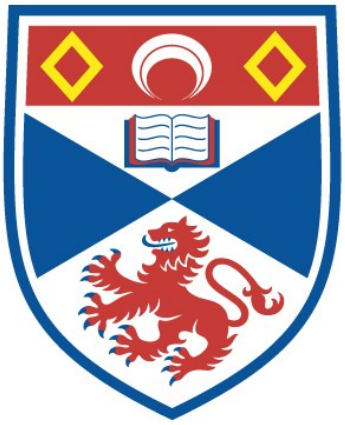
THE ECOLOGY OF HARD-SUBSTRATUM EPIFAUNAL ASSEMBLAGES : EFFECTS OF LARVAL RECRUITMENT, COMPETITION AND GRAZING

Stephanie Jane Turner

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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THE ECOLOGY OF HARD-SUBSTRATUM EPIFAUNAL ASSEMBLAGES: EFFECTS OF LARVAL RECRUITMENT, COMPETITION AND GRAZING.

by

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being a thesis submitted to the University of St. Andrews in candidature for the degree of Doctor of Philosophy.

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Declaration

I declare that the research reported in this thesis is my own, and that no part of it has been previously submitted for any other degree. The research was conducted at the Gatty Marine Laboratory, University of St. Andrews, between August 1983 and October 1988, under the direction of Dr. C.D. Todd.

Signed

(candidate)

Certificate

I certify that Stephanie Jane Turner has fulfilled the conditions laid down under Ordinance General Number 12 and Resolution of the University Court 1967 Number 1, of the University of St. Andrews; and that she is qualified to submit this thesis in the application for the degree of Doctor of Philosophy.

Signed

(supervisor)

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for Mum, Dad, Paul and Paul,
with much love

ABSTRACT

Artificial substrata were employed at sites on the east and west coasts of Scotland, in such a manner as to model the habitat found on the undersides of boulders on the shore. Panel treatments were devised to examine the effects of substratum 'age' and larval availability, and the presence or absence of varying densities of herbivorous molluscan grazers on the development of the epifaunal assemblages. The importance of inter- and intraspecific competition in structuring the bryozoan component of the assemblage was also examined.

A necessary pre-requisite for the settlement of many marine invertebrate larvae may be the development of a microfouling film, the nature of which may vary depending on its 'age', with corresponding effects on the 'attractiveness', or otherwise, to potentially settling larvae. The lowest numbers of recruits were frequently recorded on the 'youngest' panels, and greater numbers generally occurred on panels immersed for longer periods. Also of overriding significance, however, was the seasonal variability in larval availability. The assemblages were characterized by high levels of post-settlement mortality.

The outcomes of the overgrowth interactions between 18 species of encrusting bryozoans were highly variable and complex, each species of an interacting pair won some encounters, and neither consistently overgrew the other. Therefore, the pattern of competitive abilities was

neither entirely intransitive or transitive. Variations in outcome were found to be at least partially attributable to differences in the encounter angle between colonies. The competitive ability of a species also varied among sites and between years.

The herbivorous grazing gastropod *Gibbula cineraria* was found to have a markedly deleterious effect on the developing assemblages. Furthermore, individuals and colonies of the epifaunal species were apparently unable to achieve an 'escape-in-size' under the experimental conditions employed.

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1. GENERAL INTRODUCTION

1.1. SUCCESSION

The concept of succession - "...a pattern of changes in specific composition of a community after a radical disturbance..." (Horn, 1974, p.25) - has been regarded as "...a fundamental tenet of ecological theory" (Anderson, 1986, p.269). Much of the classical successional theory derives from the detailed vegetational studies of Clements (1916). Clements (1916) regarded succession as being a progressive and deterministic change, which could be reduced to a number of basic processes: nudation, migration, ecesis, competition, reaction and stabilization. Although recognizing the role of the physical environment, Clements (1916) regarded the underlying motive forces in the continuation of succession as reaction and competition - i.e. the communities themselves play the major role in bringing about succession (Odum, 1959). Reaction is the effect which a species or community exerts upon its habitat, producing physical conditions unfavourable to its performance, but advantageous to invaders of the next stage. Central to Clements' theory is the concept that succession is analogous to the development of an organism, in which the organism itself controls its development subject to environmental conditions (Tansley, 1920).

The idea that succession is a process of "community development" led Margalef (1962) to consider changes in the composition of communities during succession to be

comparable to the maturing and ageing of an organism. Margalef (1962) also suggested that by a process of succession the community becomes more precisely adjusted to the environment, specifically in terms of the maintenance of a maximum total biomass with minimum relative energy dissipation. The bioenergetic basis of succession is also fundamental to Odum's (1969) model of succession. Odum (1969) proposed a tabular model of succession, documenting the changes that occur in major structural and functional characteristics between the developmental and mature stages of a community. He defined succession in terms of the following 3 parameters:- (i) it is an orderly and reasonably directional process of community development; (ii) it is community controlled; (iii) it culminates in a stabilized ecosystem. He recognized the "strategy" of succession as "...increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations" (Odum, 1969, p.262). Sutherland and Karlson (1977) examined the fouling community at Beaufort, North Carolina in the context of Odum's successional model, and concluded that succession in the classical sense did not occur. Rather, community composition was always changing, the rate and direction being determined by the regime of larval recruitment, and the longevity and ability of the resident assemblage to resist larval invasion. They considered that this may be characteristic of many temperate and subtropical fouling communities and concluded that, despite many apparent

similarities between fouling communities and terrestrial plant communities, succession does not occur in the former. Three potential differences between the systems were recognized: (i) organisms in the fouling community growing on hard substrata do not alter the habitat in the same manner as pioneers ameliorate habitat conditions for later stages in vegetation succession (i.e. the "reaction" of Clements, 1916); (ii) fundamental differences exist in the mode of entry or establishment in the habitat; and (iii) in the longevity of the species.

There has been considerable subsequent criticism of the developmental models of succession. Horn (1974) suggested that since structural and functional characteristics take time to develop, they might be expected to do so as a consequence of the passage of time during succession, rather than as a result of internal control. Drury and Nisbet (1973) concluded that changes in the structural and functional properties of a community are not consistently associated with changes in species composition. An essential feature of the classical models of succession is that it is a community phenomenon. Drury and Nisbet (1973) suggested that a complete theory of succession should be sought at the organism level rather than in the emergent properties of communities. Breitburg (1985) found that an explanation of succession based on the general interactions between earlier and later stages, rather than on particular

interactions between earlier and later species, would prove totally inadequate. The former would only predict effects on the rate of succession; while the latter must be considered to predict changes in species composition. Drury and Nisbet (1973) argued that most of the phenomena of succession could be ascribed to differences in the colonizing ability, growth and survival of species specialized to exist in a limited range of environmental conditions; the distinct successional stages are merely the result of a sequential conspicuousness of the species, attributable to these differences.

Succession is directional because certain adaptive strategies are mutually exclusive (Krebs, 1978). The biological adaptations of species characteristic of early successional stages (short-lived, rapidly growing, massive reproductive potential and high dispersal capacity) would thus be expected to differ greatly from those of late successional species (longer-lived, slower growing, reduced reproductive output, but at a competitive advantage through, for example, larger size at maturity); *viz.* so-called "r-selected" and "K-selected" species (Pianka, 1970). Also critical are differences in the vulnerability of individual organisms to death or injury from natural enemies and physical disturbance, between successional stages (Sousa, 1980). Greene *et al.* (1983) have examined the adaptive significance of solitary and colonial strategies in succession within fouling communities. Observations by Chalmer (1982) on fouling community succession support the predictions of

differences between early and late successional stages: *Balanus* spp. and *Spirorbis* spp. were predominant early in succession because they settled rapidly and abundantly; *Anomia trigonopsis*, *Ostrea* spp. and encrusting bryozoans settled in relatively low densities and because growth was necessary before they occupied a substantial area they tended to predominate at a later stage in succession; *Mytilus edulis* settled on panels of all ages, but the period necessary for *M.edulis* to reach a large individual size acted to delay the time at which this species became predominant. Drury and Nisbet (1973) considered that a theory of succession based on these premises more closely corresponds with the theory of natural selection, in that it does not relegate the majority of species and communities to "successional" status with less than maximal fitness.

Connell and Slatyer (1977) proposed 3 alternative models to explain how the sequence of species in successions may be determined. All the models agree that certain species usually appear first because they have evolved certain "colonizing" characteristics. However, critical distinctions between the models lie in the mechanisms that determine subsequent establishment of species in the sequence, and in the cause of death of the early colonists; in essence, they are based upon different viewpoints of the organization of ecological communities.

