlement on the top of the box had been five times greater than expected when the dark half of the box was overhead (compare with Table 4.4-3), the number of settlers on the top of box when the dark half was on the side was reduced to around twice the expected value. Settlement on the faces of the box remained significantly different from a random distribution (Trial 1 - $G=7.6$ $df=2$ $P<.05$, Trial 2 - $G=9.0$ $df = 2$ $P<.05$, Table 4.4-4a,b). These data were better suited to analysis by a 3x2 contingency table, but the lack of settlement on the bottom of the box produced errors in calculation and precluded this.

With the dark half of the box on the bottom, i.e. facing up (Fig. 4.4-2d,e), the gravity and light stimuli were opposed. In the first set of trials (with tape on only the outside half of the box) 21% of larvae settled on the dark lower half. In the second set of trials (dark half taped on the inside and outside) this figure was increased to 40%. In both sets of trials 10% of the animals settled on the bottom, i.e. upward facing, surface. Hence, with opposing stimuli settlement occurred on all faces and, in both sets of trials, produced distributions of settled larvae that did not differ from random (Trial 1 - $G=7.2$ $df=3$ $P>.05$, Trial 2 - $G=1.1$ $df=3$ $P>.5$, Table 4.4-5a,b).

It is important to note that only when the darkened half of the box was on the bottom, i.e. facing uppermost, did larvae settle on the base of the box. With the box turned on its side a small darkened area was facing up, yet this did not recieve settlers.

Not only did light influence the face on which larvae settled, it also influenced the time that larvae took to settle. The interval between individual trials in the dark and light box is indicative of how quickly larvae settled. After a larva was observed to settle the box could be prepared for the next trial. The interval between trials was relatively short when the dark half was uppermost (9±1.6 minutes ($\bar{x}\pm$SE) n=20) or on the side (16±2.3 minutes ($\bar{x}\pm$SE) n=28). Trials took more than twice this long when the dark half of the box was facing up (35±5.2 minutes ($\bar{x}\pm$S.E) n=24). A component of the interval between trials is the time taken to locate a larva for the next trial. However, this period of time can be assumed to be unrelated to the orientation of the box.

Low rates of larval encounter and settlement on horizontal and vertical surfaces in 1985 hampered *in situ* confirmation of the PVC settlement box results. In 1984 the feasibility of conducting field observations of larval encounter and settlement was assessed and the rates of encounter and settlement were noticeably higher than those observed in 1985. Unfortunately the low rates in 1985 render comparisons between surfaces of different orientation inconclusive. In 7.5 hours of observations no larvae were observed to encounter horizontal surfaces, whereas encounter was observed on the vertical surfaces (Table 4.4-6). Rates of encounter and settlement were higher on vertical surfaces placed perpendicular to the current than on vertical surfaces parallel to the current. Horizontal surfaces were parallel with the current and should only be compared with the encounter and settlement of larvae on vertical surfaces that are also parallel to the current. In both years the rate of settlement onto vertical surfaces placed perpendicular to the current was approximately half of the number encountering the substratum.

ii) Post-settlement Survival

The correlation of potential sources of mortality with vertical and horizontal faces:

Potential sources of mortality were related to the inclination of rock surfaces. Grazers were more abundant on horizontal than on vertical rock surfaces, but total densities varied between sites. At The Gap, Port Noarlunga, grazers were absent from boulder sides and were at such low densities on the tops of boulders that they were not significantly different from zero densities (Fig. 4.4-5). Densities of three species of gastropod grazer were quantified at The Gap. In order of decreasing density they were Calliostoma sp., Turbo (Subninella) undulatus, and Turbo torquatus Gmelin. Low densities of the echinoid Heliocidaris erythrogramma (Valenciennes) were also present at this site. A markedly different fauna and much higher densities of grazers were apparent at the Inner Reef, Port Noarlunga. The total density of grazers, in $0.17m^2$ quadrats, on the tops of rock walls (11.6 ± 2 ($\bar{x} \pm SE$)) was significantly greater than the densities on vertical faces (3.3 ± 0.7 ($\bar{x} \pm SE$) - $t=3.82$ $df=21$ $P < .001$). Data were transformed by square root to homogenize the variances ($F_{max}=3.3$ $df=11,10$ ns). In order of decreasing density, the following gastropods were counted; Turbo (Subninella) undulatus, Clanculus limbatus Quoy and Gaimard, Cantharidus eximus (Perry), Phasianella ventricosa Swainson, Monodonta (Austrocochlea) constricta Lamarck. Mean densities of each species are presented in Figure 4.4-5. It should be noted that these data represent underestimates of total grazer density as the small limpets were not included in the analysis. The accuracy of limpet counts was questionable owing to their small size. In addition some gastropods, for example abalone, Haliotis spp., actively forage on rock surfaces at night (pers. obs.) and all counts reported here were made during the day.

The density of macroalgae and the cover of turfing algae were significantly higher on horizontal surfaces ($P < .001$ in both instances - Table 4.4-7). The stipe densities of macroalgae per $0.18m^2$ was, on average, 2.1±0.4 (SE) on horizontal faces and only 0.5±0.2 (SE) on vertical faces. The mean cover of turfing algae was, on average 78.4±0.4% (SE) on horizontal faces and only 23.9±0.5% on vertical faces.

The weight of sediment (milligrams per cm^2), determined with the syringes, was an order of magnitude heavier on horizontal surfaces than on vertical faces ($t=3.42$ $df=4$ $P < .05$, Table 4.4-8)

The effect of sediment:

Measurements of the rate of sedimentation underneath apparatus that had been designed to increase or decrease sediment flux were fraught with inconsistencies (Fig. 4.4-6). Two patterns did emerge however. In conditions of low turbidity the sediment traps under bowls accumulated less sediment than traps in the open (controls). In more turbid conditions the bowl which had been deployed closer to shore, consistently trapped much larger concentrations of sediment than controls. It is noteworthy that sediment traps deployed even closer inshore than the one beneath the bowl trapped less sediment. As noted in Chapter 2, conditions at Edithburgh are generally much less turbid than those observed at Port Noarlunga. It was therefore anticipated that the bowl apparatus would reduce the flux of sediment at Edithburgh, despite the initial expectation that this apparatus might increase sediment flux. This was indeed the case. The weight of sediment beneath the bowls was significantly lower than in the treatment without the bowls ($F=5.78$ $df=1,8$ $P < .05$, Table 4.4-9). However, recruit survival was not significantly different between the ambient sediment flux treatment and the reduced sediment flux treatment (t= 0.2 df= 8 P >.5, Fig. 4.4-7). The mean numbers of recruits surviving were 5.2 (SE= 0.8) and 5.4 (SE= 0.4), respectively (Table 4.4-10).

In the analysis of recruit survival it should be noted that the penultimate data set (February 1986) was used. The number of recruits surviving into the last period of monitoring (March 1986) had become confused by the proliferation of zooids on the plates and this is reflected in the drop in survival observed in these two treatments on the final date of monitoring (Fig. 4.4-7)

Changes in sediment flux did not influence the survival of recruits. The percentage mortality of recruits in the first week of this experiment showed no significant relationship with the sediment flux received by each trap during this period (Fig. 4.4-8)

The effect of algae:

Turfing algae did not disrupt the settlement or post-settlement survival of Podoclavella. However, colonies among long strands of algae were found at reduced densities and were also smaller in size.

No significant difference was found in the number of larvae settling between turf clearance areas and untouched turf controls. A two factor ANCOVA did, however, detect a significant difference between the two pilings (Table 4.4-11). The height of each quadrat above the sea bed was treated as a covariate, but was not significant. Prior to doing the ANCOVA, a test for the equality of regression slopes revealed no significant differences between groups (F= 2.3 df= 3,4 P >.2).

Survival in these turf treatments was recorded for over 320 Podoclavella settlers. Around 70% of these animals were still alive after 14 days (Table 4.4-12). Survivorship curves and 75th quartile survival estimates (survival was too high to calculate median survival), generated for the 14 day period of monitoring, did not indicate differences in ascidian survival between the treatment and control (Fig. 4.4-9, Table 4.4-12). The effect of the treatments and a covariate, height above the sea bed, on survival was tested using a Cox proportional hazards regression model (Hopkins, 1983). Comparisons of submodels with the full model revealed no significant differences in larval survival between the cleared and untouched substrata (χ^2=2.1 df=2 $P > .35$)

Damage to colonies of Podoclavella appeared to be a function of algal height. Long strands of algae measured, on average, 75±8.4mm (SE, n=6) while short turfing algae were 17.2±3.1 (SE, n=6) in height. Significant differences in colony density and size were detected between plates with long and short algae. Colony density was roughly half the figure observed among short algae (F= 10.2 df= 1,10 $P < .01$). There was no indication that initial recruitment had been depressed on these plates when they were initially submerged (Table 4.4-13).

Colony size was also roughly halved in the presence of long algae (F= 9.4 df= 1,33 $P < .01$, Table 4.4-14). Commensurate with this reduction in colony size was a significant reduction in zooid height (F= 213 df= 1,1 $P < .05$, Table 4.4-15).

Figure 4.4-1 The light and dark PVC box used in settlement trials (15x15x15cm). The box was constructed of clear PVC and one half was then taped on the outside with black tape. The opaque box was constructed in the same manner of grey PVC sheet.

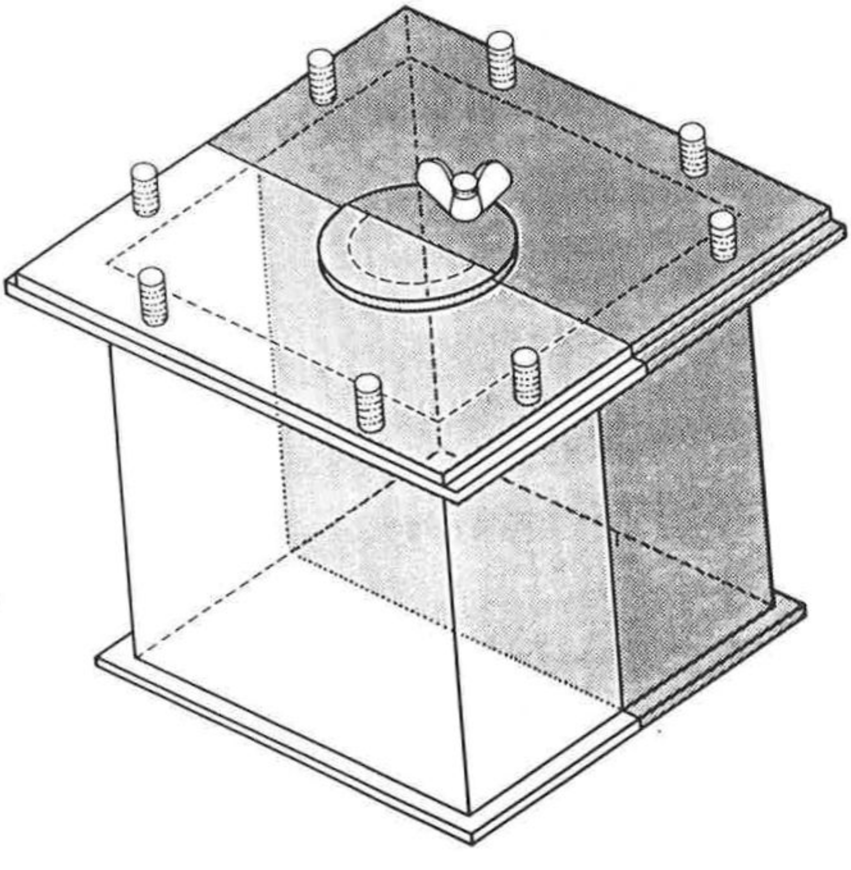


Figure 4.4-2 Orientations of the light and dark box in the settlement trials. Nineteen trials were done at orientation d) while twenty were done at all other orientations. In e) the box was taped on the inside as well as the outside.

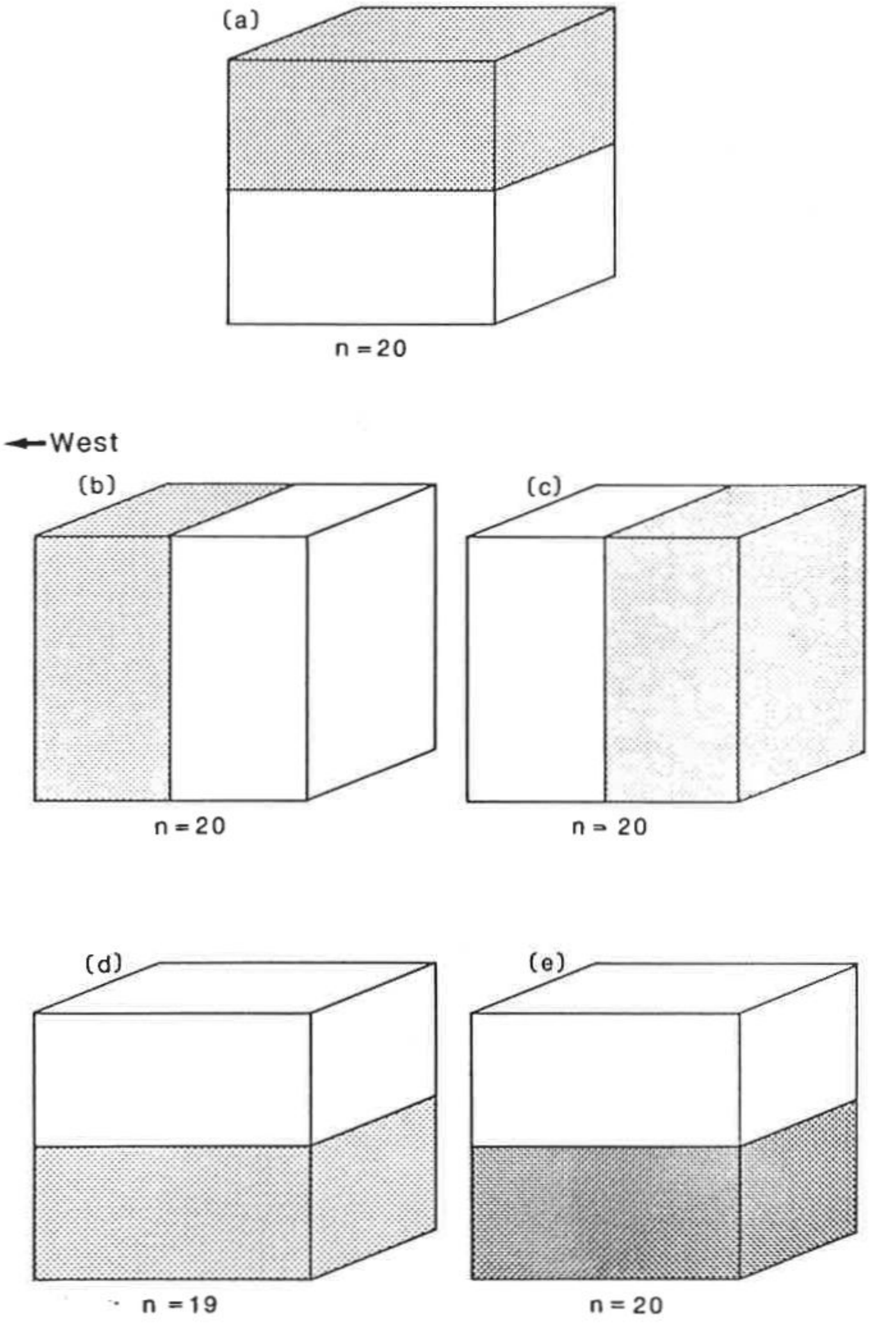
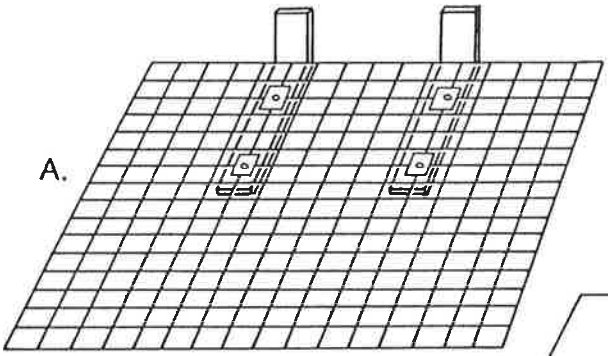

(a)
n = 20
West
(b)
(c)
n = 20
n = 20
(d)
(e)
n = 19
n = 20

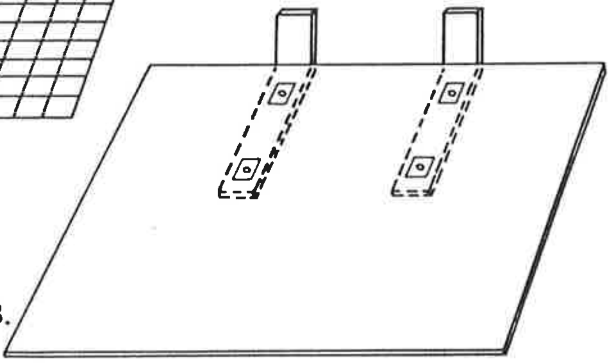
Figure 4.4-3 Apparatus tested for its effectiveness in increasing or decreasing the incident flux of sediment. A 20x20cm perspex plate and 'mesh' control were also tested but are not illustrated. The inverted salad bowl was the piece of apparatus selected to reduce incident sediment flux in the experiment.

A	40x40cm 'mesh' control
B	40x40cm perspex plate
C	Sieve with 350 micron plankton mesh
D	Inverted plastic bowl

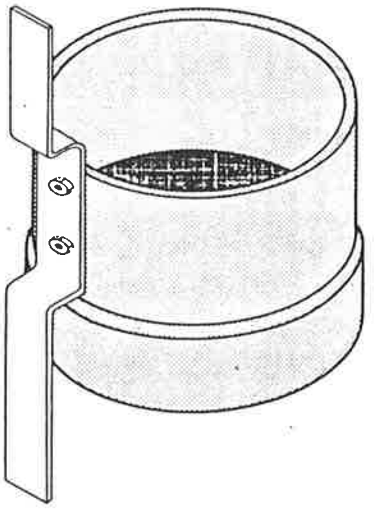
A.



B.



C.



D.

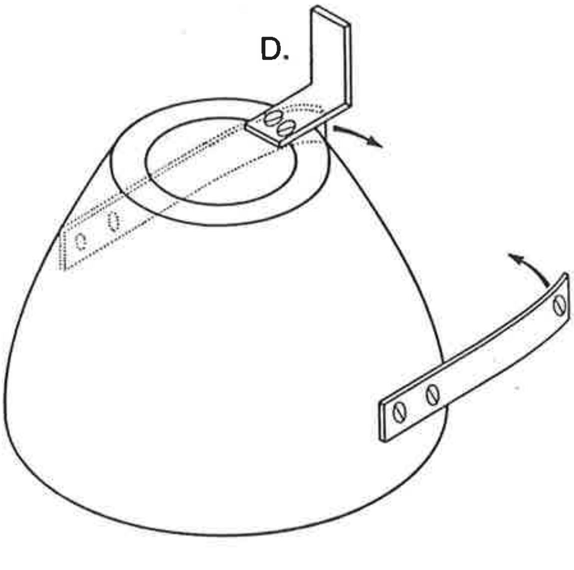


Figure 4.4-4 Apparatus used to assess the impact of sediment on the survival of recruits. While the survival of recruits was monitored the incident sediment flux was measured simultaneously with a sediment trap. Sediment traps were capped with screw tops during their removal and replacement.

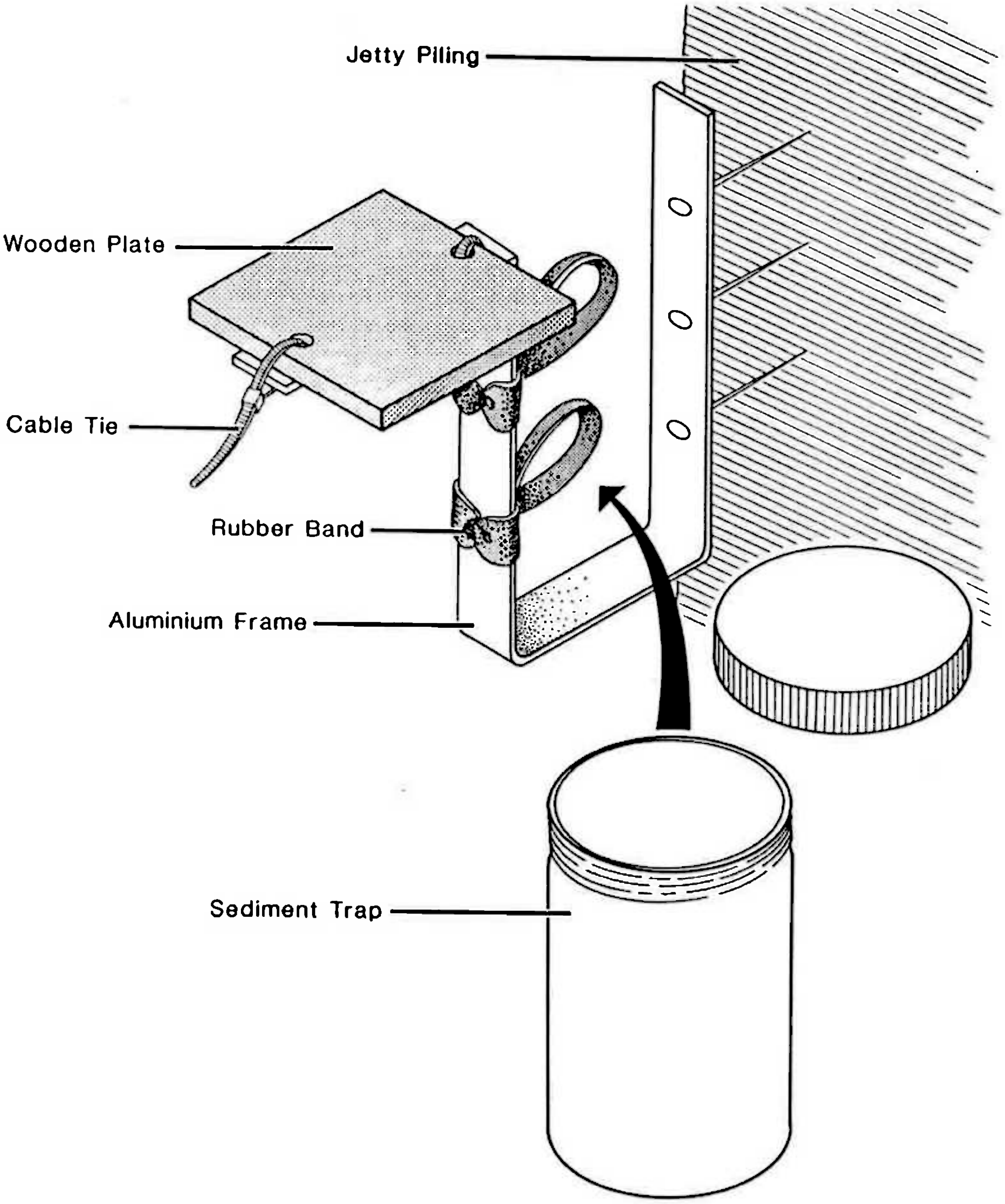

Jetty Piling
Wooden Plate
Cable Tie
Rubber Band
Aluminium Frame
Sediment Trap

Figure 4.4-5 The mean density of the most common grazing gastropods during the day at the Inner Reef and The Gap, Port Noarlunga. Means were calculated from counts within 0.5m^2 quadrats placed haphazardly on vertical and upward facing rock surfaces. Error bars are 95% confidence intervals around the mean, n=11 at the Inner Reef and 12 at The Gap.

Vertical Surfaces

▲ Inner Reef
△ The Gap

Horizontal (Upward-Facing) Surfaces

■ Inner Reef
□ The Gap

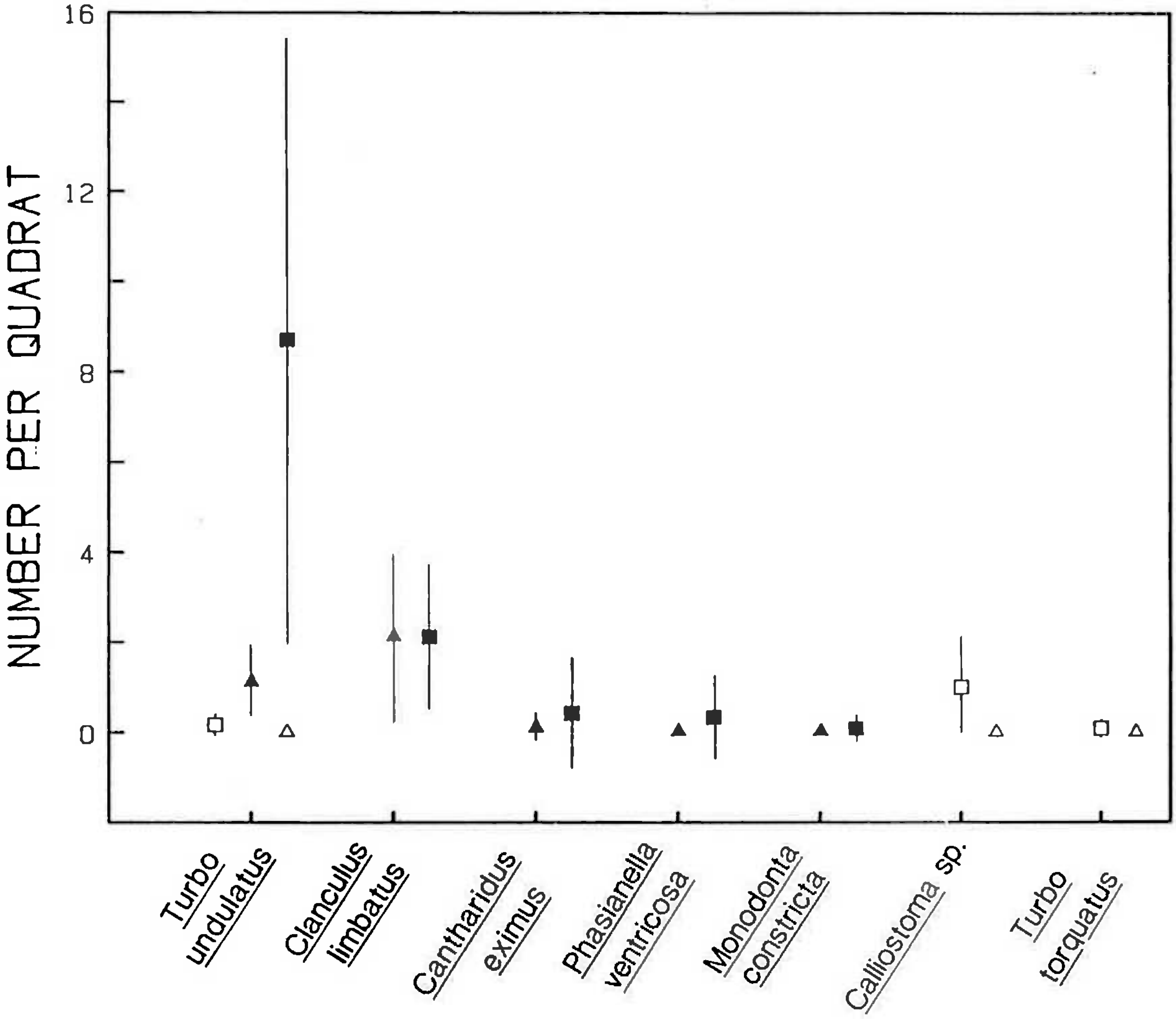

16
12
8
4
0
NUMBER PER QUADRAT
Turbo undulatus
Clanculus limbatus
Cantharidus eximus
Phasianella ventricosa
Monodonta constricta
Calliostoma sp.
Turbo torquatus

Figure 4.4-6 The weight of sediment trapped beneath apparatus during pilot tests of their effectiveness in reducing or increasing incident sediment flux. The weight of sediment was plotted as g (dry weight) per cm^2, per day (x1000).

□ ☐	Plates (small and large)
⊞ ▦	Mesh Controls (small and large)
⊙	Plastic Bowl
*	Sediment trap only (no apparatus)
in	Apparatus on inner (nearshore) half of Jetty
ou	Apparatus on outer (offshore) half of Jetty

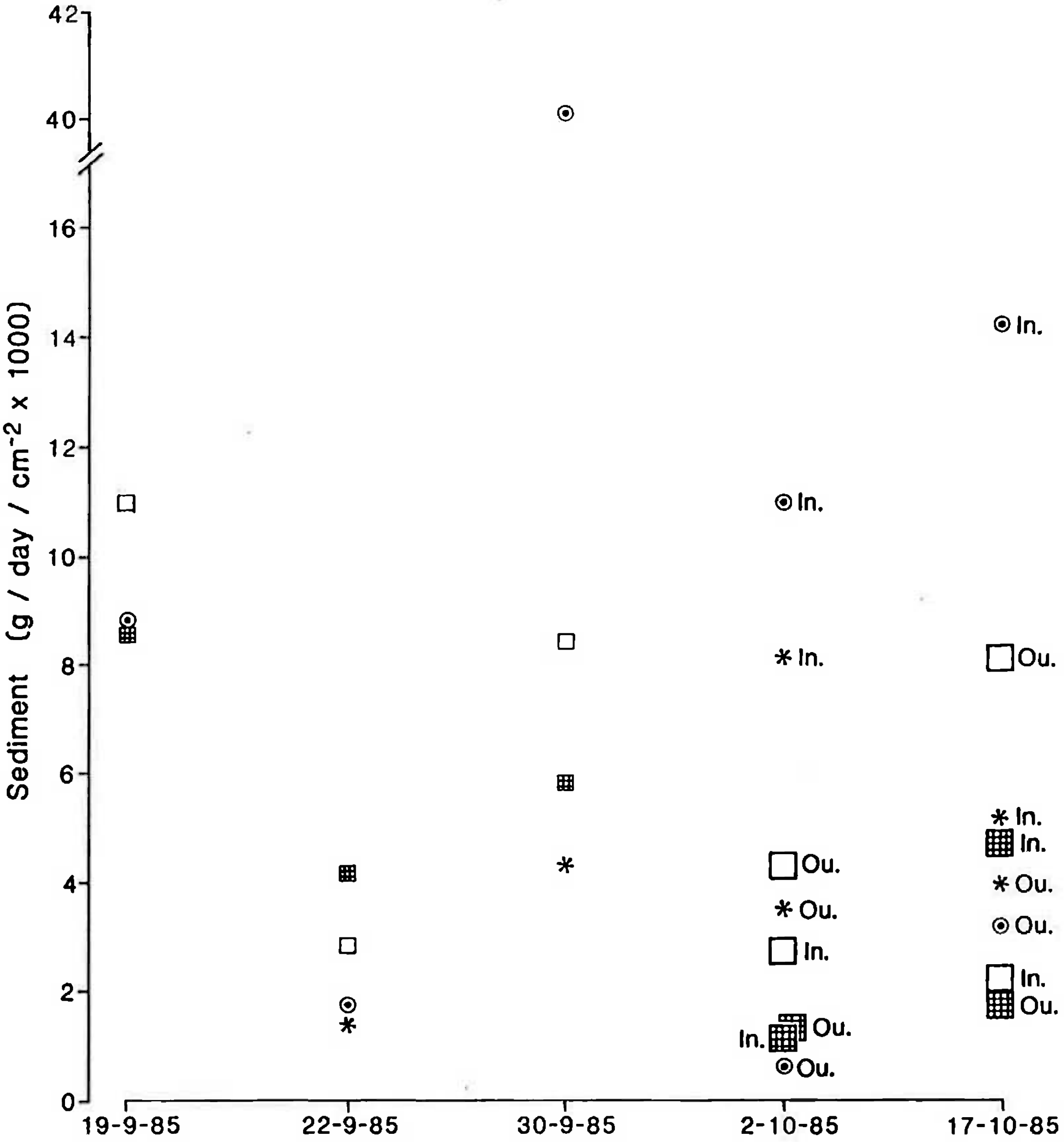

Sediment (g / day / cm^{-2} x 1000)
0
2
4
6
8
10
12
14
16
40
42
19-9-85
22-9-85
30-9-85
2-10-85
17-10-85
In.
In.
Ou.
Ou.
In.
In.
Ou.
In.
Ou.
In.
Ou.
In.
In.
Ou.
Ou.
In.
Ou.

Figure 4.4-7 The survival of recruits at ambient and below ambient levels of sedimentation over time. Recruits were on horizontal upward-facing surfaces during the experiment. Error bars are standard errors of the mean, n=5.

□—·——·—□ Ambient Sedimentation

○--------○ Below Ambient Sedimentation

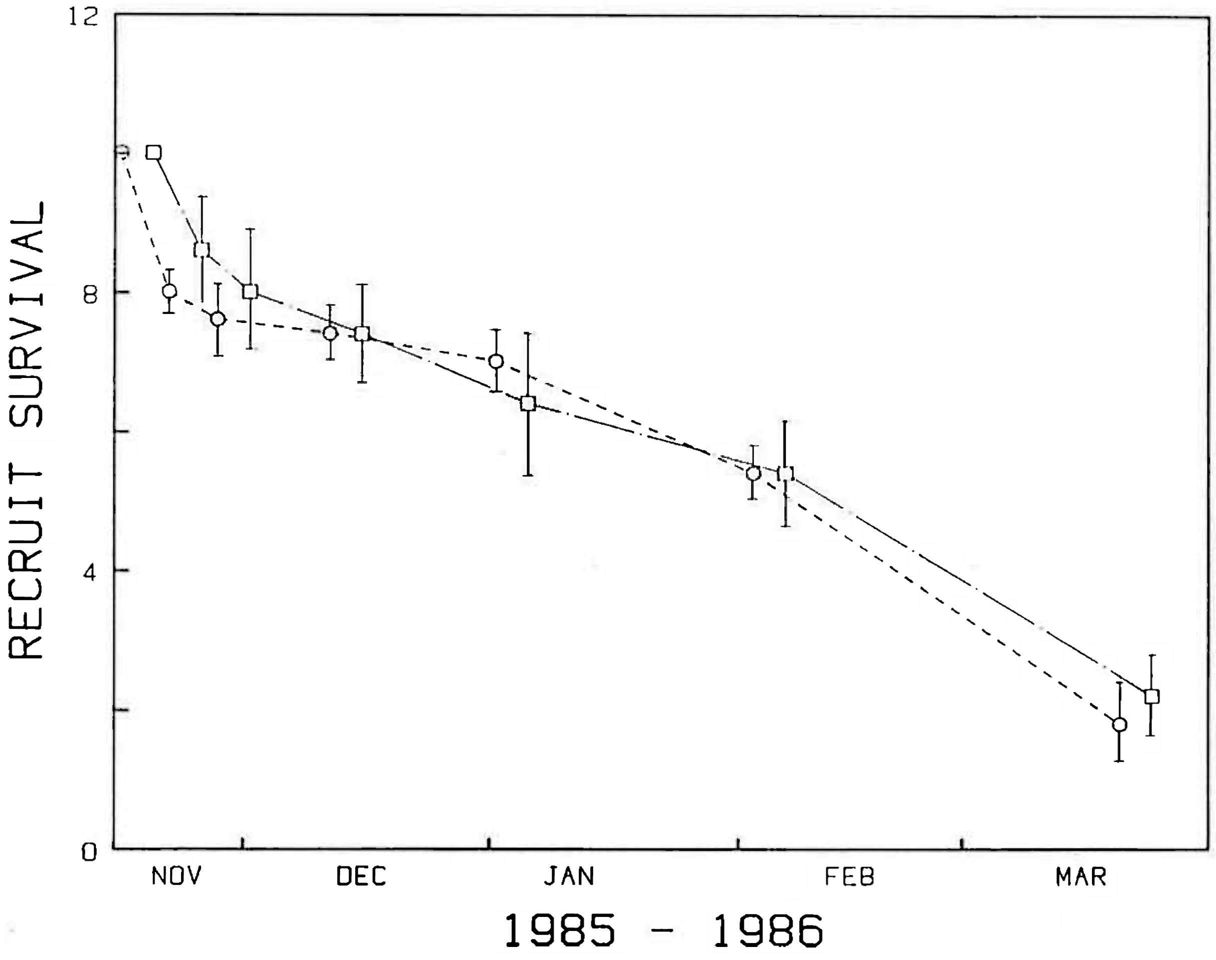

12
8
4
0
RECRUIT SURVIVAL
NOV
DEC
JAN
FEB
MAR
1985 - 1986

Figure 4.4-8 The percentage mortality of recruits versus the weight of incident sediment to which they were exposed during the first 7 days of the experiment. The weight of sediment falling into sediment traps beside both treatment and control wooden plates are plotted. Weight is plotted as g (dry weight) per cm^2, per day (x1000).

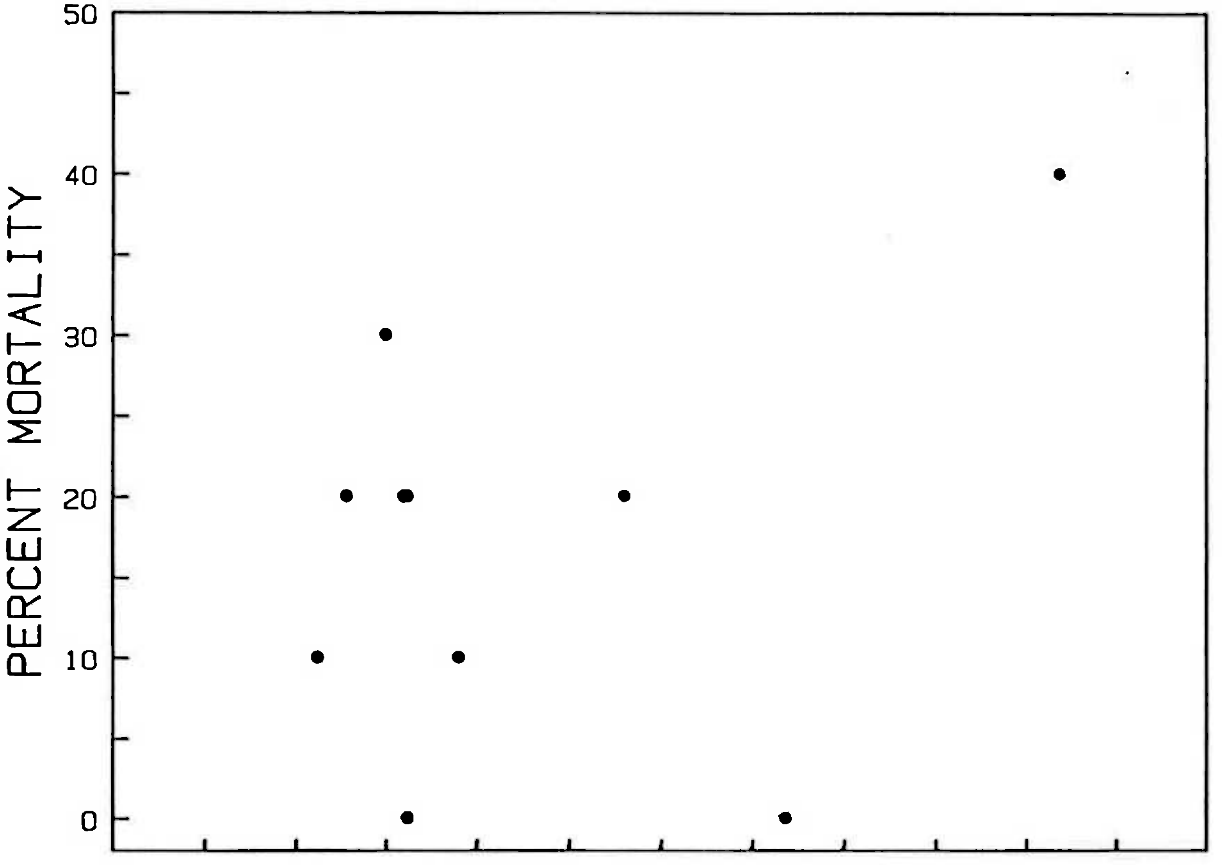

PERCENT MORTALITY
50
40
30
20
10
0
0
.5
1
1.5
2
2.5
3
SEDIMENT (GM/DAY/CM-2 * 1000)

Figure 4.4-9 Survivorship curves of settled *Podoclavella* larvae for the turf clearance and control quadrats. Plots were generated by the actuarial life table method (Cutler & Ederer, 1958) BMDP survival package 1L.

○——○ Turf Clearance Quadrats

●——● Turf Control Quadrats

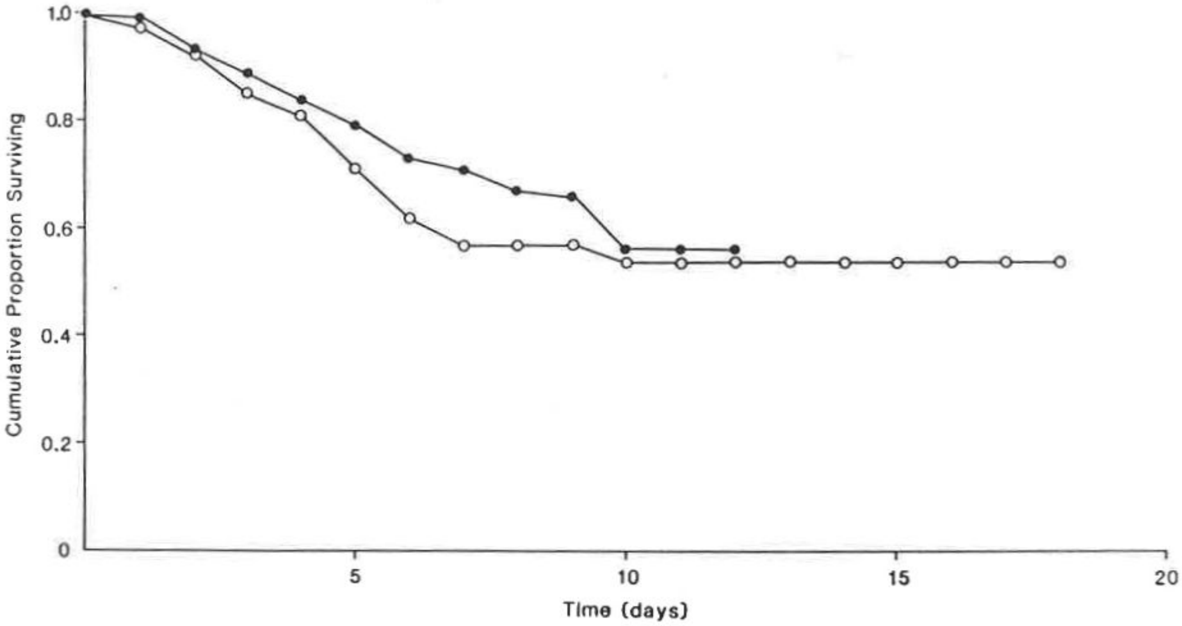

1.0
0.8
0.6
0.4
0.2
0
Cumulative Proportion Surviving
5
10
15
20
Time (days)

Table 4.4-1 Settlement in the opaque PVC box. Observed and expected frequencies of settlers on box faces, and G-test for goodness of fit.

Face	Observed Frequency	Expected Frequency	Difference (Obs.-Exp.)
Top	11	3.3	7.7
Vertical	9	13.3	-4.3
Bottom	0	3.3	-3.3

G-test Statistic = 19.2 df = 2 $P < .001$

Table 4.4-2 Test for independence of settlement in the light and dark halves of the clear and dark PVC box with the five orientations of the box (Fig. 4.4-2). Data were analysed with a 5x2 contingency table.

Box Orientation	Light	Dark
Dark half facing down	0	20
Dark half facing west	15	5
Dark half facing east	17	3
Dark half facing up [a]	15	4
Dark half facing up [b]	12	8

$G = 42.7$ $df = 4$ $P < .001$

[a] n=19, for all other treatments n=20

[b] For this set of trials the inside, as well as the outside, of the box was taped.

Table 4.4-3 Settlement in the clear and dark PVC box - Top half dark. Observed and expected frequencies of settlers on box faces, and G-test for goodness of fit.

Face	Observed Frequency	Expected Frequency	Difference (Obs.-Exp.)
Top	15	3.3	11.7
Vertical (dark)	5	6.7	-1.7
Vertical (light)	0	6.7	-6.7
Bottom	0	3.3	-3.3

G-test Statistic = 42.2 df = 3 $P < .001$

Table 4.4-4a Settlement in the clear and dark PVC Box - Dark half on side, first set of trials (dark half facing west). Distribution of settlers on the faces of the box, observed and expected frequencies of settlers, and G-test for goodness of fit.

Surface	Dark	Light
Top	4	1
Vertical Faces	11	4
Bottom	0	0
TOTALS	15	5

Face	Observed Frequency	Expected Frequency	Difference (Obs.-Exp.)
Top	5	3.3	1.7
Vertical	15	13.3	1.7
Bottom	0	3.3	-3.3

G-test Statistic = 7.6 df = 2 $P < .05$

Table 4.4-4b Settlement in the clear and dark PVC box - Dark half on side, second set of trials (dark half facing east). Distribution of settlers on the faces of the box, observed and expected distribution of settlers, and G-test statistic for goodness of fit.

Face	Dark	Light
Top	4.5*	2
Vertical	12.5	1
Bottom	0	0
TOTALS	17	3

Face	Observed Frequency	Expected Frequency	Difference (Obs.-Exp.)
Top	7	3.3	3.7
Vertical	14	13.3	0.7
Bottom	0	3.3	-3.3

G-test Statistic = 9.0 df = 2 $P < .05$

* Individuals settling on the interface between the top and vertical faces of the box were split between these two categories.

Table 4.4-5a Settlement in the clear and dark PVC box - Dark half facing up, first set of trials (box only taped on outside). Observed and expected frequencies of settlers on box faces, and G-test for goodness of fit.