(i) The Facilitation Model:- (cf. the successional model of Clements (1916) and the "Relay Floristics Model" of Egler (1954)). Early successional species modify the environment so that it becomes more suitable for later colonists to invade and grow to maturity; the sequence continues until the resident species no longer modify the habitat in ways that facilitate further invasion. There are numerous examples which suggest that facilitation may be operational in the successional processes, for example the studies of Dean and Hurd (1980) and Breitburg (1985). Turner (1983) distinguished between:

(a) non-obligate facilitation - later species may establish faster in the presence of earlier species, but they can also colonize in areas devoid of earlier species. For example, Dean and Hurd (1980) found that settlement of *Mytilus edulis* was facilitated by other species, but earlier colonists were not essential.

(b) obligate facilitation - Turner (1983), for example, found evidence of obligate facilitation in the recruitment of the dominant surfgrass, *Phyllospadix scouleri*, during secondary succession in a rocky intertidal community. Prior establishment of mid-successional algae species was necessary for this recruitment, but not all the species could equally facilitate surfgrass recruitment, the extent varied with the morphology of the species. Significantly more of the barbed surfgrass seeds attached to turf-forming algal species with a central axis approximately 1mm in diameter

and bushy side branches (e.g. erect coralline algae and the red alga *Rhodomela larix*); but seeds did not attach to blade-like algae (e.g. *Iridaea heterocarpa*) which did not provide a purchase for the seeds.

(ii) The Tolerance Model:- (cf. the "Initial Floristics Composition Model" of Egler (1954)). The earlier colonists neither increase nor reduce the rates of recruitment and growth of later colonists. Any arriving species is able to colonize in the first instance, and many of the late successional stage species may be present in the system at the outset. The successional sequence here is determined solely by life-history characteristics: that is, species that predominate later simply grow more slowly. The more tolerant species are those that are better able to utilize resources and eventually dominate. Connell and Slatyer (1977) could find little evidence in support of this model, but Greene *et al.*(1983) predicted that in fouling communities, vertical growth may ultimately transform solitary animals from inferior direct competitors for space into superior indirect competitors. This prediction was attributable to their ability to drastically alter the local flow regime and thereby, food availability.

(iii) The Inhibition Model:- Once earlier colonists have secured space and/or other resources, they may inhibit the invasion by subsequent colonists. Later species are able to invade only after the disturbance or death of earlier species, with a corresponding release of

resources. No directional mechanism is invoked; the species that eventually dominate do so simply by virtue of their life-histories, and hence the community composition will gradually shift towards species which live longer. The dominant species are those that are most resistant to damage or elimination. For example, Harger and Tustin (1973) found that settlement of the ascidian *Microcosmus kura*, on a panel fixed immediately above another panel bearing a subclimax community of adult ascidians, was initially retarded when compared with settlement on a similar panel removed 4m from any community of adult ascidians. Other examples are abundant in the literature (see, for example, Goodbody, 1961; Sutherland, 1978; Breitburg, 1985).

No one model fully describes succession in the marine environment; more than one particular kind of interaction can be operating within a single community, and furthermore, the interactions vary considerably in magnitude (Dean and Hurd, 1980). Greene and Schoener (1982) preferred to view Connell and Slatyer's (1977) models of inhibition and tolerance as 2 extremes of a more generalized successional process, rather than as distinctly different or mutually exclusive processes. Thus, resident species may influence later colonists in different ways and to different degrees, or conversely, later colonists can respond differently to different residents (Breitburg, 1985). Similarly, Sutherland and Karlson (1977) concluded that after the initial phase of colonization, subsequent changes in species composition

depended upon the ability of larvae to invade existing assemblages; this in turn depended upon the identity of residents and of the invading larvae, because species differ in their abilities to resist invasion and to establish on occupied substrata. Keough and Downes (1982) have, however, questioned how much the observed patterns of recruitment reflect active choices by larvae, and how much they reflect mortality subsequent to settlement.

A number of studies (e.g. Dean and Hurd, 1980; Greene *et al.*, 1983; Turner, 1983) have suggested that inhibition is probably a major structuring force in marine communities. Dean and Hurd (1980) concluded that not only was inhibition more frequently encountered but would also be expected to have a more profound effect on the outcome of community development. They suggested that facilitation influences only the rate of development, while strong inhibitory interactions can determine the species composition.

Alternatively, succession may have no biological basis at all; the characteristics of succession ascribed to biological or physical origins are not unique to ecological succession, but are shared by a class of statistical processes known as "Regular Markov Chains" (Horn, 1974, 1975). A Markov chain is a stochastic process in which the transition among various "states" occurs with characteristic probabilities that depend only on the current state and not on any previous state.

Succession could thus be considered as an individual-by-individual replacement process, the overall species composition depending on the probabilities that individuals will be replaced by their own or another species. Greene and Schoener (1982) have developed a stochastic "fixed lottery" model, based on Markov chains, to describe succession on marine hard substrata. The individual components of the transitional probability matrix were derived on the assumption that there is a "lottery" for living space, i.e. species do not have an equal chance to reside in the community due to variations in mortality and recruitment levels. They suggested that by adding terms to the model, direct interspecific competition could also be accounted for. In its basic form the model is analogous to Connell and Slatyers' (1977) inhibition model.

Central to all theoretical successional models is the concept of a "climax community" - that community towards which all successional development is tending. The climax community is conceived to be a relatively stable, self-perpetuating system, essentially in equilibrium with the physical and biotic environment (see, for example, Krebs, 1978). It does not, however, represent a complete halt to directional successional change; Connell and Slatyer (1977) concluded - from a lack of evidence that species composition ever reached a steady state equilibrium in a community of sexually reproducing individuals - that succession never stops. Furthermore,

in many communities, major disturbances occur sufficiently frequently to interrupt the processes of succession prior to climax formation, causing a reinitiation of the sequences.

Clements (1916) recognized a single "climatic climax", determined primarily by the regional climate, and towards which all communities develop irrespective of earlier site conditions. This "monoclimax theory" was replaced by the "polyclimax theory" (Tansley, 1939, cited in Krebs, 1978) which envisaged a number of climax communities forming a mosaic corresponding to habitat heterogeneity. Whittaker (1953, cited in Whittaker, 1975) proposed a "climax-pattern hypothesis" interpreting climax communities as a series of intergrading communities corresponding to a sequence of environmental gradients. This is more in line with current theories of the climax as being a changing mosaic of successional stages, maintained by sources of perturbation acting locally within the community (see, for example, Sousa, 1979, 1984).

Directly related to the concept of the climax is that of community stability. Stability is frequently surmised to increase through succession to produce a stable climax (see, for example, Odum, 1959, 1969), by virtue of an increasing number of species and a consequent complexity of biological interrelationships, which are expected to confer resistance to external perturbations. There is, however, increasing evidence that

diverse and complex communities are generally less stable than comparable communities with fewer or less interdependent species (Horn, 1974). Furthermore, Drury and Nisbet (1973) stressed that there are no comparative studies which confirm the generally accepted hypothesis that populations fluctuate less in areas of greater ecological diversity. Frank (1968) has warned of the tautology in reasoning that mature communities are stable, when in reality the reasons for their constancy lies in the predominance of long-lived species. Horn (1974) surmised that the dilemma is a matter of definition - if stability is defined as an absence of species turnover and fluctuation then stability would be expected to increase with succession; conversely, if dynamic stability is recognized as resistance to perturbation, or the ability of a community to return to its original state after a temporary disturbance, then stability decreases through succession. In other words: "Disturb early succession and it becomes early succession. Disturb a climax community and it becomes an early successional stage that takes a long time to return to climax" (Horn, 1974, p.32). Smedes and Hurd (1981), for example, from a study of the stability of an estuarine fouling community, found that in terms of most community characteristics and their physical structure, older communities were less stable when subjected to patch forming perturbations, showing a greater rate and amplitude of deflection from the ground state, and a slower recovery, than younger systems. Sutherland (1981)

suggested that stability and instability are evident in all communities, depending on how the system is viewed; that is to say, taking into account which resident assemblage, which perturbation and over which time scale. Smedes and Hurd (1981) also stressed that stability is relative, and not an absolute property of a community, and they suggested that the stability of a community is further dependent on the criteria and measurements employed. Smedes and Hurd (1981) concluded that because of the relative scarcity and inconsistency of available evidence, any hypothetical relationship between stability and other community properties is at present far from being conclusive.