Face	Observed Frequency	Expected Frequency	Difference (Obs.-Exp.)
Top (light)	5	3.2	1.8
Vertical (light)	10	6.3	3.7
Vertical (dark)	2	6.3	-4.3
Bottom (dark)	2	3.2	-1.2

G-test Statistic = 7.2 df = 3 P>.05

Table 4.4-5b Settlement in the light and dark PVC box - Dark half facing up, second set of trials (both inside and outside of the dark half of the box taped). Observed and expected frequencies of settlers on the faces of the box, and G-test statistic for goodness of fit.

Face	Observed Frequency	Expected Frequency	Difference (Obs.-Exp.)
Top (light)	4	3.3	0.7
Vertical (light)	8	6.7	1.3
Vertical (dark)	6	6.7	-0.7
Bottom (dark)	2	3.3	-1.3

G-test Statistic = 1.1 df = 3 P>.5

Table 4.4-6 Mean number of Podoclavella larvae encountering and settling upon horizontal and vertical substrata within replicate 15 minute periods. Area observed during each period was $400cm^2$ in 1985 and $570cm^2$ in 1984. All observations were made on bare wood.

Face	Orientation with respect to current	Larvae encountering $\bar{X}$	SE	larvae settling $\bar{X}$	SE	n	(hours)
1985							
Vertical	Perpendicular	0.75	0.13	0.33	0.14	12	(3)
	Parallel	0.63	0.06	0	-	16	(4)
Horizontal	Parallel	0	-	0	-	29	(7.5)
1984							
Vertical	Perpendicular	3.16	1.7	1.5	0.81	6	(1.5)

Table 4.4-7 Density of macroalgae (stipe number) and the percent cover of turfing algae within $0.17m^2$ quadrats on vertical and horizontal rock faces at the Inner Reef, Port Noarlunga. All macroalgae occurring within quadrats were *Ecklonia radiata*. Stipe counts were square root transformed prior to calculation of the t value (Cochran's C = 0.65 k=2 df= 17 ns). The percent cover of turfing algae was estimated by projecting quadrats at half their size onto a grid of 464 regularly arranged dots. Percent cover was arcsin transformed prior to the calculation of the t value (Cochran's C = 0.5 k=2 df=9 ns).

Face	No. of macroalgal stipes			Percent cover of turfing algae		
	mean	SE	n	mean	SE	n
Vertical	0.5	0.2	18	23.9	0.5	10
Horizontal	2.1	0.4	16	78.4	0.4	10
	t= 4.9	df= 32	P < .001	t= 7.4	df= 18	P < .001

Table 4.4-8 Dry weight of sediment (mg per cm^2) on horizontal and vertical faces at the Inner Reef, Port Noarlunga. Samples obtained with a modified syringe. Cochran's C=.96 k=2 df=2 ns.

Face	mean	SE	n
Horizontal	81.4	21.0	3
Vertical	8.2	4.1	3

t value = 3.4 df = 4 $P < .05$

Table 4.4-9 Weight of sediment trapped beneath bowls and in control sediment traps. Numbers are dry weights of sediment in g/day/cm^2x 1000. Data in ANOVA table have been square root transformed. Cochran's C=0.89 k=2 df=4 ns.

Treatment	mean	SE	n
Treatment (with bowl)	0.47	0.03	5
Control (no bowl)	0.78	0.12	5

ANOVA TABLE

Source	SS	df	MS	F	P
Between	0.89	1	0.89	5.78	<.05
Within	1.23	8	0.15		
Total	2.12	9			

Table 4.4-10 Survival of colonies at ambient and below ambient levels of sedimentation. Data are from 100cm^2 plates on which 10 larvae were settled. Both treatments were horizontal and the below ambient treatment was produced by positioning a bowl over that plate. Samples from penultimate sampling date. Cochran's C=0.8 k=2 df=4 ns.

Treatment	Mean Survival	SE	n
Ambient Sediment (no bowl)	5.2	0.8	5
Below Ambient (with bowl)	5.4	0.4	5

t value = 0.2 df = 8 P >.5

Table 4.4-11 Analysis of Covariance of total number of larvae settling in the turf clearance experiment. Factors are treatment (fixed), with two levels: cleared and uncleared, and pilings (random) also with two levels. The covariate was the height of each quadrat above the seafloor. Cochran's C=.52 k=4 df=2 ns.

Source	SS	df	MS	F	P	Regression Coefficient
Treatment	109.4	1	109.4	0.56	>.1	
Pile	409.6	1	409.6	6.19	<.05	
T x P	193.6	1	193.6	2.93	>.1	
Covariate	192.3	1	192.3	2.91	>.1	-25.32
Error	463.0	7	66.1			

Table 4.4-12 Sample sizes in turf survival experiment, including survival estimates (75th Quartile) in days and Standard Error (SE). Survival was too high to calculate median survival so 75th quartile is reported.

Treatment	Total	Dead	Alive at end	Percent Alive at end	75th Quartile	SE
Clearance	146	44	102	69.9	4.59	0.4
Control	178	47	131	73.6	5.71	0.5
Totals	324	91	233			

Table 4.4-13 Mean density of Podoclavella colonies amongst long and short strands of algae and analysis of data. Means were calculated from 3, 81cm^2 quadrats placed haphazardly on each plate. Initial density of Podoclavella recruits was estimated by one quadrat placed centrally on each plate two weeks after plates were submerged. Data were analysed by a two factor nested ANOVA. The random plate factor was nested within the fixed algal factor. The plate factor was later pooled with the residual mean square. Cochran's C = .45 k=4 df=2 ns.

Algal Type	Plate No.	Initial density	mean	SE
Long Strands	1	11	2.7	0.7
	3	18	1.0	0.6
Short Turf	2	19	5.0	1.5
	4	8	5.7	1.4

ANOVA TABLE

Source	SS	df	MS	F	P
Algae	36.7	1	36.7	49	>.05
Plates	0.8	1	0.8	0.2	>.5
Residual	35.4	9	3.9		

AFTER POOLING

Source	SS	df	MS	F	P
Algae	36.7	1	36.7	10.2	<.01
Pooled residual	36.2	10	3.9		

Table 4.4-14 Mean colony size (number of zooids) among long and short algal strands and analysis of colony size with a two factor nested ANOVA. The nested plate factor was later pooled with the residual mean square. Data were square root transformed to homogenize variances. Fmax = 5.9 df= 2,3 ns. As no difference in colony size was detected between plates of each algal type the means below are pooled across plates.

Algal Type	Mean Zooid Number	SE	n
Long strands	7.7	2.3	11
Short turf	24.0	3.9	16

ANOVA TABLE

Source	SS	df	MS	F	P
Algae	20.7	1	20.7	38.7	> .05
Plates	0.5	1	0.5	0.24	> .5
Residual	72.3	32	2.3		

AFTER POOLING

Source	SS	df	MS	F	P
Algae	20.7	1	20.7	9.4	<.01
Pooled Residual	72.8	33	2.2		

Table 4.4-15 Mean heights of zooids in Podoclavella colonies among long strands and short turfing algae. Means were calculated from 5 measurements of the highest zooids in each 81cm^2 quadrat. Data were analysed with a two factor nested ANOVA. As no difference in colony size was detected between plates of each algal type the means below are pooled across plates. Fmax=1.2 df=24,29 ns. No zooids were present in one of the quadrats placed among long strands of algae, hence the difference in sample size.

Algal Type	Mean Zooid Height	SE	n
Long strands	16.6	0.9	25
Short turf	27.6	0.7	30

ANOVA TABLE

Source	SS	df	MS	F	P
Algae	1600.3	1	1600.3	213.3	<.05
Plates	7.5	1	7.5	0.4	>.5
Residual	1074.5	53	20.3		

Interpretation

Low numbers of recruits were observed on horizontal upward-facing surfaces. Larvae were not rejecting these surfaces, they simply were not encountering them. In more than 7.5 hours of field observations of such surfaces no larvae were observed to touch them, while encounter and often settlement were observed on vertical surfaces. Thus, patterns of settlement were strongly influenced by the likelihood of larvae touching a substratum, which was influenced, in turn, by the responses of larvae to light and gravity. Podoclavella larvae were photonegative and geonegative at settlement and light- and gravity-sensitive organs, the ocellus and statolyth, were clearly visible under a binocular microscope at 10x magnification.

In the settlement boxes larvae only settled on upward facing surfaces when a light gradient was present and the darkened surface was facing uppermost. But even in these circumstances only 10% of larvae settled on the bottom of the box and time to settle was longer than when the darkened half of the box was at any of the other orientations (Fig. 4.4-2). Hence, even if dark upward-facing surfaces were encountered in the field, larvae are unlikely to settle.

I have stressed the significance of settlement as the determinant of recruit and ultimately adult distribution and abundance on vertical and horizontal surfaces. However, this is not to suggest that post-settlement mortality has no influence on these patterns. Potential sources of post-settlement mortality on vertical and horizontal surfaces, namely sediment, algae and grazers, were more prevalent on the tops of horizontal faces, but much of the evidence for their reducing the survival of recruits was equivocal, based partly on correlations. Owing to uncooperative gastropods the influence of only two of the three potential agents of mortality were considered.

A significant reduction in the levels of sediment flux did not detectably alter the survival of recently settled recruits. It could be postulated that Podoclavella recruits are extremely tolerant of smothering or interfence of feeding by sediment but an alternative explanation is that ambient levels of sedimentation at Edithburgh are too low to kill recruits. Indeed, rates of sedimentation are markedly lower at Edithburgh than at the more exposed, Port Noarlunga, site. It may not be appropriate to consider rates of sedimentation integrated over time. The rate of sediment deposition varies considerably with the resuspension of sediments following wave action or influx of sediment associated with land run-off. Perhaps only levels of sedimentation above a threshold level are sufficient to kill recruits, and these levels were not reached at Edithburgh at the time of my experiments. There was never any evidence of the burial of recruits on the horizontal plates at Edithburgh.

Young & Chia (1984) Documented heavy mortality among ascidian recruits transplanted onto upward-facing surfaces, relative to the mortality of recruits on downward-facing controls. Their experiments may, however, overestimate the impact of sediment. Recruits were placed in the field in small petri dishes and it is highly likely that the sides of the dishes would have retained sediment, thereby increasing the probability of recruit burial.

Short turfing algae did not influence the settlement or post-settlement survival of Podoclavella. In contrast, the presence of long strands of algae was correlated with a reduction in the density and size of Podoclavella colonies. Sweeping by algae can interfere with the settlement of intertidal barnacles and increase their post-settlement mortality (Hawkins, 1983). Yet the net effect of plants on neighbouring organisms may not be adverse, particularly if the organisms are not subject to some of the harmful effects of plants (sweeping, especially). For example, the individual growth rate of a suspension feeding bivalve was significantly greater within a seagrass meadow than in control plots on open sand (Petersen et al., 1984). These workers suggested that bivalve growth rates were enhanced because the seagrass blades were acting as baffles and retaining nutrients.

The examination of post-settlement mortality in this section has produced somewhat tentative results. Without further experiments it is not possible to determine if long algal strands do, in fact, reduce the survival of recruits or if sediment has little influence. The influence of grazers on the survival of recruits was not assessed, but it would certainly be feasible to fix substrata, on which larvae had been settled, onto upward-facing horizontal surfaces in the field. Fences could be erected to exclude gastropods and recruit survival in experimental and control plots compared. This section has, nevertheless, underscored the significance of settlement as a determinant of the distribution and abundance of recruits and adult colonies of Podoclavella.

4.5 DISCUSSION

Settlement was the major proximate determinant of the patterns of recruitment in Podoclavella. The lesser importance of post-settlement mortality stemmed not from well defended or invulnerable newly settled recruits, but from the ability of larvae to discriminate and settle on 'safe sites'. Such behavioral attributes are clearly advantageous and have been observed in a number of invertebrate taxa, including ascidians, barnacles, bryozoans and tube-building polychaetes (Connell, 1961; Grosberg, 1981; Young & Chia, 1981, 1984; Olson, 1983; Woodin, 1985; but see Harriot, 1983).

In Podoclavella the selection of 'safe sites' was a two tiered process involving pre- and post-attachment phases. During the pre-attachment phase larvae showed a negative phototaxis and a negative geotaxis. They were, therefore, more likely to touch vertical or downward-facing horizontal surfaces (overhangs) than upward-facing surfaces. It follows, then, that they were unlikely to settle on upward-facing surfaces and be swept by algae, buried or abraded by sediment, or 'bulldozed' by grazers. Preferential settlement on vertical or downward-facing surfaces has been documented for the larvae of several invertebrate taxa (Cole & Knight-Jones, 1939; Crisp & Ghobashy, 1971; Crisp, 1974). The larvae of these taxa possess light and, often, gravity sensitive structures (Burke, 1983). With the demonstration that mortality is markedly higher on upward-facing than on downward-facing surfaces (Olson, 1983; Young & Chia, 1984), Young and Chia suggested that "post-settlement mortality may... represent selective pressures that maintain negative phototaxis in the behavioral repertoire of ascidian tadpoles" . I agree with these authors and view post-settlement mortality as the ultimate determinant of the distribution and abundance of Podoclavella on vertical and horizontal surfaces.

On touching a substratum, Podoclavella larvae attached and the second tier of the settlement process ensued - acceptance or rejection of that substratum. On accepting a substratum larvae metamorphosed, while rejection was accomplished by detachment and swimming away. Larvae settling in a diverse epifaunal community may encounter a large number of potentially suitable substrata and Podoclavella larvae were highly discriminating, consistently rejecting some substrata and accepting others. The rejection of substrata by invertebrate larvae is not always preceded by contact (Young & Chia, 1981), but an important component of the discrimination between substrata by Podoclavella was the attachment of the larvae to the surface of the substratum, indicating that surface properties were important.

Surface contour and surface chemistry are important determinants of the settlement preferences of invertebrates (Crisp & Barnes, 1954; Dyrynda, 1984). The influence of surface contour on the settlement of Podoclavella was not assessed. However, ascidian larvae possess sensory receptors on their adhesive papillae (summarized in Burke, 1983) and there is strong evidence that chemical properties of the surface are an important determinant of larval preference (Table 4.3-2,3).

Many epibenthic taxa, particularly colonial species, possess secondary metabolites which presumably function to deter epibionts, endobionts and predators (Dyrynda, 1984). The effectiveness of these chemicals as deterrents will depend, at least partly, on their toxicity and, indeed, in the Porifera the degree of fouling has been negatively correlated with the toxicity of these metabolites (McCaffrey & Endean, 1985; Thompson et al., 1985). At settlement Podoclavella showed the highest preference for bare wood, a substratum that does not produce toxic metabolites. On the other hand the relatively unfouled and presumably toxic sponges Dendrocia sp. and Mycale sp. were often rejected (Table 4.3-1, Fig. 4.3-1). The consistent rejection of Mycale sp. was probably a response to negative chemical cues, since in the field, extracts of Mycale sp. were most often rejected.*

The toxicity of these secondary metabolites is a potentially potent selective force in moulding the settlement preferences of larvae. For example, the exposure of larvae to tissue excised from several taxa, including Porifera, Cnidaria, Bryozoa and Ascidiacea, can result in the death of a high percentage of larvae within 5 hours (Dyrynda, 1984). Hence, settling on these substrata would almost certainly result in death or disadvantageous sublethal effects, such as a reduction in fecundity. The avoidance, by Podoclavella larvae, of the unfouled matrix of what appear to be the two most toxic sponge species, Mycale sp. and Dendrocia sp., suggests that mortality stemming from exposure to toxic metabolites should be uncommon. It was the settlement of larvae on ephemeral, rapidly overgrown or easily dislodged substrata that was one of the most important sources of early-recruit mortality observed at Edithburgh Jetty. This mortality stemmed largely from the inability of larvae, in the absence of searching behaviour, to determine the proximity and taxonomic identity of neighbouring organisms.

The number of adult Podoclavella colonies was largely determined by the number of settling larvae. Positive relationships were apparent between the number of settling larvae and subsequent recruitment, and between the number of recruits and adult colonies. Variation in recruitment, equivalent (from the above) to variation in settlement, had a marked influence on the subsequent mortality experienced by recruits. At low levels of recruitment (less than 1 recruit per dm^2), mortality was invariably 100% and at high recruitment levels (more than 10

*** See addendum on back cover**

recruits per dm^2) mortality was also high, although rarely 100%. At moderate levels of recruitment, mortality was markedly lower but varied between years. Mortality at moderate densities of recruits fell to as low as 20% in 1984 but went no lower than 65% in 1985. At low densities of recruits few if any adults survived, while at high densities some adults were almost always produced as mortality rarely reached 100%. Recruit densities of between 3 and 12 per dm^2 usually produced an adult colony density of 1 per dm^2. Adult colony densities at Edithburgh were not observed to exceed 3 colonies per dm^2 and this would seem to be the upper limit of adult density. The maximum theoretical density of adult colonies, based on the area of attachment of a colony 100 zooids in size (Fig. 2.2), was 10 per dm^2. The area of attachment probably represents an underestimate of the area required by a colony, however.

This chapter underscores the significance of the density of settlement from the plankton as an important determinant of the distribution and abundance of the adults of marine invertebrates. Several workers have been advocating a shift in emphasis from the examination of factors operating on the distribution and abundance of organisms after their arrival from the plankton, to consideration of the influence of the vagaries of larval settlement (Dayton, 1979; Denley & Underwood, 1979; Dayton & Oliver, 1980; Underwood & Denley, 1984). Where the influence of initial settlement has been examined it was often an important determinant of the distribution and abundance of species, even community structure (Yoshioka, 1982; Connell, 1985a; Gaines & Roughgarden, 1985; but see Stoner, 1986).

Post-settlement mortality acted in concert with settlement to produce the patterns of recruit and adult distribution and abundance, but daily observations of permanent quadrats could not identify many of the sources of post-settlement mortality to which Podoclavella was exposed. In the following chapter I assess experimentally the influence of one of these, namely predators.

CHAPTER FIVE

The Effect of Predators

5.1 INTRODUCTION

On rocky intertidal shores, predators may act to free space which might otherwise be occupied by competitive dominants (e.g. Paine, 1974). Jackson (1977) predicted that predation would be of less significance in the subtidal zone as colonial organisms are not so vulnerable to predators. Whereas predation is usually fatal to solitary organisms, the removal of portions of colonies rarely proves fatal (Randall & Hartman, 1968; Reiswig, 1973) and the subsequent regrowth of damaged colonies permits rapid recovery from predation events (Ayling, 1981). In addition, colonial organisms may be protected by skeletal elements, such as spicules and spines (Yoshioka, 1982; Keough, 1984a). Possession of toxic chemicals may also deter predators (Russell, 1966; Burkholder, 1973).

Empirical evidence that predators are inconsequential to colonial organisms is provided by the observations of Bak *et al.*, (1981) and the manipulations of Keough & Butler (1979). It appears that the prediction of Jackson holds for *adult* colonies at all but intense grazing pressures (Sebens, 1985). However, predators may have a profound effect on the early benthic stages of colonial organisms. Soon after settlement, many colonial animals are vulnerable to predators and their removal may have a profound effect on community structure (Russ, 1980; Ayling, 1981; Keough, 1984a).

In this chapter I examine the effect of predators on *Podoclavella*, placing particular emphasis on early benthic stages of the life cycle; recruits and juvenile colonies.

Clavelinid ascidians are renowned for their ability to regenerate following damage, so it was important to determine if predators were in fact capable of killing colonies. Colonies of different ages (sizes) were artificially 'preyed upon' and their subsequent survival observed.

The impact of predators on recruits of Podoclavella was examined in two caging experiments and by tethering predators. The aim of the pilot caging experiment was to determine if predators had a detectable impact and, if so, how this impact varied in different areas. The second caging experiment examined the relative impact of crab and fish predators. Finally, crabs were tethered over recuits to distinguish direct predation from trampling.

The interpretation of caging experiments may be hampered by artifacts (Hulberg & Oliver, 1980; Underwood & Denley, 1984). Cages are likely to modify incident light, sediment flux, and water movements. Appropriate cage controls were difficult to design for the pilot experiment as the predators of Podoclavella were not known. Keough (1981) and Choat (1982) have suggested that in such instances it should be assumed that caging artifacts are present. They stress the importance of demonstrating that changes in abundance result from mortality in uncaged areas and not preferential settlement within cages. In the caging experiments described in this chapter, recruits of Podoclavella were large enough for me to distinguish mortality from preferential settlement.

A large number of animal groups have been observed feeding on ascidians (Millar, 1971). At Edithburgh several likely candidates as predators of Podoclavella can be ignored based on studies of their diets or occurrence. Starfish were unimportant as predators of Podoclavella, although the eleven armed starfish, Coscinasterias calamaria (Gray), was occasionally observed consuming this ascidian (Keough & Butler, 1979). The magpie perch, Cheilodactylus nigripes Richardson, was observed foraging on pilings, but Cappo (1980) demonstrated that this fish did not consume colonial benthic invertebrates. The urchin, *Phyllacanthus irregularis* Mortensen, occurs at very low densities and was not observed on the jetty pilings.

Based on my own observations two groups could not be excluded as predators of *Podoclavella*, namely crabs and monacanthid fishes. Three crab species were commonly observed on the pilings, the dromiid *Cryptodromia octodentata* (Haswell), the grapsid *Plagusia chabrus* (Linnaeus) and the majid *Schizophrys aspera* (M. Edwards). Schools of juvenile monacanthids, the horseshoe leatherjacket *Meuschenia hippocreppis* (Quoy & Gaimard) and the six spined leatherjacket *Meuschenia freycineti* (Quoy & Gaimard), were often observed under the jetty. The second caging experiment was designed to separate the effects of these two groups.

5.2 MATERIALS AND METHODS

Simulated predation:

The ability of juvenile (two to three months old) and adult (seven to nine months old) Podoclavella colonies to survive damage was examined by experimentally removing tissue. Colonial ascidians, particularly the clavelinids, are renowned for their regenerative ability. Therefore, to examine the affect of predators on survival, it was necessary to inflict considerable damage to colonies. Each 'predation event' consisted of the removal of all zooids at their point of attachment to the colony. Zooids were removed with a razorblade. Control colonies were touched in the same position with the blunt side of the razorblade. Following damage, the growth and survival of colonies was monitored for up to five months or until the animal died.

In the initial experiment (July 20, 1983) two stages of adult colony development were damaged; colonies with functional zooids and colonies with degenerate zooids. Six 'degenerate' colonies and six 'functional' colonies were selected, half of these were then damaged, as outlined above, and the remainder served as controls (Table 5.1). Damage in the degenerate colonies consisted of removal of all elevated 'white-blobs', leaving approximately the same thickness of colony adherent to the piling as in colonies with functional zooids. This experiment was repeated in 1984 (May 21) but only colonies with functional zooids were damaged. Eight colonies were selected, half of these were damaged and the remainder served as controls.

In assessing the impact on juvenile colonies, ten colonies each of around ten zooids in size were selected on January 26, 1984. Half of these were damaged just as the adult colonies had been and the remainder were controls. The size of colonies was reexamined on February 24.

Caging Experiments:

The impact of predators on newly settled recruits was assessed in two caging experiments. The first, a pilot experiment, served to determine patterns of spatial variation in predation and facilitated calculation of the power of the controlled (second) experiment (Table 5.2). In the pilot experiment predators were excluded from areas of substratum using cages, with uncaged areas serving as controls. Thirty two areas measuring 40x30cm were cleared of epifauna on four pilings. Clearances were made with a diving knife, then areas were thoroughly scrubbed to ensure the complete removal of invertebrates that were capable of regrowing from small remnants. Sixteen cages, measuring 20x30x6cm, were constructed of zinc-plated trellis wire (one mesh per 12.6mm, wire diameter = 0.8mm). Four cages were nailed into place on each piling and four uncaged areas were delineated with a small galvanized-iron nail. All treatments were arranged between 2 and 4 metres above the seabed. The arrangement of caged and uncaged areas on the four pilings is summarised in Fig. 5.1.

Clearances of epifauna and the erection of cages were performed just prior to the release of larvae in 1983. Counts of the number of recruits and later zooids (when individual colonies became difficult to distinguish) were performed periodically with a 25x16.6cm quadrat. To facilitate counts this quadrat was split into six subquadrats of equal area (69cm^2).

At first monitoring, the cages were opened at the top with side cutters, allowing entry of the quadrat. After monitoring the cage was closed, by bending the mesh, and reopened on subsequent monitoring. Cages became fouled with algae and hydroids and were scrubbed every three to five weeks.

On the date of final monitoring the numbers of zooids in caged and uncaged areas were compared with a two factor analysis of co-variance (ANCOVA). The factors were pilings (random) and treatments (fixed) with height of cages above the sea bed as a covariate.

The second caging experiment was done in 1985. This experiment was designed specifically to investigate the impact of monacanthid fishes and crabs on newly settled recruits. Complete cages excluded both groups of animals. Roofs excluded monacanthid fishes but permitted the entry of crabs. Monacanthid fishes orient perpendicular to the substratum when feeding (Ayling, 1981) and were therefore excluded by roofs. Fences, constructed with tops turned outwards, were designed to keep out crabs and allow fish access. Areas upon which structures were not erected served as controls. The construction of the treatments is illustrated in Figure 5.2 and the experimental design summarized in Figure 5.3.

Cage design was slightly modified from that used in the pilot experiment. Their height was increased from 6 to 7cm, while the other dimensions remained at 20x30cm. The mesh size of the trellis wire was increased (one mesh per 25.4mm, wire size=1.6mm) in an attempt to reduce light attenuation by algal and hydroid fouling. Cages, fences and roofs were scrubbed every three to four weeks and did not become as fouled as the cages in the pilot experiment.

This experiment was initiated just prior to larval release and settlement in 1985. Zones measuring 50cm wide were cleared of epifauna on five pilings. Care was taken to ensure the complete removal of all encrusting benthic invertebrates. The lower boundary of these clearings was 2.75m above the sea bed. The four treatments were haphazardly positioned, one onto each of the four main compass directions on each piling.

In the ensuing three months this experiment was monitored on three occasions. On first monitoring, recruitment was measured in all treatments twenty days after the experiment was initiated. Six weeks after initiation the number of colonies in each treatment was counted and for two of the pilings, selected at random, the size of every colony was recorded. Finally, three months after the experiment had been initiated, the total number of zooids in each treatment was counted. Unfortunately it was no longer possible to distinguish between colonies. Counts were made with the same quadrat as used in the pilot study. The quadrat was placed against the piling in the fenced and open areas, while counts were performed through the mesh of the roof and total exclusion cage. The much larger mesh size used in this experiment facilitated these counts through the mesh.

I had intended to analyse this experiment as a two factor ANOVA with repeated measures on the two orthogonal factors, fishes (fixed) and crabs (fixed), on the five replicate pilings. Jennrich et al. (1983 p.372) discuss the analysis of an analagous design. However, in the course of this experiment it became clear that patterns of settlement into the treatments were strongly influenced by current direction. Treatments on the downcurrent side of pilings received large numbers of settlers owing to eddies increasing the chance of larvae encountering the substratum. As treatments had been placed haphazardly on pilings it was not feasible to consider the orientation of treatments as a factor in the analysis. Instead, colony survival or zooid number were converted to the percentage of initial recruits and these data analysed.

The species and number of crabs on each of the pilings on which the experiment was established were counted regularly. The sizes of schools of monacanthid fishes observed in the vicinity of the experiment were estimated and recorded. Counts of crabs were analysed as a two factor ANOVA, with crab species (fixed) and pilings (random) as factors.

Times were treated as replicates, with census intervals of several days to several weeks.

An experiment to distinguish the relative impact of crab feeding and 'trampling' on recently settled *Podoclavella* recruits was done just after the annual settlement of *Podoclavella* had finished at Edithburgh Jetty (late December, 1986). Crabs with the movable finger of each chela removed, and normal crabs, were tethered over recruits of *Podoclavella*. Normal crabs could potentially have a trampling *and* feeding effect whilst any effect due to crabs without functional chelae would result from trampling alone. Two crab species, *Plagusia chabrus* and *Schizophrys aspera*, were tethered onto a 40cm race of Nichrome wire supported 6cm above the substratum by two nails 8cm in length. A thin 10cm long wire trace was attached to the nichrome wire with a fishing swivel and the free end was fixed to a crab by inserting a plastic anchor tag (FLOY FT-1, commonly used to tag commercially fished crabs) into the suture between the carapace and first abdominal segment.

In this experiment there were 4 treatments, each crab species with and without clipped chelae, and a control (nichrome wire but no tethered crab). Three replicates were used in each treatment, with only one tethered crab in each replicate. The placement of replicates in this experiment was not random. All replicates were positioned 1.75m above the seabed, on the northern face of pilings. Areas of predominantly bare space with a moderate to high density of recruits were selected. Treatments were assigned to areas randomly.

The number of recruits within a 0.18m^2 quadrat, placed over each length of nichrome, was counted before and 15 hours after crabs were tethered. This experiment was run overnight as these crab species were more active at night (pers. obs.).

This experiment was run for only 15 hours as it was feared that crabs deprived of their usual prey may alter their behaviour and perhaps damage or consume recruits of Podoclavella as an artifact of being tethered. Furthermore there was a risk of crabs being eaten by predators.

5.3 RESULTS

Simulated predation:

These experiments revealed that adult colonies were capable of sustaining high levels of damage and surviving. In both years all treatment (damaged) and control colonies survived, irrespective of whether the zooids removed had been functional or degenerate. In addition, the rate of regeneration of these ascidians was remarkable. Plots of changes in colony size show that damaged colonies rapidly assume sizes (zooid numbers) which are comparable to the undamaged control colonies (Fig. 5.4). So rapid was their regeneration that no differences in colony size were detected among any treatments on the first date of monitoring after colony damage (1983 (25 days after damage) - F=1.6 df=1,10 $P > .05$, Table 5.3; 1984 (36 days after damage) - t=.24 df=6 $P > .5$). Terms were removed from the 1983 ANOVA model using the pooling procedures of Winer (1971), but the treatment effect remained non-significant (Table 5.3).

Also apparent in the plots of colony size was a depression in the size of control colonies in August, 1983. This was most likely the result of degeneration and subsequent regeneration of these controls.

Damaged colonies may have been able to assume the size of control colonies so quickly by producing small zooids. This was not the case, however. Measurements of zooid heights in 1984 revealed no significant differences between damaged and undamaged colonies 36 days after manipulation (F=0.2 df=1,6 $P > .05$), although considerable inter-colony variation in zooid heights was observed (F=21.2 df=6,32 $P < .001$, Table 5.4). *

The survival of juvenile colonies was very poor following similar levels of damage. At first monitoring, 24 days after damage had been

*** See addendum on back cover**

inflicted, all damaged colonies had disappeared while control colonies remained healthy (Table 5.5). The positions of only four of the five replicate colonies in each treatment were relocated.

Predators:

Only two predators were positively identified in more than 650 hours of observations at Edithburgh Jetty . The most abundant of these, numerically and in biomass, was the side-gilled sea slug, Pleurobranchus hilli (Hedley). This mollusc occurred seasonally at Edithburgh and was not observed at Port Noarlunga. The presence of large numbers of spawn coils (Fig. 5.5) and the frequency of copulating pairs indicates that these molluscs move into the shallow waters of Edithburgh Bay to reproduce. Observations during the day, and at night, indicated that these large pleurobranchs (the smallest individual observed was 13.25 cm in length) seldom venture onto pier pilings and no individuals were ever observed more than 1.5m above the sea bed on a piling. The removal of two individuals from pilings and examination of their gut contents revealed them to be packed full of Podoclavella zooids, which indicates that this mollusc may have a significant impact on these ascidians, particularly colonies at the bases of pilings. The second predator, a flatworm, Pseudoceros sp., occurred at both sites but was seldom encountered.

Caging Experiments: Interpretation of the results of the pilot caging experiment was hampered by a significant interaction term in the two factor ANCOVA ($F=4.45$ $df=3,23$ $P < .05$). Plots of mean zooid numbers in caged and uncaged treatments on each piling indicated that predators affected recruit survival on two pilings but not on the remaining two (Fig. 5.6a,b). Uncaged areas on two pilings had significantly depressed numbers of zooids, with mean values per piling of 12 and 13.7 zooids. All other areas had mean zooid numbers of 260 or greater. An a-posteriori comparison between means using Tukey's HSD showed that the two uncaged treatments with low survival were significantly different from all other treatments (Table 5.6). The covariate, height of area above the seabed, was not significant.

It is noteworthy that through December caged areas on all pilings showed an increase in zooid numbers. Over the same period, uncaged areas on three piling showed either stasis or a reduction in zooid numbers (Fig. 5.6a,b).

The second caging experiment, investigating the impact of crabs and monacanthid fishes on the survival of recruits, revealed that treatments to which crabs had access, the roofed and open areas, showed significant reductions in colony survival 20 days after recruitment was quantified (Table 5.7). The percentage of colonies surviving in the presence of crabs was, on average, around 60%. When crabs were excluded survival within cages was almost 90% and over 110% in fenced areas. Survival values exceeding 100% resulted from settlement after the initial monitoring at 21 days.

Colony sizes of recruits after 6 weeks revealed the same pattern. Colonies exceeding 5 zooids in number were common only in treatments from which crabs had been excluded and no colonies of this size were recorded in the open treatments (Fig 5.7).

The mean number of zooids in each treatment after 3 months revealed the same pattern as that observed after 6 weeks (Table 5.8, Fig. 5.8). Treatments to which crabs gained access had significantly reduced numbers of zooids, with one exception, the roofed treatment on piling 4. As this treatment was on the upcurrent side of this piling it received a low number of recruits, but, unexpectedly, subsequent survival was remarkably high. High survival in this treatment on this piling was responsible for the heteroscedasticity which was detected (Cochran's C=.73 k=4 df=4 $P < .05$). A log transformation failed to reduce this heterogeneity and the raw data were analysed instead.

The results of this experiment were consistent with my own observations. Crabs, particularly the grapsid, *Plagusia chabrus*, were often observed moving across the roof and open control treatments. The fenced treatment and complete exclusion cages were effective in excluding crabs. No effect due to monacanthid fishes was detected and although schools of monacanthids were observed in the vicinity of the experiment, they were not observed to feed in any of the treatments (Fig. 5.9).

The densities of crabs were not significantly different among the 5 pilings in this experiment (Table 5.9). However, significant differences in the densities of different crab species were detected. The dromid, *Cryptodromia octodentata*, was twice as abundant as the other two crab species, with a mean density (pooled across time) of 1.6 individuals per piling. Densities of *Plagusia chabrus* and *Schizophrys aspera* were not significantly different with, on average, 0.5 and 0.8 individuals per piling, respectively.

The analysis and interpretation of the crab tethering experiment was hampered by the loss of replicates. Several specimens of *Plagusia* broke free from their tethers and most individuals of *Schizophrys* died just prior to their being tethered to pilings. *Plagusia* was a large, fast moving grapsid with an approximate carapace width of up to 10cm. Three of the tethered individuals pulled out the plastic tag and escaped. One of these crabs had escaped within 30 minutes of initiating the experiment and so this replicate was dropped from the analysis. The other two individuals broke free during the night and data from these replicates were included in the analysis. Surprisingly, a fourth individual died just prior to being tethered on a piling, despite its chelae not being clipped.

Schizophrys was a more gracile species with a maximum carapace width of approximately 5cm. All individuals with clipped chelae died just prior to initiating the experiment. In addition, one undamaged individual died. At the time it was unclear whether these crabs were simply feigning death so all individuals were tethered and replicates with dead crabs were later included with the controls in the analysis.

The number of recruits in each $0.18m^2$ quadrat varied between 54 and 430 prior to the introduction of crabs and the percentage change in the number of recruits was calculated (Table 5.10). Small errors in the counting of recruits produced an apparent increase of up to 4% during the experiment. Heterogeneity among the variances was implied (Fmax = 247) although there were insufficient degrees of freedom to confirm this suspicion. This heterogeneity stemmed from a large variance associated with the Plagusia treatment that had clipped chelae. The reduction in the number of recruits was large (41%) in one replicate and much smaller in the other (11.4%). In view of their inherent heterogeneity these data were analysed by a non-parametric test, the Kruskal-Wallis test (Sokal & Rohlf, 1981). Significant differences were detected among the treatments and control ($H= 8.4$ $df= 3$ $P < .05$) and an a-priori comparison of the two treatments of interest, Plagusia with and without clipped chelae, showed no significant differences ($t=0.32$ $df=2$ $P > .5$). As no differences were detected in the later comparison, the violation of the assumption of homogeneity between the variances did not matter (Underwood, 1981).

Attempts to observe the feeding behaviour of both crab species at night proved unsuccessful. Schizophrys was occassionally observed standing over colonies of Podoclavella in a feeding posture, but as soon as the torch beam was directed at the crab it would raise its chelae in threat or move away. The behaviour of Plagusia was also altered by attempts to make observations at night. These crabs struck opportunistically at plankters attracted by the bright light, although some individuals appeared to be searching for gastropods.

Figure 5.1 The arrangement of caged and uncaged treatments on the four pilings of the pilot caging experiment.

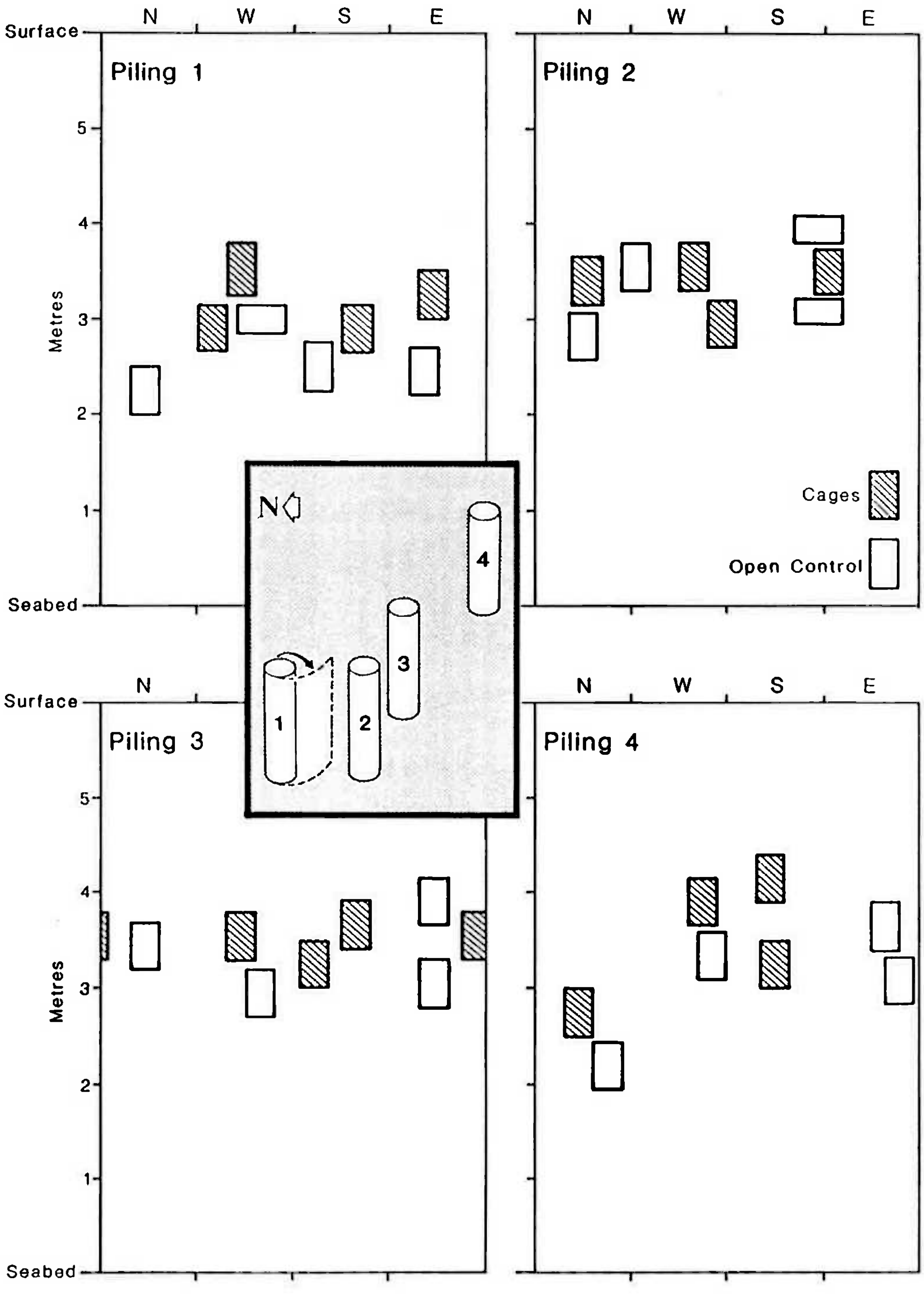
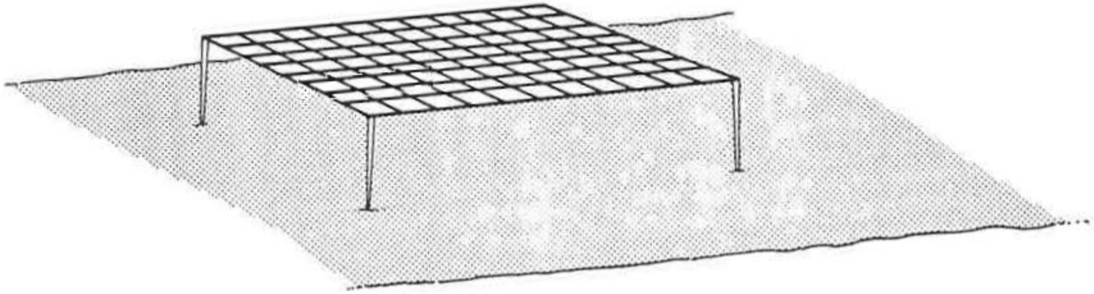
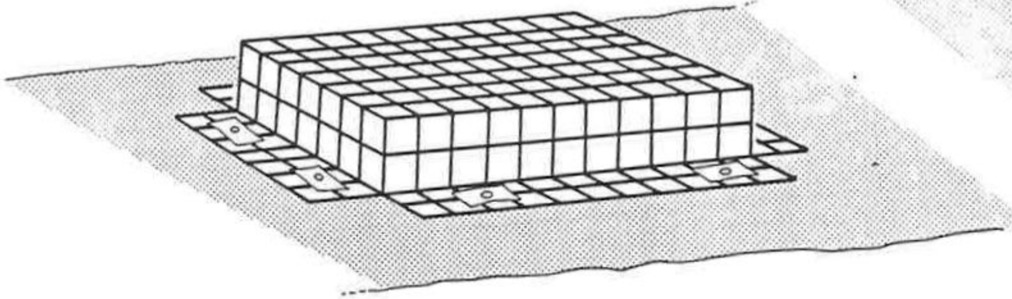

Surface
N
W
S
E
Piling 1
Piling 2
Piling 3
Piling 4
5
4
3
2
1
Metres
Seabed
Cages
Open Control
N
1
2
3
4

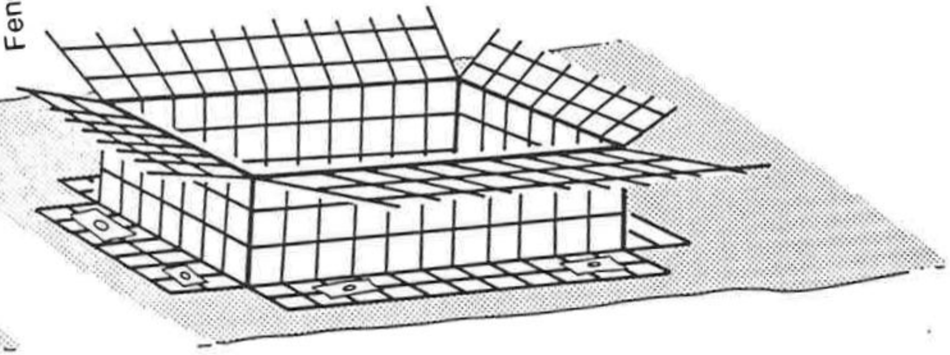
Figure 5.2 The caging treatments used in the experiment to separate the impact of crabs and monacanthid fishes.



Roof



Cage



Fence

Figure 5.3 The experimental design and arrangement of treatments in the caging experiment examining the impact of crabs and monacanthid fishes on recruits of *Podoclavella*. Numbers represent the number of replicates.

R = Roof
C = Cage
F = Fence
O = Open (Control)

	+ Fish	− Fish
+ Crabs	5	5
− Crabs	5	5

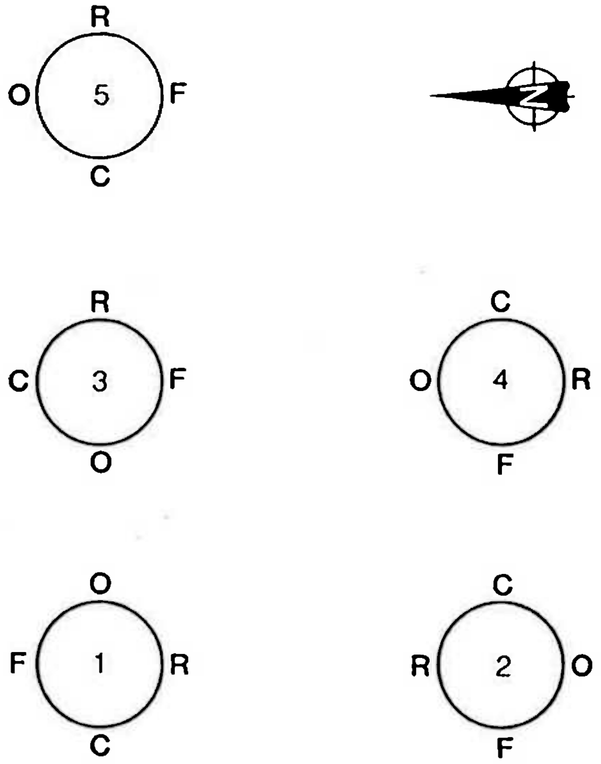


Figure 5.4 Changes in colony size, as a percentage of premanipulation size, following the infliction of artificial damage to adult colonies of *Podoclavella*. Arrows indicate the date on which damage was inflicted. Data are means (1983 - n=3, 1984 - n=4). Error bars represent standard errors of the mean.