It is thus evident from this brief examination of the concept of succession that this important process is poorly understood. Indeed, the most striking feature of the process of succession is its very unpredictability. An all-encompassing and definitive interpretation of the successional process remains elusive and it may prove impossible to present a singular model. Horn (1974, p.26), among others, concludes that "...a universal and unifying theory is a fanciful goal."

1.2. THE AIMS OF THIS STUDY

This thesis is concerned with a study of early succession and assemblage organization on artificial substrata, placed in the intertidal and subtidal zones of rocky shores in such a manner as to model the habitat found characteristically on the underside of boulders. This is a structurally simple habitat, ideally amenable to study and manipulation: it is protected from desiccation and heavy wave action, and because of low light levels is lacking in algal competitors (Keen and Neill, 1980).

Three aspects have been considered:

(i) The influence of the timing of space availability, which is recognized to be of fundamental, if not paramount, importance in successional processes (see, for example, Osman, 1977; Sutherland and Karlson, 1977; Breitburg, 1985), and the subsequent 'age' of a surface on the recruitment of invertebrate epifauna into the understone habitat. Artificial substrata (panels) were first initiated at different times and then examined over similar total lengths of time. As a result, colonization of panels of varying 'age', could be evaluated over short contemporaneous periods - the 'age' of a panel is here defined as the length of time that it has been immersed. Thus, the number of individuals or colonies recruiting on to a newly submerged set of panels could readily be compared, between similar sampling dates, with the numbers establishing on panels previously

submerged for different lengths of time. The hypothesis under examination is that differences between sets of panels may result from contrasts in the 'attractiveness' of panels of different 'ages'.

(ii) It is generally recognized that competition for limited resources, primarily space, is of widespread importance in influencing the structure of epifaunal assemblages (see, for example, Jackson, 1977a). Examined in this study was the potential role of competition in organizing the bryozoan assemblages typical of understone habitats. Species may frequently be ranked in terms of their competitive ability, and Connell (1983) suggested that if the rank order remains the same, and if interspecific competition is stronger than intraspecific competition in the superior or dominant species, then the theoretically inferior or subordinate species should eventually be eliminated. This is commensurate with predictions from some successional models. If, however, the rank order of competitive ability is reversed, that is, the "direction" of competition is not consistent, then competitive elimination is less likely. It is therefore of interest to examine the interactions observed between pairs of bryozoan species in the understone habitat, to determine whether one species always wins, whether each species of the pair wins some of the contests (i.e. there is an "equivalence" of the outcomes between species) or whether neither species ever wins outright. The hypothesis under evaluation is that the angle of encounter between 2 colonies, which is one

of a number of variables which have been recognized as possibly determining the outcome of competitive overgrowth, may alter the rank order of the competitive superiority within a pair of species. Connell (1983) concluded that the process is further complicated because competition may not only vary in the degree to which species compete, but also in time and space. Competition would only be expected to be intense in those places and at those times when resources are in short supply - interactions cannot be invoked where resources are apparently adequate (Underwood, 1986). Therefore, variations in the spatial and temporal aspects of competition have also been considered in this study.

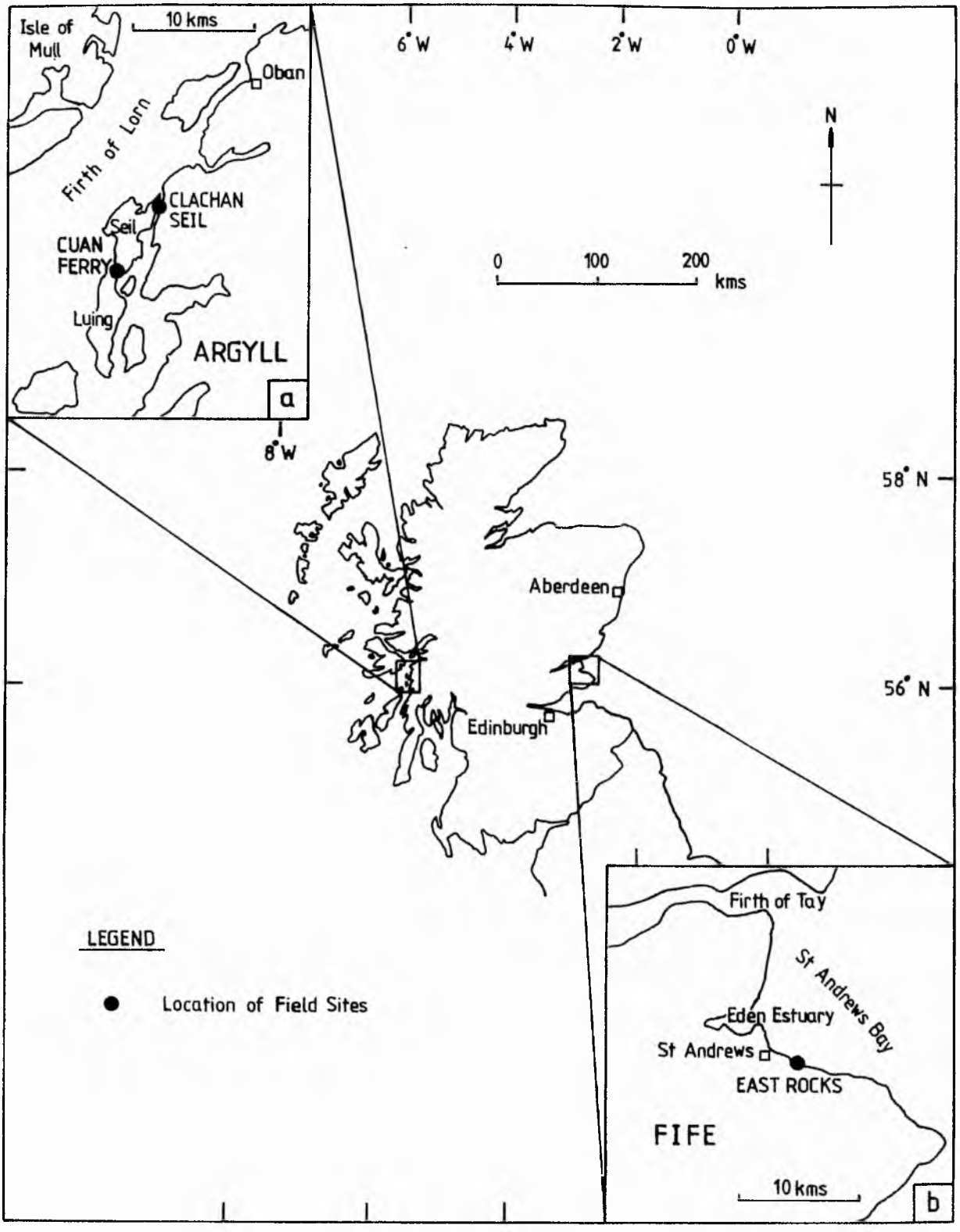
(iii) There is considerable evidence within the literature that the process of succession may be disrupted by physical and biological disturbances. For example, Breitburg (1985) and Van Tamelen (1987) found that invertebrate grazers could greatly influence successional processes and subsequent species composition of the community; Harris and Irons (1982) found that predation was a major determinant in fouling community succession. Osman (1977) and Davis and Wilce (1987) have examined the development of communities on boulders with respect to the frequency of physical disturbance by wave action. The present study examined the influence of controlled densities of 3 vagile invertebrates found commonly in the local habitat, on the early successional stages of assemblage development. The adopted

experimental approach was in accordance with that proposed by Underwood and Denley (1984), and Underwood (1985), who have suggested that experimental designs should incorporate comparisons with a range of densities of invertebrates to determine non-linear effects, rather than the total removal of all invertebrates and comparison with otherwise untouched controls.

Although recruitment, competition and grazing were considered independently in this study, in the natural assemblage they, and a host of other variable parameters, are complexly interrelated. Numerous models have been proposed in an attempt to explain the processes operational in natural assemblages (e.g. Connell, 1975, 1978, 1979; Menge and Sutherland, 1976). Underwood and Denley (1984) although conceding that evidence may exist to support such theories, suggested that alternative explanations must also be sought. They argued that the importance of competitive interactions and the effect of predators on them, are likely to be highly variable because of fluctuations in the recruitment of juveniles to the community. Variations in the intensity of recruitment of potential competitors will determine whether competition occurs. Thus, the dynamic and interrelated nature of the processes operating in assemblage development and organization must be continuously borne in mind. This will be considered again, in the final chapter.