Functional Colonies	Damaged	●————●
	Undamaged	○---------○
Degenerate Colonies	Damaged	▲·—·—·—·▲
	Undamaged	△··········△

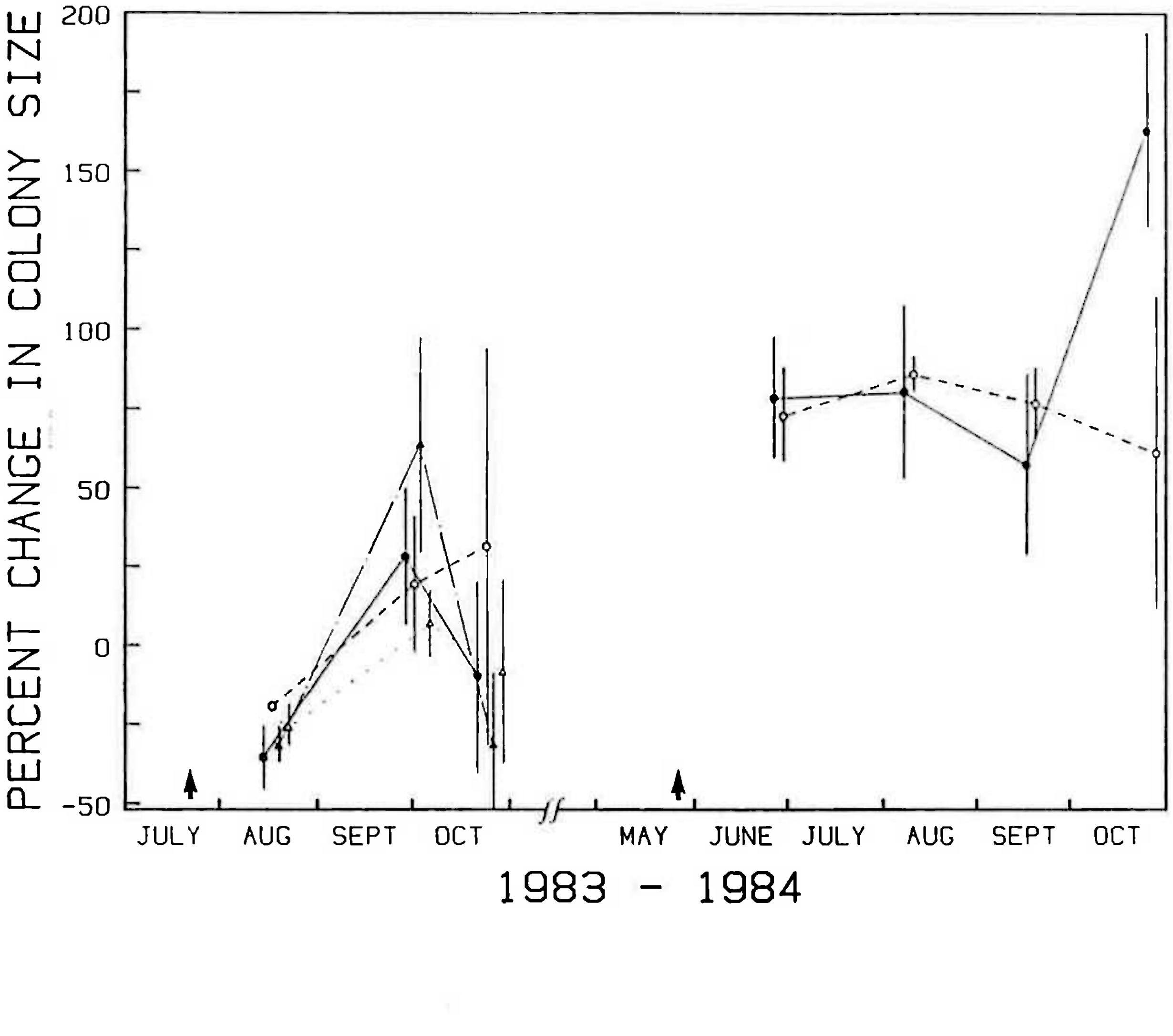

PERCENT CHANGE IN COLONY SIZE
200
150
100
50
0
-50
JULY
AUG
SEPT
OCT
MAY
JUNE
JULY
AUG
SEPT
OCT
1983 - 1984

Figure 5.5 Frequency of occurrence of the pleurobranch, *Pleurobranchus hilli* and the spawn coils of this mollusc over three years beneath Edithburgh Jetty. On each occassion all *P. hilli* individuals and spawn coils were counted beneath the Jetty (1600m^2). So few counts were made in 1983 that they were not joined to the remainder of the data set.

▲———▲ *Pleurobranchus hilli*

●- - - -● Spawn coils

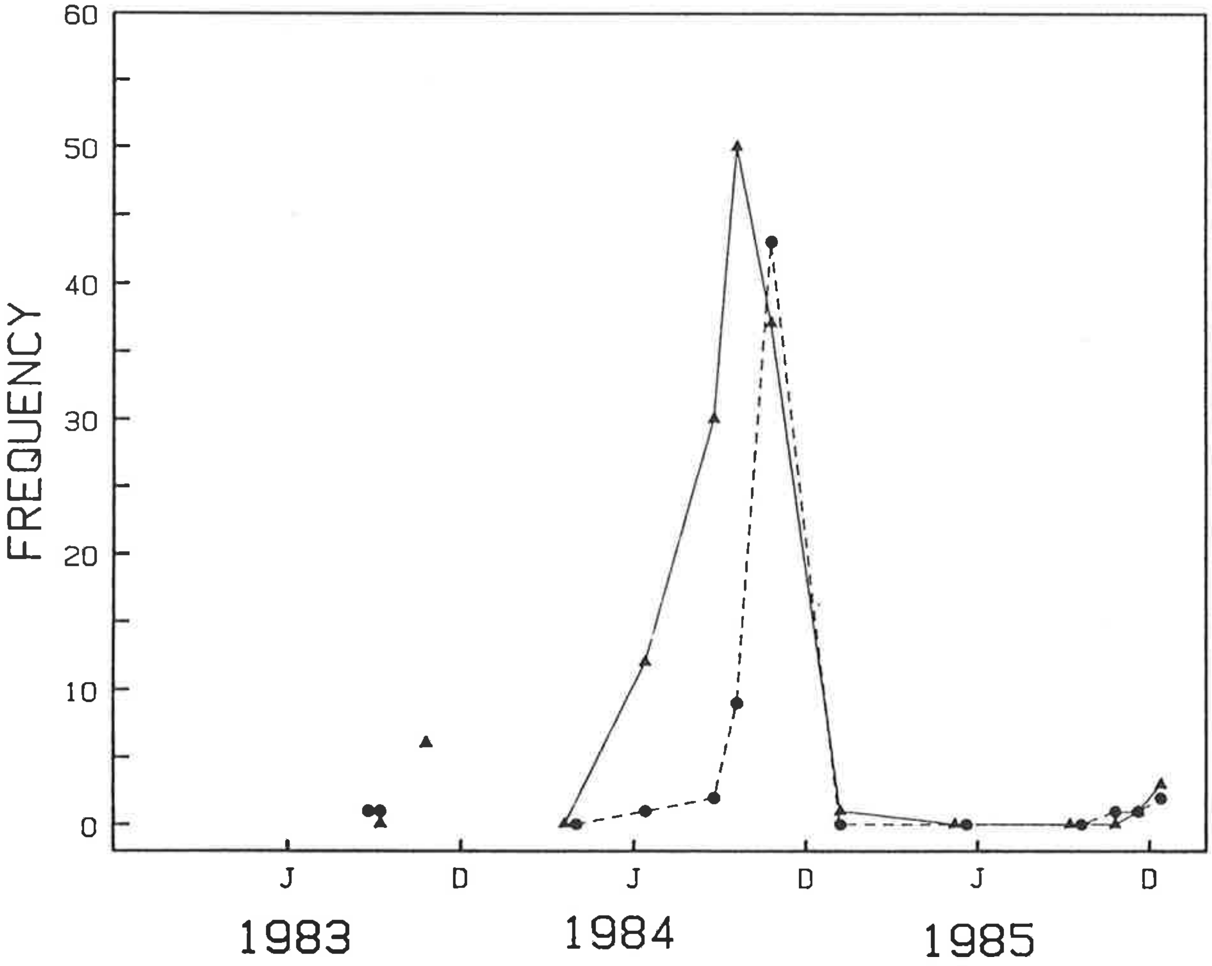

60
50
40
30
20
10
0
FREQUENCY
J
D
J
D
J
D
1983
1984
1985

Figure 5.6 Changes in zooid number with time in the pilot caging experiment. Data are means (n=4) and error bars represent the standard error of the mean.

A

Piling 1
Caged ●———●
Uncaged ○———○

Piling 2
Caged ■- - - - -■
Uncaged □- - - - -□

B

Piling 3
Caged ●———●
Uncaged ○———○

Piling 4
Caged ■- - - - -■
Uncaged □- - - - -□

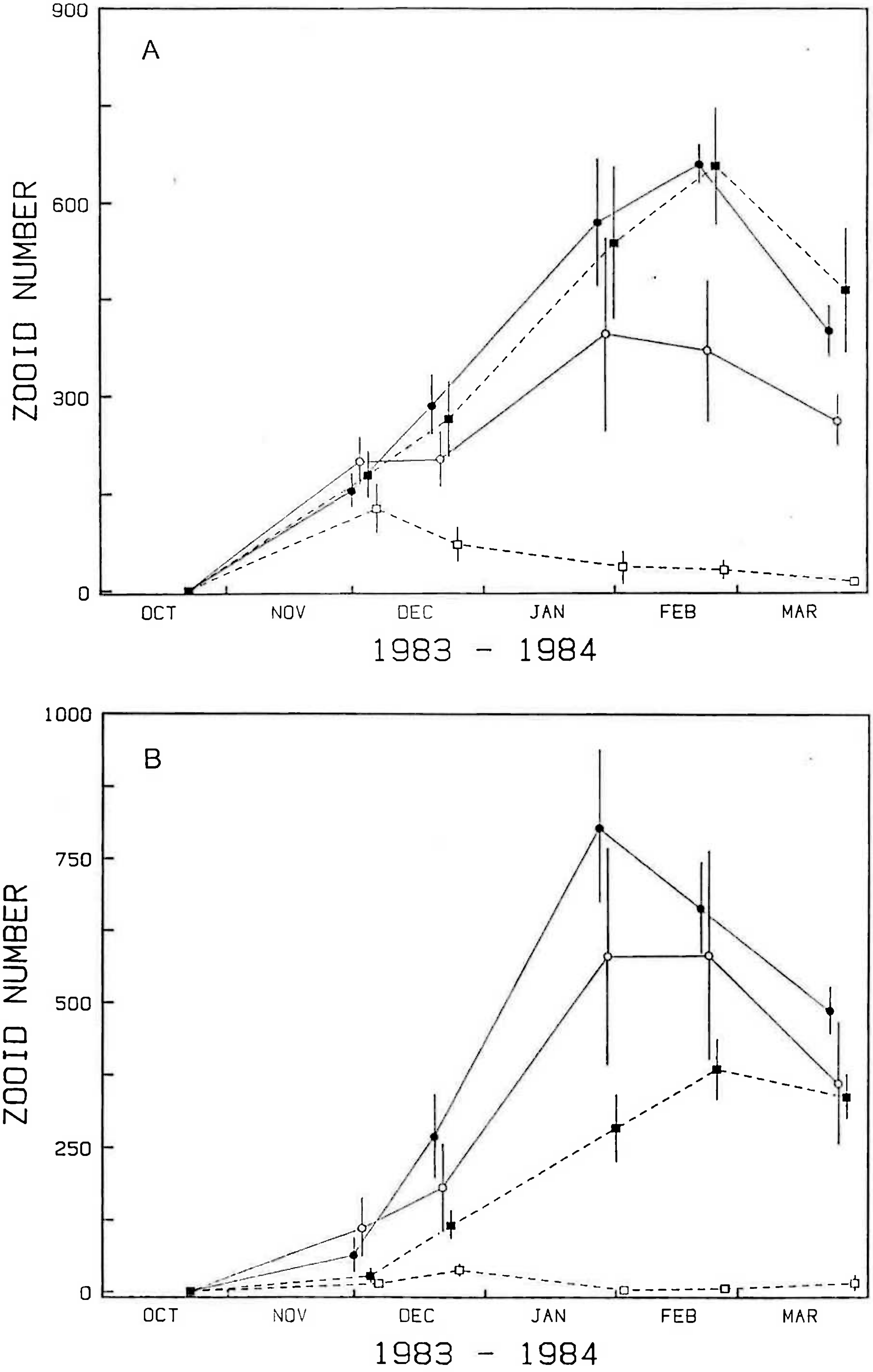

A
900
600
300
0
ZOOID NUMBER
OCT
NOV
DEC
JAN
FEB
MAR
1983 - 1984
B
1000
750
500
250
0
ZOOID NUMBER
OCT
NOV
DEC
JAN
FEB
MAR
1983 - 1984

Figure 5.7 Mean frequencies of colony size in the crab and fish caging experiment. Data were obtained by detailed censusing of all treatments on two pilings. Error bars represent standard errors of the mean, n=2.

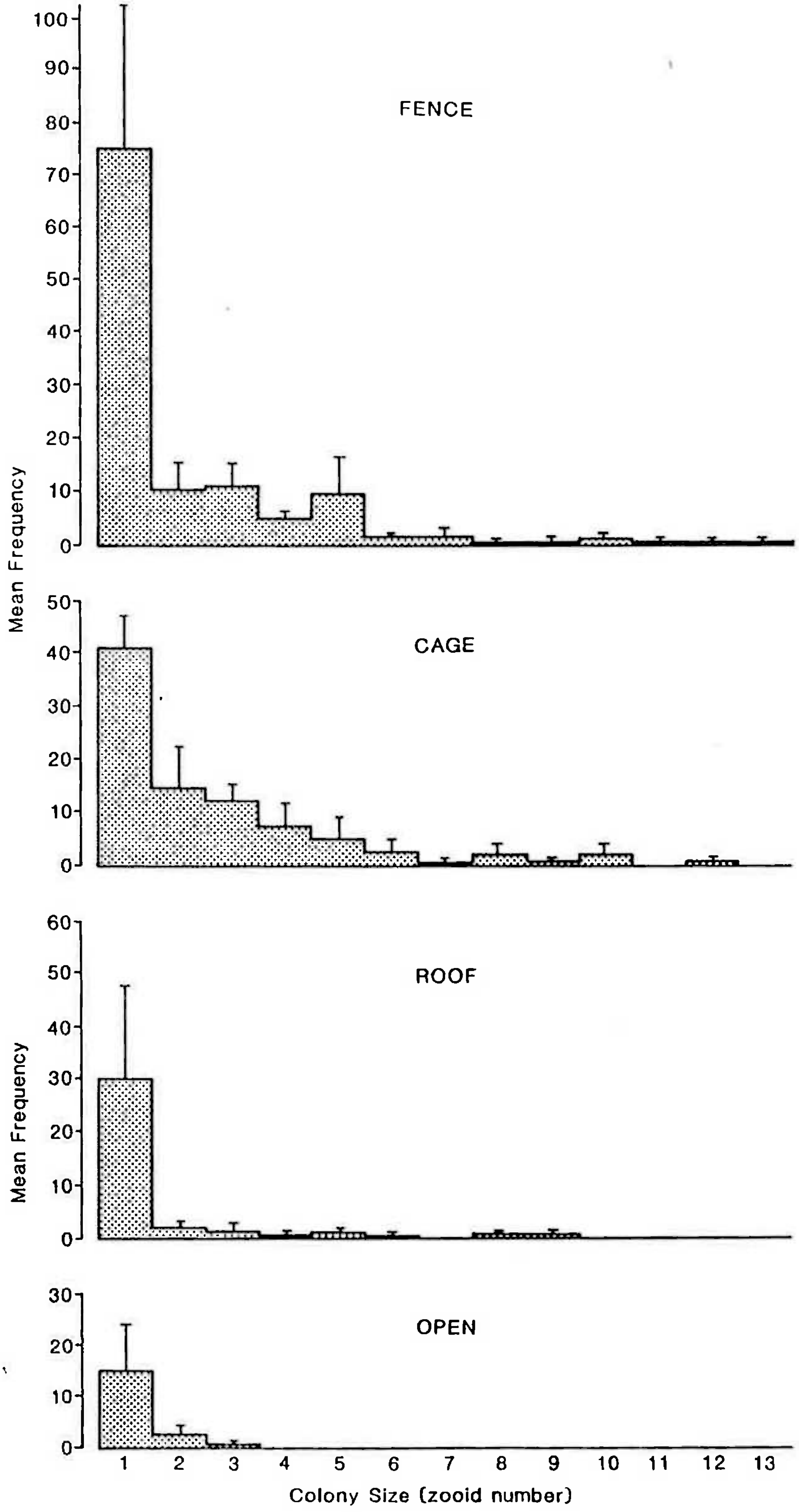

FENCE
CAGE
ROOF
OPEN
Mean Frequency
Mean Frequency
100
90
80
70
60
50
40
30
20
10
0
50
40
30
20
10
0
60
50
40
30
20
10
0
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
Colony Size (zooid number)

Figure 5.8 Mean ratio of zooid number/number of recruits as used in the analysis of the crab and fish caging experiment. Means were calculated from the five pilings used in the experiment and error bars are standard errors of the mean.

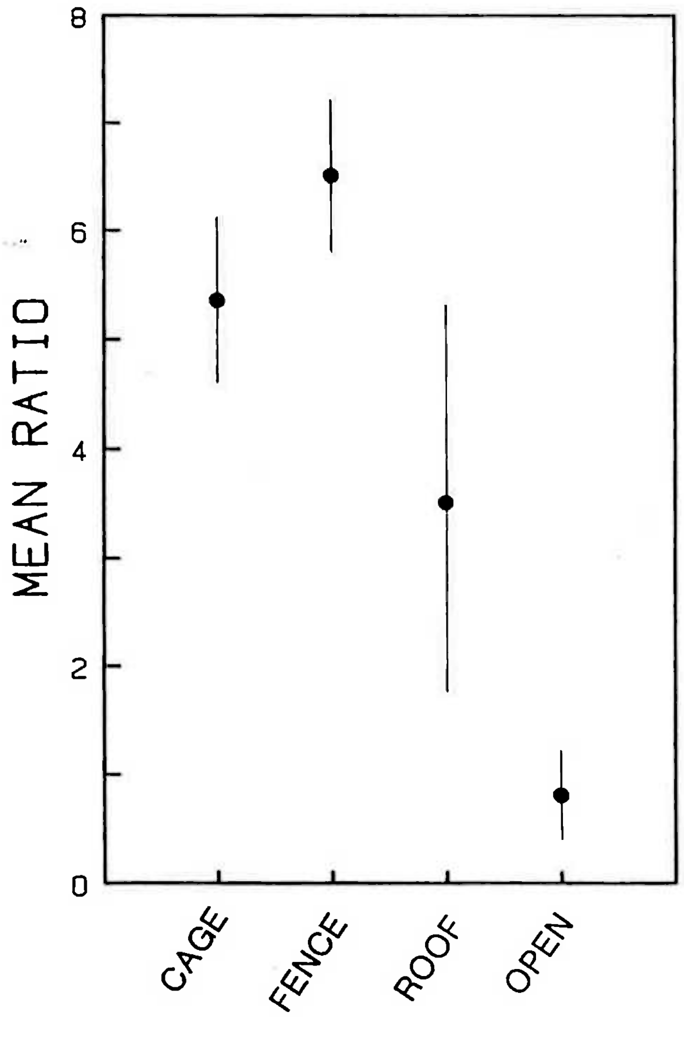

8
6
4
2
0
MEAN RATIO
CAGE
FENCE
ROOF
OPEN

Figure 5.9 Estimated size of schools of monacanthid fishes observed over three years beneath Edithburgh Jetty.

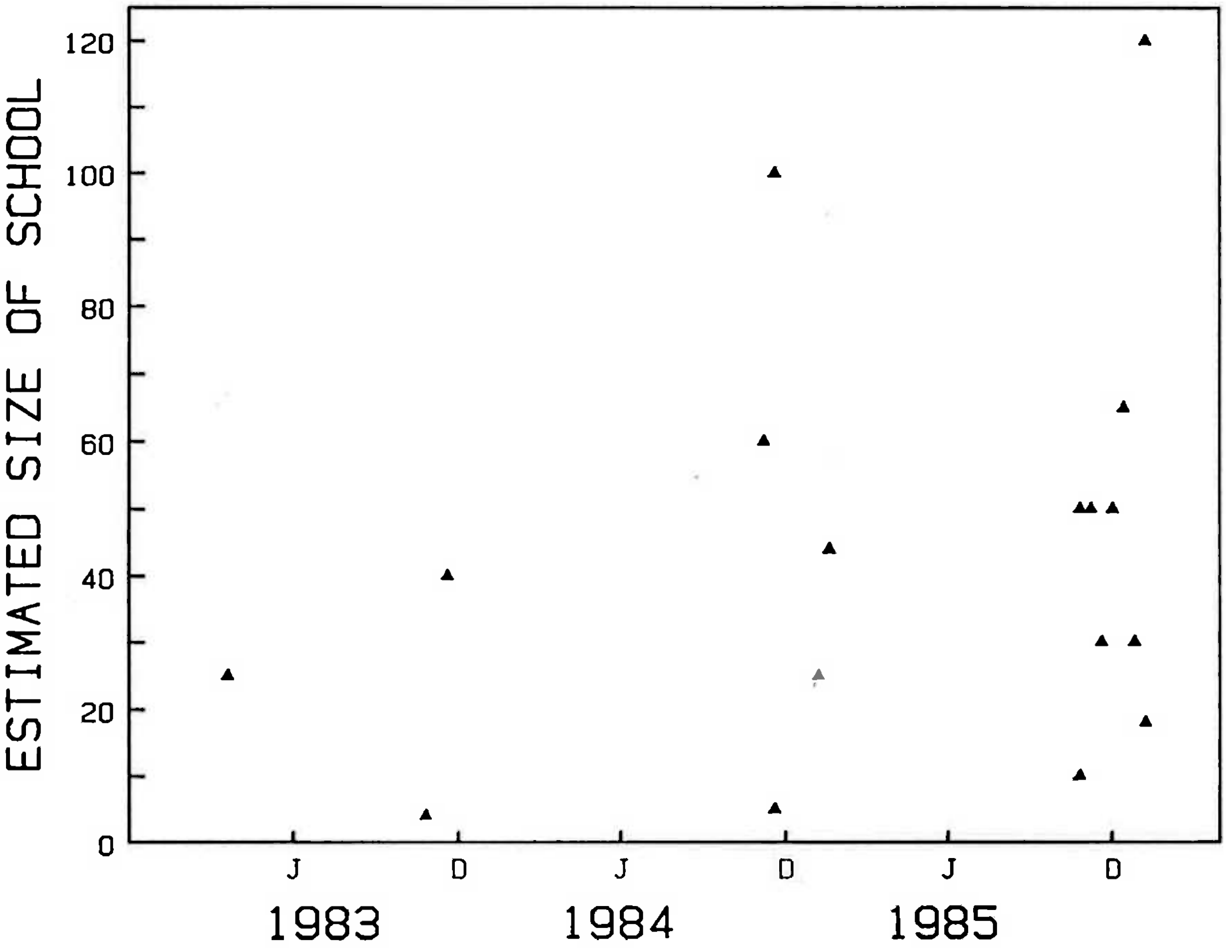

ESTIMATED SIZE OF SCHOOL
0
20
40
60
80
100
120
J
D
J
D
J
D
1983
1984
1985

Table 5.1 Design of initial 'simulated predation' experiment. Numbers refer to the number of replicates.

	COLONY TYPE	
	Functional	Degenerate
Treatment (Damaged)	3	3
Control (Undamaged)	3	3

Table 5.2 Determination of sample size and the power of the caging experiment designed to investigate the influence of crabs and fish on recruits. Under the alternative hypothesis of an effect due to crabs and fish, estimates of zooid numbers and treatment effects were obtained from the pilot experiment for the cage and open treatment.

Treatment	Cage	Roof	Fence	Open
Mean Zooid No.	400	150	150	100
Variance	15000	15000	15000	15000
Treatment Effect	+200	-50	-50	-100

$$\phi = \sqrt{\frac{55000n}{60000}}$$

Sample Size (n)	2	3	4	5	6
ϕ (Non centrality parameter)	1.35	1.65	1.91	2.14	2.34
Degrees of freedom (a(n-1))	4	8	12	16	20
Probability of Type II error (B)	.72	.49	.22	.10	.05
Power (1-B)	.28	.51	.78	.90	.95

Table 5.3 Mean percent change in colony size and analysis of variance table for artificially damaged adult colonies 25 days after damage was inflicted. Analysis was by a two - fixed - factor ANOVA. Cochran's C=.75 k=4 df=2 ns. Following initial analysis, the factor 'Colony Type' and the interaction term were removed from the analysis using the pooling procedures recommended by Winer (1971).

Treatment	Colony type	Mean	SE
Damaged	Functional	-35.5	16.0
	Degenerate	-32.2	6.1
Undamaged	Functional	-19.5	1.6
	Degenerate	-26.3	6.8

ANOVA TABLE

Source	SS	df	MS	F	P
Treatment	341.3	1	341.3	1.33	>.05
Colony Type	8.3	1	8.33	0.03	>.05
T x C	75.0	1	75.0	0.29	>.05
Error	2045.6	8	255.7		
Total	2470.3	11			

AFTER POOLING

Source	SS	df	MS	F	P
Treatment	341.3	1	341.3	1.6	>.05
Error (pooled)	2128.9	10	212.89		
Total	2470.3	11			

Table 5.4 Mean zooid heights per colony measured 36 days after damage was inflicted in the simulated predation experiment (1984). Heights of the largest five zooids were measured for a total of eight colonies, four treatment (damaged) and four controls. Treatment effects on zooid height were examined with a two factor nested ANOVA. The fixed factor, 'treatment', had two levels; damaged and undamaged. The nested factor, 'colonies', had four levels. Cochran's C = .38 k=8 df=4 ns.

Treatment	Colony no.	mean height (mm)	SE
Control	1	20.4	0.4
	2	21.0	1
	3	14.2	2.2
	4	21.0	1.3
Treatment	5	12.4	1.1
	6	24.4	1.7
	7	9.6	0.7
	8	23.4	0.7

ANOVA TABLE

Source	SS	df	MS	F	P
Treatment	28.9	1	28.9	0.2	>.05
Colony	1018.7	6	169.8	21.1	<.001
Error	256.8	32	8.0		
Total	1304.4	39			

Table 5.5 The presence of juvenile colonies 25 days after artificial damage was inflicted. NP signifies 'not present'. Means are the colony size (number of zooids) ± standard error of the mean. Numbers in parentheses are sample sizes.

Date	Control	Damaged
26-i-84	12.0 ± 1.8 (5)	9.2 ± 1.2 (5)
19-ii-84	19.5 ± 5.5 (4)	NP (4)

Table 5.6 Analysis of zooid numbers in caged and uncaged treatments of the pilot caging experiment with a two factor ANCOVA. The factor 'piling' (random) had four levels and the factor 'treatment' (fixed) had two. The covariate was height of the areas above the seabed. Cochran's C = .55 k=8 df=3 P <.05. Data were square root transformed but this did not remove the heteroscedasticity so the analysis was performed on the raw data. A-posteriori comparison among means was by Tukey's HSD. Treatments joined by lines were not significantly different. 'U' = uncaged and 'C' = caged.

Source	SS	df	MS	F	P	Regression Coefficient
Piling	271313	3	90438	9.1	<.001	
Treat	535328	1	535328	12.2	<.001	
PxT	131972	3	43991	4.4	<.05	
Covar	13536	1	13536	1.4	>.25	-.58
Error	227318	23	9883			

Tukey's HSD = 232.8

Piling	2	4	1	4	3	1	2	3
Treat	U	U	U	C	U	C	C	C
Mean	12	13.7	260	335	360	399	462	485

Table 5.7 Analysis of the percentage of colonies surviving in the caging experiment designed to separate the effect of crabs and monacanthid fishes. Data (number present at 41 days / number present at 20 days) were analysed by two factor ANOVA with repeated measures on pilings. The crab and fish factors (both fixed) were orthogonal each with two levels; present and absent. Cochran's C= .3 k=4 df=4 ns.

Source	SS	df	MS	F	P
Crab	9768.2	1	9768.2	240.3	< .001
Error	132.8	4	33.2		
Fish	824.3	1	824.3	2.8	> .05
Error	1185.4	4	296.3		
Crab x Fish	763.8	1	763.8	5.7	> .05
Error	533.3	4	133.3		

Table 5.8 Analysis of zooid number in the caging experiment designed to separate the effect of crabs and monacanthid fishes. Data (number of zooids / number of recruits) were analysed by two factor ANOVA with repeated measures on pilings. The crab and fish factors (both fixed) were orthogonal each with two levels; present and absent. Cochran's C= .73 k=4 df=4 $P < .05$.

Source	SS	df	MS	F	P
Crab	71.3	1	71.3	16.4	<.01
Error	17.3	4	4.3		
Fish	2.9	1	2.9	0.4	>.5
Error	25.0	4	6.3		
Crab x Fish	18.0	1	18.0	3.1	>.1
Error	23.0	4	5.7		

Table 5.9 Anova table of crab densities on pilings of crab and monacanthid fishes caging experiment. Data were analysed with a two factor ANOVA. Factor 'crab species' (fixed) had 3 levels, and the 'piling' factor (random) had 5 levels. Cochran's C = .14 k=15 df=5 ns.

Source	SS	df	MS	F	P
Crab species	17.3	2	8.6	9.9	<.01
Piling	1.4	4	0.4	0.3	>.05
Crab x Piling	6.9	8	0.9	0.7	>.05
Error	88.3	75	1.2		
TOTAL	114	89			

Table 5.10 The mean percentage change in the number of Podoclavella recruits after 15 hours with a crab tethered over them. Variances appeared heterogeneous (Fmax = 247) although there were insufficient degrees of freedom to test this suspicion. Data were analysed with a Kruskal-Wallis test (Sokal & Rohlf, 1981). the sample size was initially three but was subsequently altered by escapes and mortality. Hence the increase in the number of replicates in the control. One replicate was omitted as the crab broke free within 30 minutes of initiating the experiment.

Crab Species	Chelae Treatment	Mean Percent Change in the Number of Recruits	SE	n
Plagusia chabrus	Clipped	-26	14.8	2
	Unclipped	-23	1.0	2
Schizophrys aspera	Clipped	-	-	0
	Unclipped	-1	1.0	2
Control (no crabs)		0.5	0.9	8

H= 8.4 df=3 P < .05

5.4 DISCUSSION

Jackson (1977), in predicting that colonial organisms are less susceptible to predation than solitary organisms, appears to have ignored the vulnerability of recruits soon after settlement. Prior to the growth of modular units the recruits of colonial organisms are effectively solitary, Even small colonies may be susceptible to damage and, indeed, juvenile Podoclavella did not survive high levels of artificially inflicted damage. These findings indicated that this stage of the life cycle of Podoclavella was highly susceptible to attacks by predators.

It might be expected generally that juveniles of benthic invertebrates would be less well defended than adults owing to their small size and lack of structural defenses, such as a thick test or large numbers of spicules (Keough, 1984a). However, juveniles may utilize other defences. For example they may select habitats which are inaccessible to predators (Connell, 1961; Keough & Downes, 1982) or they may be better chemically defended than adults of the species. This is indeed the case for some temperate brown algae (P.D. Steinberg, pers. comm.). Juveniles may also avoid predators in time as well as space.

Caging experiments were used to examine the real impact of predators and revealed significant improvements in recruit survival and colony size, relative to controls, when crabs were excluded. It was unclear, however, whether the damage caused by crabs resulted from the direct consumption of recruits or indirectly from their 'trampling'. A significant reduction in recruit survival as a result of trampling by crabs has been observed elsewhere (Young and Chia, 1984). It could be argued that lower survival in the presence of mobile organisms is the important result and that the exact mechanism producing this result is of less interest. However, in the evolution of defenses, anti-predator adaptations will be very different from those to deter trampling organisms.

The tethering experiment and observations of crabs in the vicinity of the second caging experiment, indicated that the significant effect due to crabs in this caging experiment resulted from trampling by the grapsid, Plagusia chabrus. This crab species was often observed moving beneath roofs and across open controls in the caging experiment. It could be argued that the trampling effect was an artifact. Firstly, it might stem from contact of the thin wire trace that tethered crabs with Podoclavella recruits. This was not the case, however, as the short wire trace was stiff and did not come into contact with the substratum. The reduction in the numbers of recruits resulted from their being dislodged by the sharp dactyls of these crabs. A second potential artifact was that tethering alters the behaviour of the crabs and under normal circumstances they do not dislodge recruits. Shizophrys aspera appeared to behave normally when tethered, while Plagusia chabrus were intent on escaping and may have had more impact on recruits than under more natural conditions. There is evidence that dislodgement is not an artifact of tethering however. Rents, produced by the sharp dactyls of Plagusia, were apparent on many of the delicate sponges within some replicates in the caging experiment. Similar marks were often observed in delicate sponges in other areas, indicating that the dactyls of this crab species damage encrusting species under natural conditions. Had two counts been made in each quadrat of the tethering experiment, one at the border and the other in the centre, it would have been possible to estimate the significance of this tethering artifact. If the trampling effect had been purely an artifact then the number of recruits in the centre of the quadrat would not be expected to change significantly. In contrast, numbers at the border of the quadrat, where crabs struggle to pull free, should change appreciably. Unfortunately these counts were not made.

Incidental observations on the other crab species, *Schizophrys aspera*, provided circumstantial evidence that this species may consume *Podoclavella*. On two occasions individuals of this crab species were found within larval traps (Fig. 3.1) from which the plastic jars had been removed. In both instances the *Podoclavella* colony within each trap had been characteristically shaved of all or most of its zooids. Examination of the gut contents of both crab individuals was inconclusive: nothing in their guts could be identified.

It was noteworthy that 'shaved' *Podoclavella* colonies were not observed in the field. I conclude that colony 'shaving' occurred within the larval trap because of the amelioration of some feeding constraints. Perhaps the traps offered protection from predators on crabs, maybe other crab species. Elevation of 'feeding efficiency' as a result of the amelioration of physical factors under cage controls has been observed in several studies (Underwood, 1980).

It was highly unlikely that either the pleurobranch, *Pleurobranchus hilli*, or flatworm, *Pseudoceros* sp., influenced the results of the caging experiments. *P. hilli* did not venture high enough on pilings and the flatworm was capable of entering both treatments and controls.

The results of the pilot caging experiment indicated that the impact of crabs was unpredictable, with zooid numbers significantly reduced in some uncaged areas but not in others. Upon closer scrutiny, however, the impact of predators was not unpredictable, but was restricted to pilings with low levels of recruitment. The near stasis, or reduction, in zooid numbers observed in Figure 5.6a,b indicates that crabs reduced the survival of recruits in all uncaged treatments. The subsequent effect of this reduction depended upon the density of recruits. If levels of recruitment were low then the effect of predators was profound. If, on the other hand, recruitment was high, predators simply acted to release space and allowed the surviving colonies to grow larger. Hence no difference was detected in zooid numbers between caged treatments and uncaged treatments on pilings that had received high levels of recruitment.

The high survival observed under the roof on piling 4 points to spatial heterogeneity in the impact of crabs. The high survival on this piling could not be explained by a low density of crabs, as no differences in crab density were observed between pilings. This finding suggests that spatial refuges from crabs exist in the sense that, by chance, some areas are not visited by crabs for a significant period of time.

Monacanthid fishes did not reduce recruit survival. The failure to detect an effect due to fish was for one (or more) of three reasons:

i) Fish may be unimportant as predators of Podoclavella. Indeed, swimming larvae were rejected by clinid fishes. Podoclavella may be chemically defended. Stoecker (1980a, 1980b, 1980c) suggested that low pH and the presence of vanadium act to deter predators, although Parry (1984) has challenged her assertion. Podoclavella contains vanadium (Hawkins et al., 1980) and this may deter fish predators.

ii) Fishes are important predators of Podoclavella but their impact is patchy in space and time. The effect of consumers which graze patchily in space and time can be totally unpredictable (J.H. Choat, pers. comm.). Indeed, it is possible that monacanthids may not have fed within any of the five fenced areas purely by chance.

iii) Fishes are important predators of Podoclavella but avoided the fenced crab exclusions. In southern Australia monacanthid fishes have previously been observed to feed within partial cages of approximately the same dimensions as used in this experiment (Russ, 1980). I did not, however, observe monacanthid fishes feeding within any of the treatments in this experiment. Perhaps their skittish behaviour in the presence of divers explains the lack of feeding observations.

Morphogenic studies of ascidian degeneration were initiated early this century (Hirschler, 1914; Sélys-longchamps, 1915). Clavelinids have exceptional ability to regenerate (Brien, 1927, 1930 and 1932). *Clavelina lepadiformis* was capable of full regeneration from stolonal fragments less than 1mm in length (Berrill & Cohen, 1936). Indeed, degeneration and subsequent regeneration was observed in newly settled *Podoclavella*, of only one zooid in size. The remarkable powers of regeneration of *Podoclavella* colonies indicates that predators are inconsequential to adult colonies, unless they consume the entire colony. I conclude that crabs are an important source of post-settlement mortality and that this results from mechanical damage associated with their foraging activities.

CHAPTER SIX

General Discussion

Most natural populations can be considered to consist of a series of interconnected subpopulations occupying more-or-less discrete patches of suitable habitat. These subpopulations will fluctuate in density as a result of local conditions and variation in the dispersal between them. To understand the dynamics of populations requires detailed knowledge of the processes occurring within patches and those affecting exchange between patches. It is this information that I sought to obtain for Podoclavella.

Podoclavella is a clonal organism. The modular construction of clonal species often presents problems in identifying the appropriate unit of study (Harper, 1977). The units of study can be: the genet, the colony or the module. In this study the colony was adopted as the unit of study, irrespective of whether it was formed sexually or asexually. The dynamics of modules (zooids) were not examined although somer information was gathered on factors influencing zooid numbers. Colonies at Edithburgh Jetty were produced almost wholly by sexual reproduction, that is, a colony was equivalent to a genet, with few exceptions. At Port Noarlunga colonies were formed both sexually and asexually. The asexual production of colonies was not an active process but resulted from the shrinkage or atrophy of stolons during colony degeneration. Rarely were daughter colonies separated by more than a few centimetres. Although colonies did not equate to genets, genets could usually be distinguished with confidence at Port Noarlunga.

Natural populations - and more so local populations - often show considerable fluctuation in density over time and ecologists have been aware of this variation for some time. In 1930 Charles Elton rejected the concept of 'the balance of nature' because natural systems were so variable and since then other workers have highlighted the significance of variability (Andrewartha & Birch, 1954, 1984; den Boer, 1968; Chesson, 1978; 1985; Underwood, 1981; May, 1986). Fluctuations in population density observed during this study were dependent on the site and time interval considered. Fluctuations in density and age structure of the population within years resulted from 'pulses' of recruitment. At Port Noarlunga the pulses of recruits were small and had little impact on population density or age structure. In contrast the average population at Edithburgh was maintained by a large annual pulse of recruits, resulting in large fluctuations in density and population age structure within years at Edithburgh Jetty.

At both sites fluctuations between years were small, even though colony densities at the two sites differed by two orders of magnitude. The longevity of colonies in the perennial population at Port Noarlunga was responsible for the near absence of fluctuations in population size. As the longevity in this population exceeded the period of my monitoring, the same individuals were being observed and only slight fluctuations would be expected (Frank, 1968; Connell & Sousa, 1983). It has been argued that to assess realistically the magnitude of fluctuations in populations requires observations after a period in which a complete turnover of the population has occurred. That is, a period exceeding the maximum longevity of all members of the population (Connell & Sousa, 1983). Complete turnover of the population at Port Noarlunga may take several years, and without a longer-term data set, little can be said about fluctuations in population density at this site.

The near constancy in adult population size observed between years at Edithburgh was surprising. This annual population was wholly maintained by recruitment yet adult densities were highly consistent in the three years of this study. Before considering why population fluctuations are so low between generations at this site it is instructive to examine the processes which influence and regulate populations generally.

Four processes which may act to change population size can be distinguished; natality, immigration, mortality, and emigration. Clearly, if populations are not to rise indefinitely or crash to zero, changes in birth and/or immigration must be compensated for by changes in death and/or emigration at least over a time commensurate with the longevity of the animals. This has been taken to suggest the need for a regulatory mechanism - some form of negative feedback to density - so that if (for example) birth rate rises, death rate will also rise. But there is no logical necessity for the compensatory changes to be causally related, nor simple, nor is there a necessity for them to be closely linked so that fluctuations are strongly damped (Andrewartha & Birch, 1954; Strong, 1984). After all, populations usually fluctuate and some do experience crashes or explosions. For example, there was a very rapid reduction in densities of echinoids associated with disease (= mortality) on both the Pacific and Atlantic coasts of the United States (Pearse & Hines, 1979; Scheibling & Stephenson, 1984). On the other hand, in 1982 El Niño resulted in the disappearance of large tracts of Macrocystis from the Californian coast. Associated with the decline in kelp was a population explosion of sea urchins (Dayton & Tegner, 1984). These rapid shifts in community structure had important implications for this and other communities (Keough & Downes, 1986; Gaines & Roughgarden, 1987). Understanding patterns in local assemblages may benefit from the consideration of regional processes (Ricklefs, 1987).

It could be argued that such unpredictable events are extremely rare and therefore of little significance, but this does not appear to be the case. El Niño occurs at intervals of two to ten years (Philander, 1983). It may be that 1982 was the only year in which dramatic changes occurred, but I suspect that the detection of changes earlier this century was hampered by a poor data base. In addition to these unpredictable phenomena associated with global weather patterns and disease, there is also evidence of predictable cycles in marine environments. Gray & Christie (1983) detected cycles with periods of 3 to 100 years from the analysis of long-term hydrographic data. There are two take-home messages here. First, changes in population density may occur very rapidly and second, much of what we observe in populations and communities may have an historic component, the causes of which are no longer apparent.

The constancy in the size of the population of Podoclavella at Edithburgh appears to result from; i) short distance dispersal and, ii) a consistent availability of suitable sites for settlement. The lecithotrophic larvae of Podoclavella move such short distances that a very high proportion settle straight back into the population from which they were released. Such a population may be regarded as effectively closed, with settlement in direct proportion to the size of the resident adult population. In contrast, species with planktotrophic larvae, which may spend weeks to months in the water column, are highly unlikely to settle in the same areas from which they were released and will be exposed to many agents of mortality during their planktonic existence. Many physical and biological factors may act to alter the concentration of larvae in the water column (e.g. Thorson, 1946; Bousfield, 1955; Mileikovsky, 1974; Hawkins & Hartnoll, 1982; Keough, 1983; Shanks, 1983). Even the act of settlement itself may reduce appreciably the number of larvae in a water mass (Gaines & Roughgarden, 1985). As settlement is dependent on the number of larvae encountering the substratum (Gaines et al., 1985) the settlement of species with planktotrophic larvae is often unpredictable over time and between sites (Connell, 1961; Gaines & Roughgarden, 1985; Wethey, 1985).

The availability of suitable sites for settlement was the major determinant of the distribution and abundance of adult colonies of Podoclavella because the larvae were so discriminating at settlement. Unlike most seeds, for which the environment decides which colonists will survive, many larvae can discern sites in which post-settlement survival is likely to be poor (Harper, 1985). The avoidance of such sites has been observed for several taxa including ascidians, barnacles, bryozoans and tube-dwelling polychaetes (Grosberg, 1981; Young & Chia, 1981; Woodin, 1985; Davis, in press). Responses of Podoclavella larvae to light and gravitational cues ensured that larvae rarely encountered upward facing surfaces and therefore seldom settled on surfaces of this orientation. In contrast, vertical faces were regularly encountered and the patterns of settlement reflected the behavioural responses of larvae to particular substrata. Some substrata were consistently rejected, while others were often settled on at first encounter. It is clearly inappropriate to consider larvae as passive particles; they were highly discriminating.

So discriminatory were Podoclavella larvae for substrata on which survival was likely to be enhanced, that settlement explained 86% of the variation in recruitment 30 days after settlement began. In addition, there was a significant relationship between the number of recruits and the number of adults present a year later. Inappropriate substrata were rejected by Podoclavella larvae, probably on the basis of negative chemical cues. Such cues have been observed to influence the settling behaviour of other invertebrate larvae (Young & Chia, 1981; Woodin, 1985).