2. MATERIALS AND METHODS

FIGURE 2.1. Map showing the location of the study sites on (a) the west coast and (b) the east coast of Scotland.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CLACHAN SEIL
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CUAN FERRY
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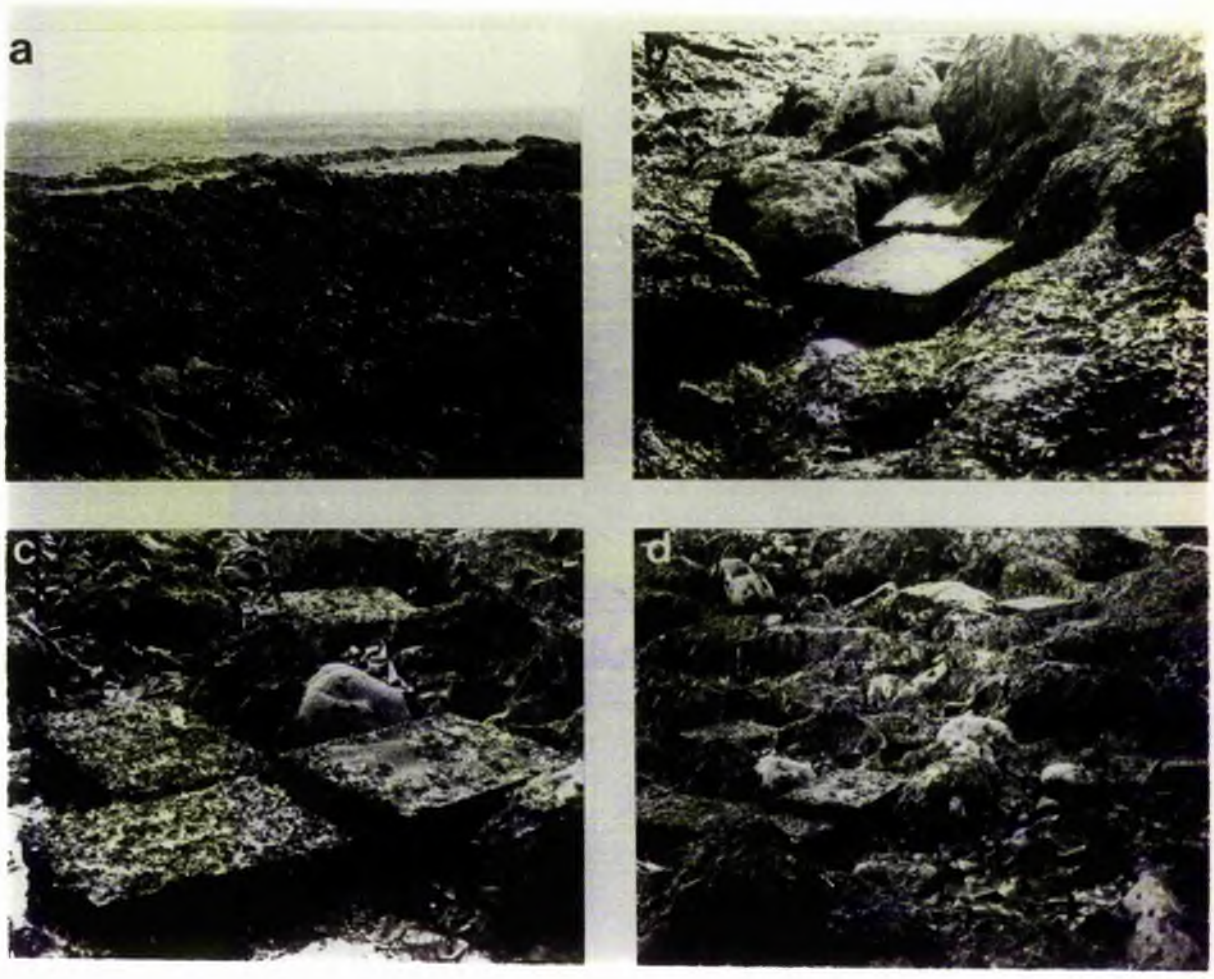
ARGYLL
a
8°W
6°W
4°W
2°W
0°W
N
0
100
200
kms
58°N
56°N
Aberdeen
Edinburgh
LEGEND
Location of Field Sites
Firth of Tay
St Andrews Bay
Eden Estuary
St Andrews
EAST ROCKS
FIFE
10 kms
b

2.1. THE STUDY AREAS

A large proportion of the field-work was carried out at St.Andrews, Fife (56°20'N, 2°47'W), on the east coast of Scotland (see Figure 2.1.). The 2 sites were on an area of rocky shore 1.5km to the south-east of the Gatty Marine Laboratory, and at the foot of the Kinkell Braes. The shore section of the Kinkell Braes consists of calciferous sandstones and igneous rocks (Laverack and Blackler, 1974); the stratified rocks are thrown into a long series of anticlinal and synclinal folds, intersected by numerous faults and pierced by the necks of ancient volcanoes (Kirk, 1925). North of the rocks there is a sandy beach (the East Sands) with St.Andrews harbour situated at the mouth of the Kinnessburn. Sublittorally St.Andrews Bay is relatively shallow - approximately 22m deep 8km offshore - and the bottom is comprised mainly of mud and sand, with some rock (Laverack and Blackler, 1974). The water at the sites was observed to contain much suspended material, especially after heavy ground swells.

Conolly and Drew (1985) estimated the degree of exposure of the shore at St. Andrews to be 12 on the Grenager and Baardseth (1966) exposure index, indicating that the shore may be classed as "exposed". Onshore seas and south-easterly or northerly winds are of a frequent occurrence, especially during autumn and winter (personal observations).

FIGURE 2.2. (a) Looking south-eastwards, the situation of the field - sites on the East rocks at St. Andrews. The 2 sites are located in the fore-ground.
(b) The upper intertidal site.
(c) The lower intertidal site.
(d) The positions of the 2 sites relative to each other, looking westwards. In the bottom left of the photograph is the lower site, and in the top right the upper site.


a
c
d

The mean monthly sea temperature for St.Andrews (taken from the Bell Rock Lighthouse) between 1948 and 1966 varied between 4.7°C in March and 12.2°C in August (Laverack and Blackler, 1974). The inshore salinity is 34.45 - 34.50‰ - in St.Andrews Bay the salinity may be influenced by freshwater input from the River Tay at Dundee, the Eden estuary and the Kinnessburn (Laverack and Blackler, 1974). Laverack and Blackler (1974) cited evidence that St.Andrews Bay is within the influence of the North Atlantic Drift, although the degree of Atlantic incursion into the North Sea fluctuates from year to year, in volume, time and direction of flow. There is a correspondingly marked effect on sea temperature and salinity.

Two field sites were studied. The first was a 'lower' intertidal site within the *Laminaria digitata* (Huds.) Lamour. zone and in a gully running parallel to the cliffs. The second was an 'upper' intertidal site, approximately 7m horizontally and 2m vertically above the lower site (see Figure 2.2.). The sites differed markedly in their periods of exposure at low tide, and it is difficult to predict total emersion periods for each site. In general, however, the lower site was exposed only on spring tides, exceptionally for 1 or 2 hours, and was inaccessible for several weeks during the winter months. Conversely, the upper site was rarely not emersed on low spring tides, and often encountered continuous aerial exposure for several hours (personal observations). The accessibility of the sites was highly

dependent on the prevailing tidal and weather conditions. The height of the tide, and distance to which it receded, was markedly affected by wind and barometric pressure (personal observations). At St.Andrews there is also a marked seasonal variation in the actual low water level of spring tides. Thus, for tides of the same predicted low water heights, the ebb is often to a lower level in summer than in winter (Laverack and Blackler, 1974; personal observations). Thompson (1914), who studied such annual and long-term fluctuations in the tidal cycles at Dundee and Aberdeen, found that the annual fluctuation was of greatest amplitude for mean low water level and occurred independently of variation in the wind and barometric pressure.

The remainder of the field-work was carried out at 2 sites on Seil Island, Argyll ($56^{o}17'N$, $5^{o}37'W$), on the west coast of Scotland (see Figure 2.1.). The sublittoral site was at Clachan Seil (hereafter referred to as Clachan), a tidal narrows between Seil Island and the mainland. The intertidal site was located at Cuan Ferry (hereafter referred to as Cuan). Further site details are given in full in Todd and Turner (1986).