What then were the suitable sites for settlement and what influenced their availability? *Podoclavella* settle in higher densities and survive better on vacant space than on any other substratum. There were clear differences in the availability of free space at the two sites, Edithburgh Jetty and Port Noarlunga (Fig. 2.12). Only very small patches of bare space are usually observed on rock walls in the subtidal (Sebens, 1985) and vacant space was rare at Port Noarlunga; patches were seldom larger than 100cm^2, even after intense wave action (pers. obs.). In contrast, vacant space was always available at Edithburgh Jetty (Kay & Butler, 1983). The largest patches at Edithburgh were up to 25 fold larger than those seen at Port Noarlunga (pers. obs.). A definite temporal component to patch formation was observed at Edithburgh. This did not correspond to the frequency of disturbance (e.g. storms), but to the dying and sloughing off of *Botrylloides leachii*, an annual ascidian. After reproducing in late spring this colonial ascidian dies and, in sloughing from pilings, often removes fauna which it overgrew during the winter months. By December the cover of *B. leachii* at Edithburgh was reduced to less than 1% and a large number of vacant patches were produced. Hence the larval release of *Podoclavella* corresponds with the maximal availablity of its preferred substratum. This correspondence may be purely coincidental, but other marine species have been observed to spawn in response to cues which are likely to maximize the availability of free space for settlement. Both intertidal mussels and limpets have been documented to spawn following storms (Suchanek, 1978; Creese & Ballantine, 1983).

If the availability of suitable settlement sites, that is free space, is an important determinant of adult population size a correlation would be expected between the size of adult populations and the amount of bare space available during the settlement of Podoclavella. This hypothesis may be tested by providing free space at some sites and examining changes in adult population size in experimental and control sites at some later date.

In the study of marine communities most emphasis has been placed on mortality as influencing population dynamics and ultimately community structure, almost to the exclusion of birth, immigration and emigration. Three agents of post-recruitment mortality have received considerable attention; predation, competition, and physical disturbance. This emphasis on post-recruitment mortality ignores two earlier phases of the life history which may be very important determinants of distribution and abundance: settlement and pre-recruitment mortality. Several workers have suggested that settlement may be equally as important as mortality in determining patterns of distribution and abundance (Dayton, 1979; Denley & Underwood, 1979). As settlement is difficult to distinguish from post-settlement mortality, a test of their assertion has awaited empirical evidence. Recent empirical studies have demonstrated that the larval settlement rate is indeed an important determinant of population dynamics (Yoshioka, 1982) and community structure (Gaines & Roughgarden, 1985). This is clearly not always the case however (Stoner, 1986).

In this study the number of larvae that were competent to settle, their behavior at settlement and the availability of sites that were suitable for settlement were the primary determinants of the distribution and abundance of adult Podoclavella colonies.

REFERENCES

Allen T.F.H. & T.B. Starr (1982) Hierachy: perspectives for ecological complexity. University of Chicago Press, Chicago. 310pp.

Andrewartha H.G. & L.C. Birch (1954) The Distribution and Abundance of Animals. University of Chicago Press Chicago 782pp.

Andrewartha H.G. & L.C. Birch (1984) The Ecological Web. More on the distribution and abundance of animals. University of Chicago Press Chicago.

Ayling A.M. (1981) The role of biological disturbance in temperate subtidal encrusting communities. Ecology 62:830-847.

Ayre D.J. (1985) Localized adaptation of clones of the sea anemone Actinia tenebrosa. Evolution 39:1250-1260.

Bak R.P.M., J. Sybesma & F.C. van Duyl (1981) The ecology of the tropical compound ascidian Trididemnum solidum. II. Abundance, growth and survival. Mar. Ecol. Prog. Ser. 6:43-52.

Beckner M. (1974) Reduction, hierachies and organicism. In, Studies in the philosophy of biology: Reductism and related problems. Ayala F.J. & T. Dobzhansky (eds) University of California Press, Berkeley pp.163-177.

Berrill N.J. (1931) Studies in tunicate development. Part II. Abbreviation of development in the Molgulidae. Philos. Trans. R. Soc. London Ser. B. 219:281-346.

Berrill N.J. (1975) Chordata: tunicata. In, Reproduction of Marine Invertebrates. Giese A.C. & J.S. Pearse (eds) Academic Press, New York & London. 2:241-282.

Berrill N.J. & A. Cohen (1936) Regeneration in Clavelina lepadiformis. J. Exp. Biol. 13:352-362.

Blomqvist S. & C. Kofoed (1981) Sediment trapping - a sub-aquatic in situ experiment. Limnol. Oceanogr. 26:585-590.

Bousfield E.L. (1955) Ecological control of the occurrence of barnacles in the Miramichi Estuary. Bull. Nat. Mus. Canada (Biol. Ser. 46) 137:1-68.

Bricelj V.M., R.E. Malouf & C. de Quillfeldt (1984) Growth of juvenile Mercenaria mercenaria and the effect of resuspended sediments Mar. Biol. 84:167-173

Brien P. (1927) Contribution à l'étude de la blastogenèse des Tuniciers. IV. Bourgeonnement de Clavelina lepadiformis (Muller). Inst. zool. Torley-Rousseau Rec. 1:31-81.

Brien P. (1930) Contribution à l étude de la régénération naturelle et expérimentale chez les Clavelinides. Soc. roy. zool. Belgique Ann. 60:33-46

Brien P. (1932) L'hétéromorphose chez les Tuniciers. La régénération bithoracique et monothoracique des fragments oesophagiens de *Clavelina lepadiformis* (Muller). Acad. roy. Belgique (Classe sci.) Bull. 18:975-1005.

Burke R.D. (1983) The induction of metamorphosis of marine invertebrate larvae: stimulus and response. Can. J. Zool. 61:1701-1719.

Burkholder P.R. (1973) The ecology of marine antibiotics and coral reefs. In, Biology and Geology of Coral Reefs. Jones O.A. & R. Endean (eds) Academic Press, New York. 2:117-182.

Burton R.S. (1983) Protein polymorphisms and genetic differentiation of marine invertebrate populations. Mar. Biol. Letters 4:193-206.

Buss L.W. (1979) Bryozoan overgrowth interactions - the interdependence of competition for space and food. Nature (London) 281:475-477.

Butler A.J. (1986) Recruitment of sessile invertebrates at five sites in Gulf St. Vincent, South Australia. J. Exp. Mar. Biol. Ecol. 97:13-36

Butler A.J. & F.J. Brewster (1979) Size distributions and growth of the fan-shell *Pinna bicolor* Gmelin (Mollusca: Eulamellibranchia) in South Australia. Aust. J. Mar. Freshwat. Res. 30:25-39.

Byte J.A.T. (1976) Physical oceanography of Gulf St Vincent and Investigator Strait. In, Natural History of the Adelaide Region. Twidale C.R., M.J. Tyler & B.P. Webb (eds) Royal Society of South Australia, Adelaide. pp.143-161

Caffey H.M. (1985) Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecol. Monogr. 55:313-332.

Cappo M.C. (1980) Some aspects of the ecology and population biology of magpie perch (*Cheilodactylus nigripes*). B.Sc. Hons. Thesis University of Adelaide, South Australia.

Chambers S.M. (1983) Genetics principles for managers. In, Genetics and Conservation. Schonewald-Cox C.M., S.M. Chambers, B. MacBryde & L. Thomas (eds) Benjamin/Cummings pp. 15-146.

Charnov E.L. & W.M. Schaffer (1973) Life history consequences of natural selection: Coles result revisited. Am. Nat. 107:791-793.

Chesson P.L. (1978) Predator-prey theory and variability. Annu. Rev. Ecol. Syst. 9:323-347.

Chesson P.L. (1985) Environmental variation and the coexistence of species. In, Community Ecology. Diamond J. & T.J. Case eds. Harper & Row New York pp.240-256.

Chia F.S., J. Buckland-Nicks & C.M. Young (1984) Locomotion of marine invertebrate larvae: a review. Can. J. Zool. 62:1205-1222.

Choat J.H. (1982) Fish feeding and the structure of benthic communities in temperate waters. Annu. Rev. Ecol. Syst. 13:423-449.

Cole H.A. & E.W. Knight-Jones (1939) Some observations and experiments on the settling behaviour of *Ostrea edulis*. J. Conserv. perm. int. Explor. Mer. 14:86-105.

Connell J.H. (1961) Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31:61-104.

Connell J.H. (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In, Ecology and Evolution of Communities. Cody M.L. & J.M. Diamond (eds) Belknap Press Cambridge Mass. pp.460-490.

Connell J.H. (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Connell J.H. (1985a) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 93:11-45.

Connell J.H. (1985b) Variation and persistence of rocky shore populations. In, The Ecology of Rocky Coasts. Moore P.G. & R. Seed (eds) Hodder and Stoughton, Sevenoaks, Kent, England. pp.56-69.

Connell J.H. & W.P. Sousa (1983) On the evidence needed to judge ecological stability or persistence. Am. Nat. 121:789-824.

Creese R.G. & W.J. Ballantine (1983) An assessment of breeding in the intertidal limpet *Cellana radians* (Gmelin) J. Exp. Mar. Biol. Ecol. 67:43-59.

Crisp D.J. (1958) The spread of *Elminius modestus* Darwin in northwest Europe. J. Mar. Biol. Ass. U.K. 37:483-520.

Crisp D.J. (1974) Energy relations of marine invertebrate larvae. Thalassia Jugosl. 10:103-120.

Crisp D.J. (1976) Settlement responses in marine organisms. In, Adaptations to environment: essays on the physiology of marine animals. Newell R.C. (ed) Butterworths, London pp. 83-124.

Crisp D.J. & H. Barnes (1954) The orientation and distribution of barnacles at settlement with particular reference to surface contour. J. Anim. Ecol. 23:142-162.

Crisp D.J. & A.F.A.A. Ghobashy (1971) Responses of the larvae of *Diplosoma listerianum* to light and gravity. In, Proceed. 4th Euro. Mar. Bio. Symp. pp. 443-465.

Cutler S.J. & F. Ederer (1958) Maximum utilization of the life-table method in analyzing survival. J. Chron. Dis. 8:699-713.

Davis A.R. (in press) Variation in recruitment of the subtidal colonial ascidian *Podoclavella cylindrica* (Quoy and Gaimard): The role of substratum choice and early survival. J. Exp. Mar. Biol Ecol.

Dayton P.K. (1971) Competition, disturbance and community organization. The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41:351-389.

Dayton P.K. (1979) Ecology: A science and a religion. In, Ecological Processes in Coastal and Marine Systems. Livingston R.J. (ed), Plenum Press, New York. pp.3-18.

Dayton P.K. & J.S. Oliver (1980) An evaluation of experimental analyses of population and community patterns in benthic marine environments. In, Marine Benthic Dynamics. Tenore K.R. & B.C. Coull (eds) University of South Carolina Press, Columbia, S.C. pp.93-120.

Dayton P.K. & M.F. Tegner (1984) Catastrophic storms, El Niño and patch stability in a southern Californian kelp forest. Science 224:283-285.

den Boer P.J. (1968) Spreading of risk and stabilization of animal numbers. Acta Biotheor. 18:165-194.

Denley E.J. & A.J. Underwood (1979) Experiments on factors influencing settlement, survival, and growth of two species of barnacle in New South Wales. J. Exp. Mar. Biol. Ecol. 36:269-293.

Devinny J.S. & L.A. Volse (1978) Effects of sediments on the development of Macrocystis pyrifera gametophytes Mar. Biol. 48:343-348.

Dixon W.J. (chief ed)(1983) BMDP Statistical Software. University of California Press. pp. 733.

Doyle R.W. (1975) Settlement of planktonic larvae: a theory of habitat selection in varying environments. Am. Nat. 109:113-126.

Dyrynda P.E.J. (1984) Chemical defenses and the structure of subtidal epibenthic communities. In, Proceed. 19th Euro. Mar. Bio. Symp. pp. 411-421.

Edson M.M., T.C. Fion & C.M. Knapp (1981) "Emergent properties" and ecological research. Am. Nat. 118:593-596.

Elton C. (1930) Animal ecology and evolution. Clarendon, Oxford.

Forster G.R. (1958) Underwater observations on the fauna of shallow rocky area in the neighbourhood of Plymouth. J. Mar. Biol. Ass. U.K. 37:473-482.

Forster G.R. (1961) An underwater survey of the Lulworth Banks. J. Mar. Biol. Ass. U.K. 41:157-160.

Frank P.W. (1968) Life histories and community stability. Ecology 49:355-357.

Frankel O.H. & Soulé (1981) Conservation and Evolution. Cambridge University Press, Cambridge.

Gaines S., S. Brown & J. Roughgarden (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, Balanus glandula. Oecologia (Berlin) 67:267-273.

Gaines S. & J. Roughgarden (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. Natl. Acad. Sci. (USA) 82:3707-3711.

Gaines S. & J. Roughgarden (1987) Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. Science 235:479-481.

Gardner W.D. (1980a) sediment trap dynamics and calibration: a laboratory evaluation. J. Mar. Res. 38:17-39.

Gardner W.D. (1980b) Field assessment of sediment traps. J. Mar. Res. 38:41-52.

Gardner W.D. (1985) The effect of tilt on sediment trap efficiency. Deep Sea Res. 32:349-361.

Gerrodette T. (1981) Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae. Ecology 62:611-619.

Goodbody I. (1961) Continuous breeding in three species of tropical ascidians. Proc. Zool. Soc. London 136:403-409.

Gray J.S. & H. Christie (1983) Predicting long-term changes in marine benthic communities. Mar. Ecol. Prog. Ser. 13:87-94.

Grosberg R.K. (1981) Competitive ability influences habitat choice in marine invertebrates. Nature (London) 290:700-702.

Harper J.L. (1977) Population biology of plants. Academic Press London England. 892pp.

Harper J.L. (1982) After description. In, The plant community as a working mechanism. Newman E.I. (ed) The British Ecol. Soc. London. pp.11-27.

Harper J.L. (1985) Modules, branches and the capture of resources. In, Population Biology of Clonal Organisms. Jackson J.B.C., L.W. Buss & R.E. Cook (eds) Yale University Press, New Haven Connecticut pp. 1-33.

Harriot V.J. (1983) Reproductive seasonality, settlement, and post-settlement mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. Coral Reefs 2:151-157.

Hartnoll R.G. (1983) Substratum. In, Sublittoral Ecology: the ecology of the shallow sublittoral benthos. Earll R. & D.G. Erwin (eds) Clarendon Press Oxford pp.97-125.

Hawkins S.J. (1983) Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). J. Exp. Mar. Biol. Ecol. 71:55-72.

Hawkins S.J. & R.G. Hartnoll (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977-1981) J. Exp. Mar. Biol. Ecol. 62:271-283.

Hawkins C.J., D.L. Parry & C. Pierce (1980) Chemistry of the blood of the ascidian *Podoclavella moluccensis*. Biol. Bull. 159:669-680.

Heyward A.J. & J.A. Stoddart (1985) Genetic structure of two species of Montipora on a patch reef: conflicting results from electrophoresis and histocompatibility. Mar. Biol. 85:117-121.

Highsmith R.C. (1982) Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7:207-226.

Hirschler H. (1914) Ueber die Restitutions -und Involutions-vorgange bei operierten Exemplaren von Ciona intestinalis Flem. Zeitschr. Zellforsch. mikro. Anat. 85:205-227.

Hiscock K. (1979) A survey of sublittoral habitats and species in the region of Padstow, Cornwall. Prog. Underwat. Sci. Rep. Underwat. Ass. (N.S.) 4:121-130.

Hiscock K. (1983) Water movement. In, Sublittoral Ecology: the ecology of the shallow sublittoral benthos. Earll R. & D.G. Erwin (eds) Clarendon Press Oxford pp.58-97.

Hiscock K. and Hoare R. (1975) The ecology of sublittoral communities at Abereiddy quarry, Pembrokeshire. J. Mar. Biol. Ass. U.K. 55:833-864

Hopkins A. (1983) Survival analysis with covariates - Cox models. In, BMDP Statistical Software. W.J. Dixon (chief ed) University of California Press. pp. 576-594.

Hughes T.P. & J.B.C. Jackson (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. Science 109:713-715.

Hughes T.P. & J.B.C. Jackson (1985) Population dynamics and life histories of foliaceous corals. Ecol. Monogr. 55:141-166.

Huitema B.E. (1980) The analysis of covariance and alternatives. Wiley & Sons, New York. 445pp.

Hurlbert S.H. (1984) Psuedoreplication and the design of ecological field experiments. Ecol. Monogr. 54:187-211.

Hulberg L.W. & J.S. Oliver (1980) Caging manipulations in marine soft-botton communities: importance of animal interactions of sedimentary habitat modifications. Can. J. Fish. Aq. Sci. 37:1130-1139.

Huxley J.S. (1926) Studies in Dedifferentiation. VI. Reduction phenomena in Clavelina lepadiformis. Staz. zool. Pub. 7:1-36.

Jablonski D. & R.A. Lutz (1983) Larval ecology of marine benthic invertebrates: paleobiological implications. Biol. Rev. 58:21-89

Jackson J.B.C. (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am. Nat. 111:743-715.

Jackson J.B.C. (1985) Distribution and ecology of clonal and aclonal benthic invertebrates. In, Population Biology and Evolution of Clonal Organisms. Jackson J.B.C., L.W. Buss & R.E. Cook (eds). Yale University Press, New Haven. pp.297-357.

Jackson J.B.C. & L.W. Buss (1975) Allelopathy and spatial competition among coral reef invertebrates. Proc. Natl. Acad. Sci. (USA) 72:5160-5163.

Jackson J.B.C. & T.P. Hughes (1985) Population dynamics and life histories of foliaceous corals. Ecol. Monogr. 55:141-166.

Jennrich R., P. Sampson & J. Frane (1983) Analysis of variance and covariance including repeated measures. In, BMDP Statistical Software. W.J. Dixon (chief ed) University of California Press. pp. 359-387.

Johnson J.K. (1972) Effect of turbity on the rate of filtration and growth of the slipper limpet, Crepidula fornicata Lamarck,1799 Veliger 14:315-320

Johnson M.S. & R. Black (1984) Pattern beneath the chaos: the effect of recruitment on genetic patchiness in an intertidal limpet. Evolution 38:1371-1383.

Karlson R.H. (1983) Disturbance and monopolization of a spatial resource by Zoathus sociatus (Coelenterata, Anthazoa). Bull. Mar. Sci. 33:118-131.

Kay A.M. & A.J. Butler (1983) "Stability" of the fouling communities on the pilings of two piers in South Australia. Oecologia (Berlin) 56:58-66.

Kay A.M. & M.J. Keough (1981) Occupation of patches in the epifaunal communities on pier pilings and the bivalve Pinna bicolor at Edithburgh, South Australia. Oecologia (Berlin) 48:123-130.

Keough M.J. (1981) Community dynamics of the epifauna of the bivalve Pinna bicolor Gmelin. Ph.D. Thesis. University of Adelaide, South Australia.

Keough M.J. (1983) Patterns of recruitment of sessile invertebrates in two subtidal habitats. J. Exp. Mar. Biol. Ecol. 66:213-245.

Keough M.J. (1984a) Dynamics of the epifauna of the bivalve Pinna bicolor: interactions among recruitment, predation, and competition. Ecology 65:677-688.

Keough M.J. (1984b) Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65:423-437.

Keough M.J. & A.J. Butler (1979) The importance of asteriod predators in the organisation of a sessile community on pier pilings. Mar. Biol. 51:167-177

Keough M.J. & H. Chernoff (in press) Effects of dispersal and weather on the population structure of the bryozoan Bugula neritina. Ecology.

Keough M.J. & B.J. Downes (1982) Recruitment of marine invertebrates: the role active larval choices and early mortality. Oecologia (Berlin) 54:348-352.

Keough M.J. & B.J. Downes (1986) Effects of settlement and post-settlement mortality on the distribution of the ascidian Trididemnum opacum. Mar. Ecol. Prog. Ser. 33:279-285.

Kitching J.A., T.T. Macan & H.C. Gilson (1934) Studies in sublittoral ecology. I. A submarine gulley in Wembury Bay, S. Devon. J. Mar. Biol. Ass. U.K. 19:677-705.

Knight-Jones E.W. (1953) Decreased discrimination during settling after prolonged planktonic life in larvae of Spirobis spirobis (Serpulidae). J. Mar. Biol. Ass. U.K. 32:337-345.

Koehn R.K. (1984) Adaptive significance of biochemical and physiological variability. Proceed. 19th Euro. Mar. Bio. Symp. pp. 425-441.

Koehn R.K., J.G. Hall, D.J. Innes & A.J. Zera (1984) Genetic differentiation of Mytilus edulus in eastern North America. Mar. Biol. 79:117-126.

Kott P. (1972) Ascidians of South Australia. Trans. Roy. Soc. S.A. 96:1-52.

Levins R. (1966) The strategy of model building in population biology. Am. Sci. 54:421-431.

Lubchenco J. & S.D. Gaines (1981) A unified approach to marine plant-herbivore interactions. I Populations and communities Annu. Rev. Ecol. Syst. 12:405-437.

Luckenbach M. (1984) Settlement and early post-settlement survival in the recruitment of Mulinia lateralis (Bivalvia). Mar. Ecol. Prog. Ser. 17:245-250.

McCaffrey E.J. & R. Endean (1985) Antimicrobial activity of tropical and subtropical sponges. Mar. Biol. 89:1-8.

McFadden C.S. (1986) Colony fission increases particle capture rates of a soft coral: Advantages of being a small colony. J. Exp. Mar. Biol. Ecol. 103:1-20.

McLay C.L. (1983) Dispersal and use of sponges and ascidians as camouflage by Cryptodromia hilgendorfi (Brachyura: Dromiacea). Mar. Biol. 76:17-32.

Marshal S.M. and Orr A.P. (1931) Sedimentation on low Isles Reef and its relation to coral growth. Great Barrier Reef Exped. 1928-1929 Brit. Mus. (Nat. Hist.) Sci. Rept. 1:94-133

May R.M. (1986) The search for patterns in the balance of nature: advances and retreats. Ecology 67:1115-1127.

Meadows P.S. & J.I. Campbell (1972) Habitat selection by aquatic invertebrates. Adv. Mar. Biol. 10:271-382

Menge B.A. & J.P. Sutherland (1976) Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. Am. Nat. 110:351-369.

Metz J.A.J., T.J. de Jong & P.G.L. Klinkhamer (1983) What are the advantages of dispersing; a paper by Kuno explained and extended. Oecologia (Berlin) 57:166-169.

Mileikovsky S.A. (1973) Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Mar. Biol. 23:11-17.

Mileikovsky S.A. (1974) On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar. Biol. 26:303-311.

Millar R.H. (1971) The biology of ascidians. Adv. Mar. Biol. 9:1-100.

Olson R.R. (1983) Ascidian-Prochloron symbiosis: The role of larval photoadaptations in midday larval release and settlement. Biol. Bull. 165:221-240.

Olson R.R. (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. Ecology 66:30-40.

Osman R.W. (1977) The establishment and development of a marine epifaunal community. Ecol. Monogr. 47:37-63.

Paine R.T. (1966) Food web complexity and species diversity. Am. Nat. 100:65-75.

Paine R.T. (1974) Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berlin) 15:93-120.

Paine R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. J. Anim. Ecol. 49:667-685.

Paine R.T. (1984) Ecological determinism in the competition for space Ecology. 65:1339-1348.

Parry D.L. (1984) Chemical properties of the test of ascidians in relation to predation. Mar. Ecol. Prog. Ser. 17:279-282.

Pearse J.S. & A.H. Hines (1979) Expansion of a central Californian kelp forest following the mass mortality of sea urchins. Mar. Biol. 12:28-41.