FIGURE 2.3. (a,b) The steel frames on the shore at the field-sites, in which the experimental substrata were positioned. (Scale bar = 30cm)
(c,d) The panels were accommodated over studs fastened at regular intervals into the base of the frame. (Scale bar = 30cm)
(e) A frame being air-lifted into position on the shore.


a


b


c


d


e

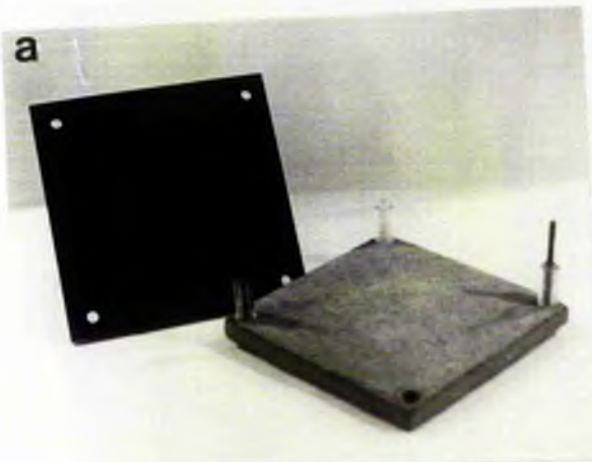
2.2. EXPERIMENTAL DESIGN

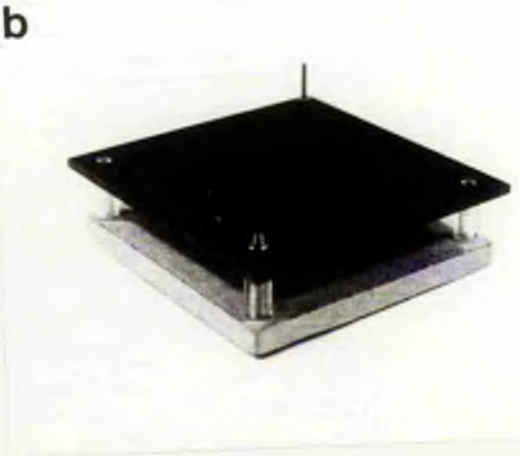
2.2.1. General Experimental Design and the Recruitment Experiment:- At the east coast sites, experimental substrata were retained in frames (overall dimensions: 92 x 65.5 x 10 cm) (see Figure 2.3.) of welded angle steel (10 x 6.5 x 0.8 cm), with steel cross struts (6.5 x 0.8 cm) welded to the base. Each frame was bolted to 2 concrete blocks (91.5 x 25.5 x 15 cm), giving the whole structure a weight of 250kg. It was not feasible to bolt the frames directly to the rock substratum itself, thus the necessity for the concrete blocks to hold the frames in position during winter storms. Removable lids (95 x 67 x 2.5 cm) of angle steel (2.5 x 2.5 x 0.3 cm), covered with a double layer of Netlon plastic mesh (mesh diameter 0.8 cm) provided protection from wave action and dislodged stones, and allowed access for collecting the experimental substrata.

Lengths (7.5cm) of stainless steel 2BA rod were bolted at regular intervals into the base of the frame. Experimental substrata could then be slotted over these pins and held, by nuts, in a position horizontal to the bottom.

The frames and lids were painted with 4-5 coats of red oxide anti-rust paint, and were placed on the shore 10-14 days before the initiation of experiments, to allow some leaching of any toxic metal ions to occur. By the end of the study, the frames and lids were beginning to support an abundant fouling assemblage.

FIGURE 2.4. (a,b,c) The arrangement of the experimental substrata.
(d) The panels in place in one of the frames on the shore.


a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Water flow through the frames was facilitated by a longitudinal groove between the frame and concrete blocks, by the mesh lid, and by a row of 1.6cm diameter holes drilled through the sides of the main frame. Furthermore, the experimental surfaces were maintained clear of the frame bottom by 1cm thick perspex blocks.

The design of the frames was based on those established on the west coast of Scotland (see Todd and Turner, 1986). The necessary modifications outlined above arose from differences in the degree of wave action between the respective localities. Those on the west coast were subject to minimal physical disturbance compared to frames on the east coast.

The experimental substrata comprised roughened black perspex panels (16 x 16 x 0.3 cm), each bolted horizontally to a slate panel of similar dimensions. Vertical separation between the panel pairs was maintained by 2.5cm long perspex cylinders or 'spacers', accommodated in holes drilled in each corner of the 2 panels (see Figure 2.4.). The panels were bolted together across one diagonal, with the 2 remaining diagonal holes accommodating the frame pins. In this way the panel pairs were maintained in a horizontal orientation with the perspex panel uppermost. The panel pair thus modelled the habitat found between the undersurface of a boulder (the bottom surface of a perspex panel), and the underlying rock substratum (the top surface of a slate panel). In

all the experiments the only surface which was examined was the underside of the upper perspex panel. The bottom slate panel had a primary role of protecting the experimental surface during transportation to and from the laboratory for sampling.

Several studies have suggested that the orientation of a surface may have important consequences on the development and nature of epifaunal assemblages (e.g. Pomerat and Reiner, 1942; McDougall, 1943; Maturo, 1959; Crisp and Ghobashy, 1971; Schmidt, 1982). Generally, the evidence suggests that horizontal surfaces support a richer epifaunal assemblage on lower surfaces than upper ones. Various factors have been proposed to control such patterns. For example, Sentz-Braconnot (1966) suggested that levels of illumination were important, while Harris and Irons (1982) concluded that sedimentation and predation interacted to exclude most species from upper horizontal surfaces.

Because of a desire to maintain a degree of comparability between the experiments all the artificial substrata were of perspex. The choice of perspex as the material was based on several considerations. Of primary importance was that it was ideally suited to the experimental requirements specific to this study, in particular the manipulative design required for the competitive overgrowth experiment (see below). The use of this material proved advantageous in the recruitment and grazing experiments because its surface was easily

marked out in a 0.5 x 0.5 cm grid to facilitate precise location of established organisms. This was an especially important consideration in the repetitive, non-destructive censusing programme of the recruitment experiment. A further advantage of perspex was that it could be cut to dimension. It was also relatively light in weight, and this facilitated transportation of panels between field sites and the laboratory. Finally, it was easily cleaned for re-use.

A wide range of artificial substrata have been utilized in fouling assemblage studies. Sutherland (1978), for example, utilized unglazed ceramic tiles; Dean and Hurd (1980) used asbestos-cement panels; and Greene and Schoener (1982) textured, white formica panels. The nature of the substratum does, however, have a potentially important effect on the characteristics of the assemblage that develops. Pomerat and Weiss (1946) submerged samples of 40 different materials and found marked differences in the populations that became established. Aleem (1958), in examining the development of fouling communities on various artificial substrata, found that although the phases in the successions were independent of the substrata nature, the latter may affect the timing of settlement, cause a retardation of growth, and affect the quantity of organisms in the community. Conversely, Scheer (1945), for example, found that changes in the community observed on glass panels were similar to those on wooden floats and metal panels.

In all studies utilizing artificial substrata a large degree of artefact is inevitably incurred, due, in the main, to a failure to adequately model the natural surface. Yamaguchi (1971) found that although the organisms recorded on artificial polyethylene "seaweeds" were similar to those on natural seaweeds, the former were covered with fouling organisms, while the fronds of real seaweeds were only partially covered. He attributed this to the excretion of mucous substances by the algae and their greater flexibility. Similarly, Harriott and Fisk (1987) found that ceramic wall tiles supported larger total numbers of coral spat than various natural coral surfaces; furthermore, colonies established on tiles were larger than those on dead coral surfaces. Conversely, some studies have indicated that there may be little difference between artificial and natural substrata. Tsuda and Kami (1973) found that tyres used in the construction of artificial reefs, were comparable to calcareous substrata (dead coral heads) for algal growth, and both supported a similar algal flora. Schoener (1982), from a review of the literature, concluded that there is a broad similarity between the processes of colonization and assemblage development on both artificial and natural substrata.

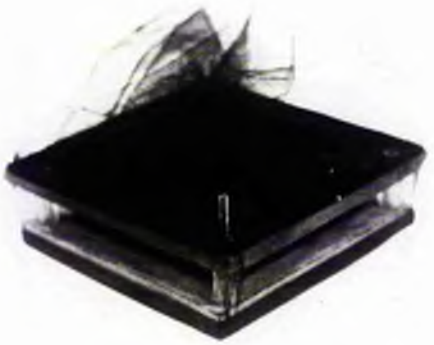
There are several advantages of artificial substrata over more natural surfaces, which have led to the frequent utilization of the former in the study of epifaunal assemblages. Often the choice is made

primarily for utilitarian reasons; for example, Fullner (1971) considered that artificial plates of hardwood were advantageous because they were light and small in size, and therefore easier to mail, hence decreasing the time spent visiting sites within a large geographical area. Generally, however, the reasons are because of the basic requirements of careful experimental design and sufficient replication (Schoener, 1982). It is more convenient to produce a series of more-or-less uniform surfaces using artificial substrata of precise and controllable dimensions and type, rather than searching for natural substrata of the required quantitative and qualitative properties (Schoener, 1982; Harriott and Fisk, 1987). It is also easier to maintain uniformly dimensioned surfaces in a retaining apparatus at a field site.

Artificial substrata are generally considered to be similar to, but simpler than natural substrata (Osman, 1982). They are presumed to present uniform, homogeneous surfaces devoid of the microhabitat variations that are associated with natural surfaces and which may lead to variability in experimental results. Conversely, it is possible to produce replicable physical structures; for example, Harger and Tustin (1973) altered homogeneous artificial substrata, creating a complex of structural matrices, by cementing hair curlers to formica panels. Russ (1980) and Dean (1981) have similarly altered the structural complexity of artificial substrata. Artificial substrata thus have major advantages over

FIGURE 2.5. (a,b) Panels were enclosed in nylon mesh in the grazer exclusion/inclusion study, which was supplemented with a more durable, thicker plastic mesh (b) in the longer-term experiment.
(c,d) The design of the panels used in the study of bryozoan competitive interactions.

a



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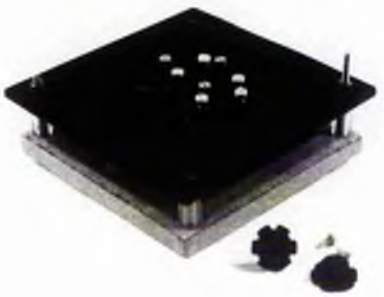


d

natural substrata in providing the potential for experimental control of biological and physical environmental variability.

However, concomitant with the wide use of artificial substrata has been a lack of standardization between studies. Not only is there considerable variation in the nature of the experimental material, but also in the sizes or surface areas of substrata (see, for example, Osman (1977, 1982), Jackson (1977b) and Keough (1984a) for the importance of substratum size in the development of communities). There are also differences in the orientation and arrangement of experimental surfaces, the water depth and geographical location of sites, and the duration of studies. Comparisons are further complicated by differences in the sampling procedures.

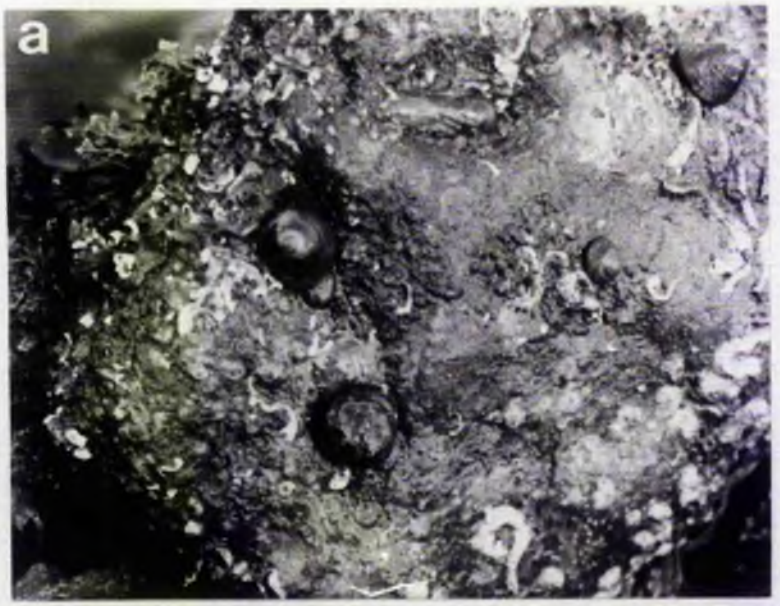
2.2.2. <u>The Grazing Experiment</u>:- To examine the influence of vagile grazing invertebrates on the initial stages of assemblage development, panel pairs were enclosed within a nylon mesh (mesh diameter = 0.15cm) (see Figure 2.5.a.); in the subsequent, longer-term experiments this was supplemented by an outer, more durable, thicker gauge mesh (mesh diameter = 0.40cm) (see Figure 2.5.b.). This was deemed necessary as some of the original 'nets' were damaged by crabs entering the frames, with consequent losses of the experimentally enclosed invertebrates. 'Nets' were retained around the edges of the panels with

FIGURE 2.6. The 3 species studied in the grazing experiment:

(a) *Gibbula cineraria* (approx. life-size).

(b) *Nucella lapillus* (approx. life-size).

(c) *Asterias rubens* (approx. 0.4 x life-size).


a


b


c

bands cut from tyre inner tubes. Fixed, but not unrealistic densities (i.e. similar to those on the underside of surrounding rocks, personal observations) of 3 invertebrate species (*Gibbula cineraria* (L.), *Nucella lapillus* (L.) and *Asterias rubens* L., see Figure 2.6.), which are locally common, were included within the 'nets'. Invertebrates of approximately the same size range were used throughout the experiments.

The most frequent method for investigating the effects of invertebrate and vertebrate predators or grazers on epifaunal assemblages is to totally exclude them by means of cages (e.g. Sutherland, 1974; Russ, 1980; Otsuka and Dauer, 1982; Breitburg, 1985). However, Keough and Butler (1979) and Keough (1984b) suggested that, since it may not always be possible to design appropriate controls for the effects of caging, a more suitable procedure may be to include predator density modifications. By fencing-in variable densities of the species concerned it may be possible to learn more about their effects on the community, although their effect will probably be over-estimated (Keough and Butler, 1979). This was the approach adopted in this study. The procedure assumes that artefacts due to caging are present and attempts to show that any differences in the abundance of sessile species between caged and uncaged substrata result from mortality in uncaged areas rather than selective recruitment of larvae into caged areas (Keough, 1984b).

In the first part of this study 15 panels were allocated to 5 treatments, each with 3 replicates:-

(i) uncaged controls - i.e. no manipulation;

(ii) caged controls - i.e. containing no vagile species which are large enough to be held by the mesh;

(iii) 1 *G.cineraria*. panel^{-1} (iii) 1 *A.rubens*. panel^{-1}

(iv) 3 *G.cineraria*. panel^{-1} or (iv) 1 *N.lapillus*. panel^{-1}

(v) 5 *G.cineraria*. panel^{-1} (v) 3 *N.lapillus*. panel^{-1}

In a subsequent experiment to determine the effects of initial protection from grazing invertebrates followed by exposure to their activities, 30 panels were allocated to 10 treatments, each with 3 replicates:-

(i) uncaged controls;

(ii) caged controls;

(iii) 1 *G.cineraria*. panel^{-1}

(iv) 3 *G.cineraria*. panel^{-1} maintained throughout the 4 months duration of the experiment

(v) 5 *G.cineraria*. panel^{-1}

(vi) 1 *N. lapillus*. panel^{-1}

(vii) 1 *G.cineraria*. panel^{-1}

(iix) 3 *G.cineraria*. panel^{-1} introduced after 2 months initial exclusion and maintained for the remaining 2 months of the experiment

(ix) 5 *G.cineraria*. panel^{-1}

(x) 1 *N.lapillus*. panel^{-1}

There has been considerable controversy over the validity of results obtained from caging experiments because of the possible artefacts introduced by the experimental methods involved. Cages may modify the light intensity, sediment deposition and water flow (Keough, 1984b) with corresponding qualitative and

quantitative effects on the assemblages that develop. Keough and Downes (1982) have stressed that differences in the abundance of taxa between controls and exclusions in caging experiments may be the result of 2 factors - the presence/absence of the predator or grazer and larval responses to the different physical regimes - and these alternatives are rarely separated. Relatively few studies have examined the effects of the cages themselves, rather than the predation or grazing, and the results are somewhat controversial. Otsuka and Dauer (1982) found that cages alone had an effect on community structure and development, selectively excluding certain species (e.g. hydroids) and acting as a structural support for others (e.g. *Molgula manhattensis* and *Botryllus schlosseri*). Schmidt and Warner (1984) carried out experiments to distinguish the various effects of predation and of caging *per se*, and found evidence that the most important effects of caging were not due to the exclusion of predators, but due to changes in the physical environment (specifically light intensity and water current velocity) which influenced larval settlement. Conversely, Breitburg (1985) found that cages and cage-roofs did not significantly alter water flow; and although light intensity was reduced by 8% compared to levels on uncaged plates, the differences between the communities developing on cage-roof and uncaged plates were few and inconsistent with the expected effects of shading. Scott and Russ (1987) tested for the effects of cages, other than that of