Peterson C.H., H.C. Summerson & P.B. Duncan (1984) The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, Mercenaria mercenaria. J. Mar. Res. 42:123-128.

Philander S.G.H. (1983) El Niño Southern Oscillation phenomena. Nature (London) 302:295-301.

Power J.H. (1984) Advection and drift migrations of larval fish. In, Mechanisms of Migration in Fishes. McCleave J.D., G.P. Arnold, J.J. Dodson & W.H. Neill (eds) Plenum Press New York & London. pp. 27-39.

Quayle D.B. (1964) Distribution of introduced marine mollusca in British Columbia waters. J. Fish Res. Board Can. 21:1155-1181.

Randall J.E. & W.D. Hartman (1968) Sponge-feeding fishes of the West Indies. Mar. Biol. 1:216-225.

Reiswig H.M. (1973) Population dynamics of three Jamaican Demospongiae. Bull. Mar. Sci. 23:191-226.

Richmond R.C., M.E. Gilpin, S.P. Salas & F.J. Ayala (1975) A search for emergent competitive phenomena: The dynamics of multispecies Drosophila systems. Ecology 56:709-714.

Ricklefs R.E. (1987) Community diversity: relative roles of local and regional processes. Science 235:167-172.

Roughgarden J. (1974) Population dynamics in a spatially varing environment: how population size "tracks" spatial variation in carrying capacity. Am. Nat. 108:649-664.

Roughgarden J., Y. Iwasa & C. Baxter (1985) Demographic theory for an open marine population with space-limited recruitment. Ecology. 66:54-67.

Russ G.R. (1980) Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. J. Exp. Mar. Biol. Ecol. 42:55-69.

Russ G.R. (1982) Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. Oecologia (Berlin). 53:12-19.

Russell F. (1966) An investigation of the palability of some marine invertebrates to four species of fish. Pacific Sci. 20:452-460.

Ryland J.S., R.A. Wigley & A. Muirhead (1984) Ecology and colonial dynamics of some Pacific reef flat Didemnidae (Ascidiacea). Zool. J. Linn. Soc. 80:261-282.

Sabbadin A. (1981) Genetics of the colonial ascidian, Botryllus schlosseri. In, Marine Organisms - genetics, ecology and evolution. Battaglia B. & J.A. Beardmore (eds). Plenum Press New York pp.195-209.

Salt G.W. (1979) A comment on the use of the term "emergent properties". Am. Nat. 113:145-151.

Sammarco P.W. (1980) Diadema and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. Exp. Mar. Biol. Ecol. 45:245-272.

Sastry A.N. (1985) Pelagic larvae: an evolutionary compromise. Maritimes 29:10-12.

Scheibling R.E. & R.L. Stephenson (1984) Mass mortality of Strongylocentrotus droebachiensis off Nova Scotia. Mar. Biol. 78:153-164.

Scheltema R. (1974) Biological interactions determining larval settlement of marine invertebrates. Thalassia Jugosl. 10:263-296.

Scheltema R.S. (1977) Dispersal of marine invertebrate organisms: paleobiogeography and biostratigraphic implications. In, Concepts and Methods of Biostratigraphy. Kauffman E.G. & J.E. Hazel (eds) Dowden Hutchinson & Ross Strousberg, Pennsylvania. pp. 73-108.

Schoener T.W. (1986) Mechanistic approaches to community ecology: A new reductionism? Am. Zool. 26:81-106.

Sebens K.P. (1983a) The larval and juvenile ecology of the temperate octocoral Alcyonium siderium Verrill. I. Substratum selection by benthic larvae. J. Exp. Mar. Biol. Ecol. 71:73-89.

Sebens K.P. (1983b) The larval and juvenile ecology of the temperate octocoral Alcyonium siderium Verrill. II. Fecundity, survival, and juvenile growth. J. Exp. Mar. Biol. Ecol. 72:263-285.

Sebens K.P. (1985) Community ecology of vertical rock walls in the Gulf of Maine, U.S.A.: small-scale processes and alternative community states. In, The Ecology of Rocky Coasts. Moore P.G. & R. Seed (eds) Hodder and Stoughton, Sevenoaks, Kent, England. pp. 346-371.

Shanks A.L. (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311-315.

Shelbourne J.E. (1957) The 1951 Oyster stocks in the Rivers Crouch and Roach, Essex. Fish. Invest. Lond. 21:1-27

Sélys-Longchamps M. de. (1915) Autotomie et régénération des viscè chez Polycarpa tenera Lacaze et Delage. Acad. sci. Comptes rendus. 160:566-569.

Snedecor G.W. & W.G. Cochran (1980) Statistical Methods. Seventh ed. Iowa State University Press Iowa. pp. 507.

Sokal R.R. & F.J. Rohlf (1969) Biometry. First ed. W.H. Freeman and Company, San Francisco 776pp.

Sokal R.R. & F.J. Rohlf (1981) Biometry. Second ed. W.H. Freeman and Company, San Francisco 859pp.

Sork V.L. (1984) Examination of seed dispersal and survival in red oak Quercus rubra (Fagaceae), using metal-tagged acorns. Ecology 65:1020-1022.

Stearns S.C. (1976) Life history tactics: a review of the ideas. Q. Rev. Biol. 51:3-47

Stocker L.J. (1984) Recruitment, growth and mortality in the subtidal ascidian Pseudodistoma novaezelandiae (ascidiacea: Polyclinidae). M.Sc. thesis. Uni. Auckland, N.Z.

Stoecker D. (1980a) Distribution of acid and vanadium in Rhopalaea birkelandi Tokioka. J. Exp. Mar. Biol. Ecol. 48:277-281.

Stoecker D. (1980b) Relationships between chemical defense and ecology in benthic ascidians. Mar. Ecol. Prog. Ser. 3:257-265.

Stoecker D. (1980c) Chemical defenses of ascidians against predators. Ecology 61:1327-1334.

Stoner D.S. (1986) Distribution of a tropical colonial ascidian: a result of settlement or post-settlement processes? In, Program of the IV International Congress of Ecology, Syracuse, New York, August 1986 p.323 (Abstract only).

Strathman R.R. (1980) Why does a larva swim fo long? Paleobiology 6:373-376.

Strathmann R.R., E.S. Branscomb & K. Veoder, (1981) Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. Oecologia (Berlin) 48:13-18.

Strong D.R. (1984) Density-vague ecology and liberal population regulation in insects. In, A New Ecology: novel approaches to interactive systems. Price P.W., C.N. Slobodchikoff & W.S. Gaud (eds). Wiley & Sons New York. pp.313-329.

Struhsaker J.W. (1968) Selection mechanisms associated with intraspecific shell variation in Littorina picta (Prosobranchia; Mesogastropoda) Evolution 22:459-480.

Suchanek T.H. (1978) The ecology of Mytilus edulis L. in exposed rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 31:105-120.

Sutherland J.P. (1981) The fouling community at Beaufort, North Carolina: a study in stability. Am. Nat. 118:499-519.

Sutherland J.P. & R.H. Karlson (1977) Development and stability of the fouling community at Beaufort, North Carolina. Ecol. Monogr. 47:425-446.

Svane I. (1983) Ascidian reproductive patterns related to long-term population dynamics. Sarsia 68:249-255.

Svane I. (1984) Observations on the long-term population dynamics of the perennial ascidian, Ascidia mentula O.F. Muller, on the Swedish west coast. Biol. Bull. 167:630-646.

Svane I. & T. Lundalv (1981) Reproductive patterns and populaton dynamics of Ascidia mentula O.F. Muller on the Swedish west coast. J. Exp. Mar. Biol. Ecol. 50:163-182.

Svane I. & T. Lundalv (1982a) Population dynamics and reproductive patterns of Boltenia echinata (Ascidiacea) on the Swedish west coast. J. Neth. Sea. Res. 16:105-118.

Svane I. & T. Lundalv (1982b) Persistence stability in ascidian populations: Long-term population dynamics and reproductive pattern of Pyura tessellata (Forbes) in Gullmarsfjorden on the Swedish west coast. Sarsia 67:249-257.

Thompson J.E., R.P. Walker & D.J.Faulkner (1985) Screening and bioassays for biologically-active substances from forty marine sponge species from San Diego, California, USA. Mar. Biol. 88:11-21.

Thorson G. (1946) Reproduction and larval development of Danish marine bottom invertebrates. Meddr. Kommn. Danm. Fisk-og. Havunders, Ser Plankton 4:1-523.

Thorson G. (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25:1-45.

Thorson G. (1964) Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia 1:167-208.

Tukey J.W. (1977) Exploratory Data Analysis. Addison-Wesley Publishing Co. Reading, Massachusetts 688pp.

Tunnicliffe V.J. (1981) Breakage and propagation of the stony coral, Acropora cervicornis. Proc. Natl. Acad. Sci. (USA) 78:2427-2431.

Turkington R. & J.L. Harper (1979) The growth, distribution and neighbour relationships of Trifolium repens in a permanent pasture IV. Fine scale biotic differentiation. J. Ecol. 67:245-254.

Underwood A.J. (1980) The effect of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia (Berlin) 46:201-213.

Underwood A.J. (1981) Techniques of analysis of variance in experimental marine biology and ecology. Ocean. Mar. Biol. Ann. Rev. 19:513-605.

Underwood A.J., E.J. Denley & M.J. Moran (1983) Experimental analysis of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. Oecologia (Berlin) 48:221-233.

Underwood A.J. & E.J. Denley (1984) Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In, Ecological Communities: conceptual issues and the evidence. Strong D.R. jr, D. Simberloff, L.G. Abele & A.B. Thistle (eds) Princeton University Press New Jersey pp. 151-180.

Vavio S., R. Chakraborty & M. Nei (1986) Genetic variation in subdivided populations and conservation genetics. Heredity 57:189-198.

Vogel S. (1981) Life in Moving Fluids. Willard Grant Press, Boston, Massachuasetts.

Waser N.M. & M.V. Price (1982) A comparison of pollen and fluorescent dye carry-over by natural pollinators of Ipomopsis aggregata (Polemoniaceae). Ecology 63:1168-1172.

Wethey D.S. (1985) Local and regional variation in settlement and survival in the intertidal barnacle Semibalanus balanoides: patterns and consequences. In, The Ecology of Rocky Coasts. Moore P.G. & R. Seed, Hodder and Stoughton, Sevenoaks, Kent, England. pp.194-202.

Wilson D.P. (1952) The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of Ophelia bicornis Savigny. Ann. Inst. Oceanogr. 27:49-152.

Winer B.J. (1971) Statistical principles in experimental design. McGraw-Hill Kogakusha, Tokyo, Japan.

Woodin S.A. (1985) Effects of defecation by the arenicolid polychaete adults on spionid polychaete juveniles in field experiments: selective settlement or differential mortality. J. Exp. Mar. Biol. Ecol. 87:119-132.

Yoshioka P.M. (1982) Role of planktonic and benthic factors in the population dynamics of the bryozoan Membranipora membranacea. Ecology 63:457-468.

Young C.M. & F.-S. Chia (1981) Laboratory evidence for delay of larval settlement in response to a dominant competitor. Int. J. Invert. Reprod. 3:221-226.

Young C.M. & F.-S. Chia (1984) Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. Mar. Biol. 81:61-68.

Appendix 1. Data used to determine the relationship between zooid number, the area of attachment and colony size (dry weight).

Colony number	Number of zooids	Attachment area (mm)	Wet weight (g)	Dry weight (g)
1	62	811	6.4014	0.4531
2	109	-	12.4024	0.9303
3	77	871	11.2904	0.815
4	26	530	3.4846	0.2415
5	52	463	8.3387	0.5167
6	28	140	1.9105	0.1398
7	64	586	8.7316	0.2704
8	26	339	2.6444	0.2316
9	98	1017	11.8243	0.8809
10	55	542	4.1307	0.2954
11	91	1015	19.479	1.3893
12	272	-	61.4987	4.3167
13	43	855	6.7927	0.4529
14	40	390	6.5357	0.4313
15	107	1408	20.3262	1.3854
16	22	627	3.1283	0.2532
17	46	398	5.9272	0.4354
18	40	421	5.7199	0.3422
19	43	575	2.7829	0.1702
20	64	387	9.5457	0.6202
21	52	437	4.2036	0.3319
22	131	976	2.624	1.3036
23	60	685	9.525	0.7358
24	94	1128	19.5877	1.353
25	28	104	2.4188	0.1654
26	54	289	7.9333	0.5161
27	37	695	17.4629	0.221
28	72	993	7.6358	0.6622
29	42	340	4.2546	0.3826
30	95	-	10.6328	0.9024
31	32	562	2.9895	0.2147
32	92	824	14.3785	1.1606
33	41	133	3.6328	0.2162
34	10	91	0.3553	0.0281
35	14	97	0.7861	0.0548
36	40	229	3.3094	0.2392
37	175	1238	24.6521	1.7656
38	89	560	9.519	0.6536
39	147	1112	26.6112	1.7121
40	192	1853	29.0892	2.3223
41	249	2046	42.2414	3.3418
42	110	946	16.1484	1.1941
43	91	629	13.1546	0.947
44	43	386	5.4509	0.3267
45	8	57	0.2921	0.0234
46	155	799	13.4701	0.9035
47	53	278	5.8342	0.3828
48	220	1061	28.7774	2.0281
49	133	1097	17.4131	1.0296
50	50	245	3.9343	0.2848

Appendix 1. (continued)

Colony number	Number of zooids	Attachment area (mm)	Wet weight (g)	Dry weight (g)
51	168	1434	35.4312	2.22
52	194	1318	25.4633	1.7725
53	80	852	11.3421	0.7342
54	12	224	1.6696	0.1177
55	87	821	12.5269	0.9252
56	152	1149	29.4429	1.9409

Appendix 2. Data obtained while larvae were followed underwater from the parent colony to settlement, Chapter 3. Note, a current speed of 0cm s^{-1} means the current was flowing at less than 5cm s^{-1}.

Date	Time	Distance Moved (m)	Time swimming (secs)	Total time to settle (secs)	Angle of dispersal (degrees)	Current speed (cm s^{-1})	Trap no.	no. of touches	Height larva settled above seabed (m)
8.11	11.32	9.5	210	210	0	7.8	2	1	1.25
8.11	13.12	6.5	200	390	0	6	1	2	10
10.11	11.11	6.5	111	130	0	8	1	2	2.5
10.11	12.21	6.8	550	550	30	5	1	4	1
10.11	16.15	1	30	40	0	5	2	5	2.5
11.11	11.07	0.1	43	43	0	0	2	1	1.6
11.11	11.5	10.1	288	598	35	6	5	11	1.5
11.11	12.05	0.1	36	36	0	6.5	2	1	1.6
11.11	12.3	0.85	40	40	0	6.5	2	1	2
11.11	12.3	0.2	45	45	0	6	5	3	2.2
11.11	13.08	0.05	67	67	0	8	5	1	2.05
11.11	13.14	0.1	15	15	0	6.5	2	1	1.6
11.11	13.17	0.1	24	24	0	6.5	5	1	2.1
11.11	13.22	0.15	32	32	0	6	5	1	2.15
11.11	13.25	1.1	74	74	0	6	2	1	2.6
11.11	13.3	0.4	38	60	10	6	1	4	2.4
11.11	13.34	0.6	109	109	10	6	2	7	1.7
11.11	13.53	1.5	137	137	0	0	1	7	3
11.11	14.1	0.5	20	40	0	0	1	8	2.5
11.11	14.2	0.2	38	38	0	0	1	1	2.2
11.11	14.25	3.6	240	240	40	0	1	1	0
12.11	10.45	0.15	51	75	0	0	5	4	2.15
12.11	13.2	2.5	89	89	0	6.5	1	1	2.5
12.11	13.35	0.08	73	73	0	9	1	1	2.1
12.11	14.03	0.25	31	31	0	7.8	1	1	2

Appendix 2. (continued)

Date	Time	Distance Moved (m)	Time swimming (secs)	Total time to settle (secs)	Angle of dispersal (degrees)	Current speed (cm s^{-1})	Trap no.	no. of touches	Height larva settled above seabed (m)
12.11	14.21	11.2	287	287	60	7	1	1	0.5
12.11	14.22	0.9	135	135	30	7	2	1	2
13.11	13.4	1.1	74	74	0	10	1	1	3
13.11	14.21	0.1	40	40	0	11	1	1	2.1
14.11	10.54	1.45	150	10800	0	5	2	12	1.7
14.11	11.03	0.45	180	180	0	5	2	10	1.7
14.11	11.52	1.15	67	67	0	0	2	1	2
14.11	12.04	0.05	15	15	0	6	2	1	1.5
14.11	12.43	8.9	272	272	35	10	5	1	0
14.11	12.57	0.2	21	21	0	10	5	1	2.1
14.11	13.03	0.15	59	59	0	11.2	2	4	1.6
14.11	13.14	0.3	120	120	0	6.5	1	3	2.1
14.11	13.2	2.5	46	46	0	6.5	5	2	2.5
14.11	13.48	10.3	240	240	20	10.1	2	1	3
14.11	14.08	11.5	0	0	35	11.5	1	4	0
15.11	16.52	0.3	40	40	0	7	2	1	1.6
17.11	11.1	0.9	60	60	30	7	2	1	2
17.11	11.19	0.9	33	33	30	7	2	2	2
17.11	11.21	0.8	105	105	30	7	2	2	2
17.11	11.23	0.05	20	20	0	7	2	1	1.5
17.11	11.32	0.8	70	70	30	6.5	2	1	2
17.11	11.37	0.5	80	80	0	6.5	2	1	1.5
17.11	11.39	4.5	275	275	30	6.5	2	1	0
17.11	11.46	0.5	99	99	0	6	2	1	1.6
17.11	12.03	0.35	158	158	0	6.8	4	1	2.2
17.11	12.09	0.5	72	72	0	6.8	2	1	1.7
17.11	12.2	0.35	52	52	0	6.8	2	1	1.6
17.11	12.23	0.2	35	35	0	6	5	1	2.1
17.11	12.24	1.2	54	54	0	6	5	1	3

Appendix 2. (continued)

Date	Time	Distance Moved (m)	Time swimming (secs)	Total time to settle (secs)	Angle of dispersal (degrees)	Current speed (cm s^{-1})	Trap no.	no. of touches	Height larva settled above seabed (m)
17.11	12.29	0.75	89	89	0	6	5	4	2.8
17.11	13.26	0.65	78	78	0	0	2	3	1.8
17.11	13.29	0.1	73	73	0	0	2	1	1.5
17.11	13.32	0.45	98	98	0	0	2	14	1.7
17.11	13.35	1.4	120	161	0	0	2	2	3
17.11	13.46	0.5	30	30	0	0	2	1	1.5
17.11	13.48	3.6	183	183	45	0	3	1	0
17.11	13.55	0.25	31	31	0	0	5	1	2.1
17.11	14.22	0.3	40	40	0	0	4	1	1.6
19.11	11.26	0.15	58	58	0	0	1	1	1.5
19.11	11.3	6.4	334	334	30	0	5	3	0
19.11	11.48	2	158	158	30	0	2	-	3.3
19.11	11.56	2.5	400	523	0	0	2	20	3.5
19.11	12.23	0.15	40	40	0	0	5	1	2.1
19.11	12.24	0.45	54	54	0	0	5	4	2.2
19.11	12.35	0.15	30	30	0	0	5	1	2.1
19.11	13.12	0.5	92	92	0	0	2	1	1.7
19.11	13.14	0.8	82	100	0	6	2	1	1.8
20.11	13.43	1	84	84	0	0	5	1	2.7
20.11	13.5	1.4	0	0	0	0	2	14	3
23.11	13.44	1.1	58	58	0	6.5	2	1	1.5
24.11	11.07	9.75	152	152	30	10	4	1	0
24.11	11.36	7	161	161	35	10.4	5	1	1.75
24.11	14.27	10.2	270	270	25	7.8	2	1	3

Appendix 2. (continued)

Date	Time	Distance Moved (m)	Time swimming (secs)	Total time to settle (secs)	Angle of dispersal (degrees)	Current speed (cm s^{-1})	Trap no.	no. of touches	Height larva settled above seabed (m)
24.11	13.39	13.8	460	460	10	9.6	2	3	0
25.11	18.3	0.2	30	30	0	6	4	1	2.1
27.11	11.37	2.35	268	268	55	0	10	1	0.25
27.11	11.55	2.15	164	164	0	5	13	6	0.25
27.11	13.19	1.65	65	65	55	8	10	1	0.25
28.11	10.35	6.1	273	273	40	8.2	10	2	0
28.11	10.43	0.05	120	120	0	8.2	10	2	1
28.11	10.54	0.4	40	40	0	6	10	1	1.2
28.11	11.35	0.05	15	15	0	8.3	11	1	1
28.11	12.27	9.3	230	230	35	8.3	13	1	0
29.11	12.06	0.15	120	170	0	0	13	3	1
29.11	12.12	0.05	59	59	0	0	14	2	1

Appendix 3. Kokkinn M.J. & A.R. Davis (1986) Secondary Production: Shooting a Halcyon for its Feathers. In, Limnology in Australia. De Decker P. & W.D. Williams (eds) CSIRO Melbourne. pp. 251-261.

M. J. Kokkinn and A. R. Davis (1986) Secondary Production: Shooting a Halcyon for Its Feathers.
Monographiae Biologicae, v. 61, pp. 251-261, 1986

Appendix 4. Davis A.R. (in press) Variation in recruitment of the subtidal colonial ascidian Podoclavella cylindrica (Quoy & Gaimard): the role of substratum choice and early survival. J. Exp. Mar. Biol. Ecol.

A. R. Davis (1987) Variation in Recruitment of the Subtidal Colonial Ascidian Podoclavella-Cylindrica (Quoy and Gaimard): the role of substratum choice and early survival.
Journal of Experimental Marine Biology and Ecology, v. 106 (1), pp. 57-71, March 1987

ADDENDUM

(See asterisks in text)

Page 63: It must be remembered that settlement depends not only on encountering a surface, but also on the suitability of that surface. If a reef happens to provide a greater density of suitable sites than pilings, then distance moved might be reduced.

Page 78: The higher densities of recruits seen in Figure 4.3-4 (recruits per cm^2) relative to those in Figures 4.2-2 and 4.2-3 (recruits per dm^2) were an artifact of density estimates being based on different sized quadrats. The densities in Figure 4.3-4 were higher because the small (81 cm^2) quadrats were selectively placed on certain substrata, one of which was bare space. Of the 54 quadrats placed on substrata, 18 (40%) of them were on bare wood. Podoclavella has high settlement and survival on bare wood (Davis, in press), and bare wood usually accounts for less than 25% of the total cover of pilings at this site (Kay & Butler, 1983). Hence the density per unit area appears higher than in larger quadrats.

Page 136: Chemicals from the sponges might, of course, act as cues to behaviour without having any toxic effect on the ascidian larvae.

Page 148: This test, based on the largest five zooids, may be insensitive if the variance in zooid size is high in damaged colonies. Casual observations, however, did not indicate any greater heterogeneity in damaged than undamaged colonies.