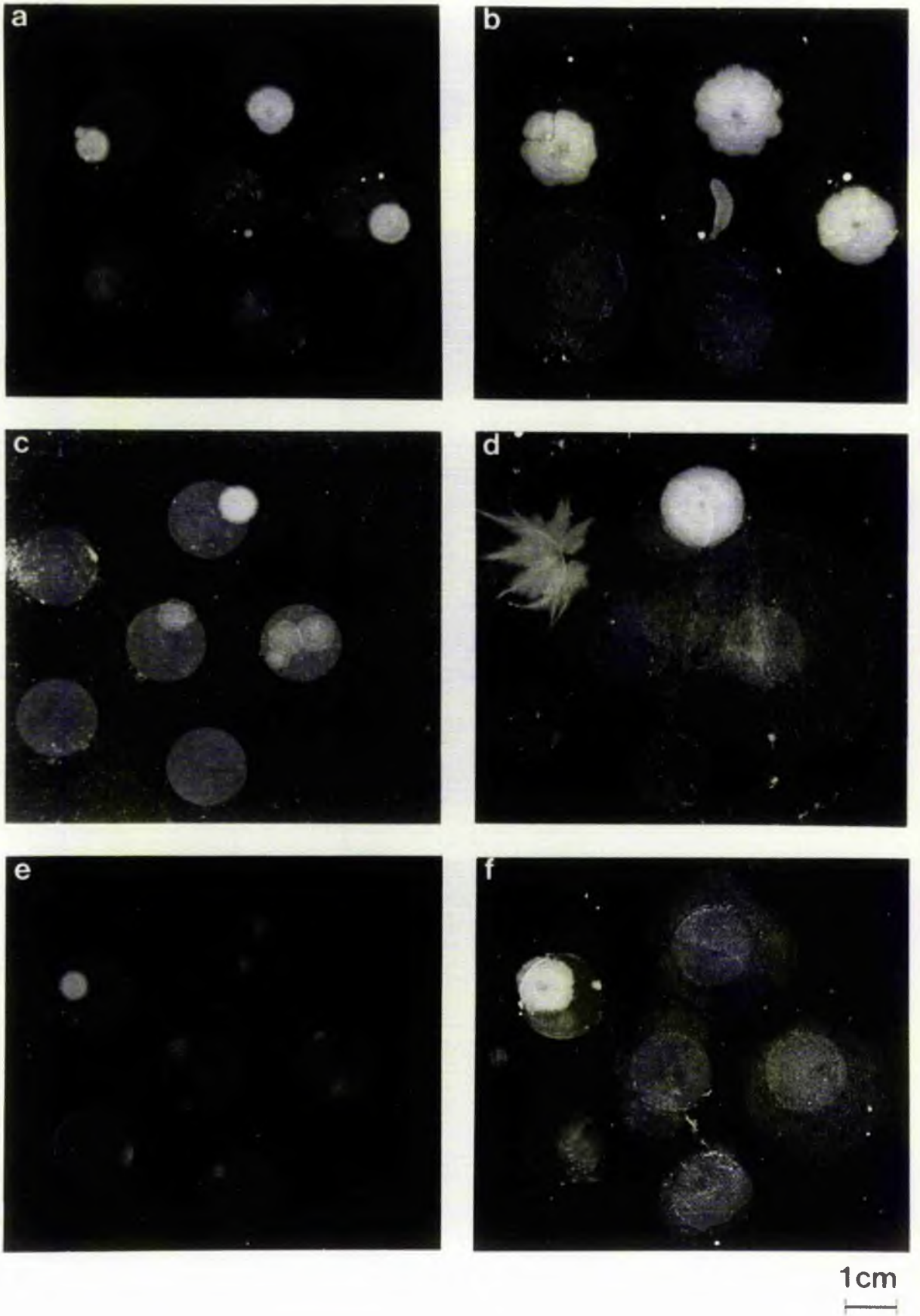
excluding large grazers, and found no significant differences in the species composition of encrusting algal communities other than those attributable to the effects of grazer exclusion. Thayer (1985) recognizing that caging provides information that is not readily attainable by other means, suggested that it remains an appropriate technique where proper controls are established, and the results are interpreted with caution.

In this study, no potential effects of the nets were tested for; however, the frames containing the netted panels were observed to accumulate considerable quantities of sediment. Sediment also accumulated on the bottom panels of pairs enclosed in the nets. This presumably was the result of the impediment of water flow. There was, however, no evidence of qualitative differences in the species recruiting to netted and unnetted panels. Thus, sponges, serpulids, barnacles, anomiids, hydroids, bryozoans, and colonial and solitary ascidians were observed on both netted and unnetted panel treatments.

2.2.3. The Competition Experiment:- Competitive interactions between encrusting bryozoan species growing on perspex panels (16 x 16 x 0.6 cm) were examined. The experimental panels were so designed that plastic 'plugs' (diameter = 1.55cm) supporting small bryozoan colonies could be fitted into holes drilled through the panels (see Figures 2.5.c. and 2.5.d.). This enabled particular species to be introduced into the developing assemblage. Initially, panels with 16 'plugs' were immersed to allow recruitment to occur, specifically of bryozoan ancestrulae. 'Plugs' bearing small established colonies were then introduced into the experimental panels. Each of these panels had 1 centrally placed 'plug' surrounded by 5 others equidistantly spaced (space between 'plugs' = 1.5cm). By rotating the 'plug', the orientation of the established colonies could be altered as required. The 'plugs' were then held in position with small plastic screws set into the top surface of the panel. This design allowed small colonies of particular species to be introduced into close proximity of one another, at predetermined angles of potential contact. The panels were then left undisturbed in the field (except for monthly censusing) and the colonies allowed to grow, and ultimately meet and interact.

With hindsight, supplemented with further knowledge of bryozoan growth rates and the sizes attained at the end of one year of growth, the design might be improved by using smaller, more closely spaced 'plugs' and increasing the number of sets of interactions that may

FIGURE 2.7. In the study of bryozoan competition, plugs bearing small colonies were introduced into the panels, the bryozoans were then allowed to grow and interact. The 3 panels illustrated were initiated at Cuan Ferry in February/March 1984, and photographed in May 1984 (a,c,e) and subsequently in June 1984 (b,d,f).

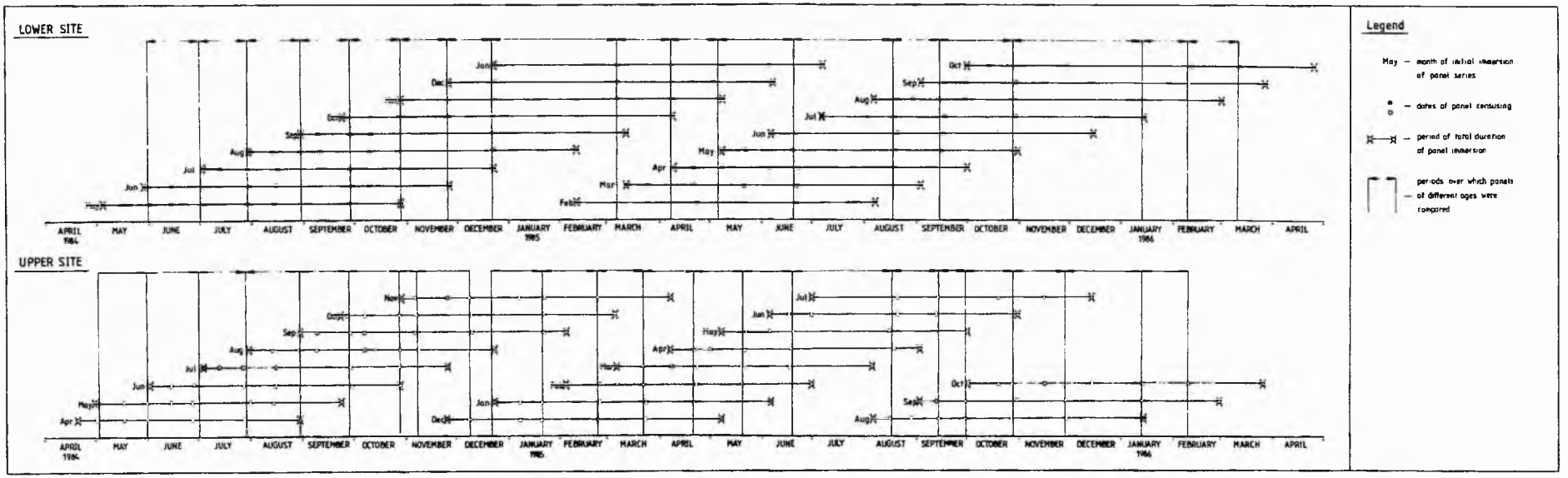

a
b
c
d
e
f
1cm

become established, for example by having 4-5 sets of 6 'plugs' per panel instead of the one set. The present design proved most appropriate for rapidly growing species that may cover a large area of substratum, for example *Alcyonidium* spp. (see Figure 2.7.), but was less adequate for slower growing, smaller species. Of necessity, the data in this study were supplemented with examination of all the bryozoan interactions that occurred on the panels.

Further, caution should be taken to ensure that all the panels are made from the same sheet of perspex. Very small differences in the thickness between sheets led to small irregularities when plugs made precisely to fit one panel were moved to a position in another panel. Such irregularities in an otherwise homogeneous panel surface may have influenced bryozoan growth rates - although the few irregularities that did occur in this study were of no greater vertical difference than would be experienced by bryozoans overgrowing, say, a small spirorbid settled on the substratum.

NOTE: Prior to immersion at the field sites all the panels were preconditioned in running seawater in the laboratory for 7-10 days and then thoroughly brushed. (See Chapter 3 and references in *Marine Biodeterioration: An Interdisciplinary Study*, edited by J.D. Costlow and R.C. Tipper (1984), Naval Institute Press, Annapolis).

FIGURE 2.8. A summary of the schedule employed in the study of recruitment onto panels of varying 'ages'. The dates of panel initiation, examination and termination during the 5 or 6 months total immersion period, at both sites on the east coast, are indicated; as well as the periods over which panels of differing 'ages' were compared in the statistical analysis.


LOWER SITE
UPPER SITE
APRIL 1984
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
JANUARY 1985
FEBRUARY
MARCH
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER
DECEMBER
JANUARY 1986
FEBRUARY
MARCH
APRIL
Legend
May — month of initial immersion of panel series
— dates of panel censusing
— period of total duration of panel immersion
— periods over which panels of different ages were compared

2.3. SAMPLING PROTOCOL

2.3.1. The Recruitment Experiment:- Triplicates of panels were immersed at the 2 sites (lower and upper intertidal) at St.Andrews, approximately every 4 weeks from April 1984 through to October 1985. Exposure was for periods of 5 months at the upper site and 6 months at the lower, because of a shortage of space in the frames at the upper site. Panels were censused non-destructively and then repositioned in the field for further colonization. Panels were always returned to the same frame and in the same position and orientation. During the early stages of panel colonization, monitorings were more frequent (approximately every 7-14 days) than at later stages, when the observation period was increased to every 4-6 weeks (see Figure 2.8.). In this way the early development of the epifaunal assemblages on each panel could be followed in some detail. Panels were monitored whenever possible at approximately the same times; the actual timing of sampling periods was dependent on commitments with field-work on the west coast, and tidal and weather conditions. Losses of sampling opportunities were most frequent during the winter months when the weather restricted the number of times that the lower site, in particular, could be visited.

At each sampling date the triplicates of panels were removed from the frames and quickly transported to the laboratory in buckets covered with polyurethane foam to

prevent desiccation, and were placed in running seawater within 15-30 minutes. In the laboratory all the panels remained submerged in large aquaria provided with running seawater which is pumped daily from St.Andrews Bay into the laboratory. All the panels were returned to the frames on the low tide 24 hours later.

In the laboratory panels were placed for examination in a dissection dish with fresh seawater, if the examination time was prolonged the seawater was frequently changed. Prior to examination, panels were rinsed in running seawater to remove any loose sediment. Panels were systematically examined under a Wild M8 stereomicroscope. The location and identification of each new individual or colony was mapped onto sheets with a set of grid squares corresponding to those marked on the panel surface. By these means new recruitment, growth of previously settled individuals and mortality of individuals could be readily monitored.

Only sessile species capable of occupying space on the substratum were censused, transient animals were not included. Otherwise, all the organisms were identified to the species level, unless proper identification could not be made without disturbing the animal, in which case it was identified only to genus. Individuals or colonies which grew onto the panel surface either from the panel sides or 'spacers' separating the panel pairs (or more rarely from short pieces of algae which became trapped against the panel surface (mainly hydroids, but occasion-

ally bryozoans)), were not included. This study also excluded contributions made by all the microorganisms (for example filamentous diatoms, blue-green algae, stalked ciliates) which occupied the apparently 'bare' space.

There has been considerable controversy as to the artefactual handling effects of relatively frequent sampling on the assemblages developing on panels, and this is related to the more general question of the relative merits of destructive and non-destructive sampling techniques (Schoener and Greene, 1981). Sutherland and Karlson (1977) suggested that all the organisms on their panels appeared healthy and unharmed by the handling procedure. Breitburg (1985) concluded that although the handling of caged panels had some effect on the community composition, the effect was minor compared to differences between experimental treatments. Todd and Turner (1988, and in prep.) found no significant handling effects on assemblage development. Conversely, Harger and Tustin (1973) recorded extreme fluctuations in numbers and a reduction in diversity of resident organisms in a community subjected to regular laboratory examinations, to the extent that subclimax stages developing on undisturbed long-term panels were not apparent. Schoener and Greene (1981) found, from a comparison of handled panels with unhandled panels, that during the early stages of panel development there was no evidence for differences in terms of the mean percentage cover and the

total number of sessile species. Results from older panels indicated that handling effects could influence panel development; handled panels had a higher percentage cover and the species numbers were significantly greater, although relatively few species were treatment specific. They therefore inferred that treatment effects may occur on handled panels at certain times during the sequence of panel colonization, although their observations were inconsistent with the outcome that might intuitively be predicted. They concluded that the nature of the handling effects was elusive and presumably dependent on complex species interactions.

2.3.2. The Grazing Experiment:- All the grazing experiments were carried out at the lower site at St.Andrews. In the first part of this experiment treatments were immersed for 2 month intervals (except during the winter when bad weather prevented access to the frames) from July 1984 through to September 1985. The *G.cineraria* experiments (hereafter referred to as *G.cineraria* panels) were initiated in July and September 1984, and February, April and June 1985 (in subsequent sections these are denoted by 'J-S84', 'S-F85', 'F-A85', 'A-J85' and 'J-A85'respectively). The *N.lapillus* and *A.rubens* experiments (hereafter referred to as *N.lapillus* and *A.rubens* panels, respectively) were initiated in August and October 1984, and March, May and July 1985 (in subsequent sections these are denoted by 'A-O84', 'O-M85', 'M-M85', 'M-J85' and 'J-S85' respectively). The

second part of the experiment, to determine the effects of initial protection from grazing on assemblage development, was repeated twice for a period of 4 months, from October 1985 to February 1986 (hereafter referred to as 'O-F86') and from February to June 1986 (hereafter referred to as 'F-J86'). After the designated period of immersion, panels were removed from the frames and returned to the laboratory, where the nets were removed and the numbers of grazers present and alive were recorded. The panels were then held in aquaria supplied with running sea-water. This method was destructive in that panels were not returned to the field after examination.

As with the recruitment experiment, panels were searched microscopically, and the location and identification, size and survivorship of all the recruits was recorded. The taxonomic grouping 'sponges' was not included in any analyses of the data sets. This decision was based on substantial evidence that small spiculate sponges were recruiting onto the panels held within the laboratory, over a period of several days; there was no evidence that recruitment occurred over a period of 24 hours, which was the maximum length of time the recruitment experiment panels were within the laboratory. The recruitment of sponges was most evident on the final series of grazing experiment panels brought into the laboratory in June 1986: on the first panel examined, a net control panel, 5 sponges were recorded compared to 5315 on a *G.cineraria* panel examined a few days later.

The pipes within the laboratory supplying seawater to the aquaria are known to support a rich assemblage of sponges, presumably the origins of the observed heavy settlement. There was, however, no evidence that any other species recruited to panels held within the laboratory.

2.3.3. Settlement and Recruitment:- In the recruitment and grazing experiments it is necessary to distinguish between the processes of settlement and recruitment. Connell (1985, p.12) defined settlement "...as the point when an individual first takes up permanent residence on the substratum" - for sessile invertebrates this phase includes metamorphosis. Recruitment combines settlement with any early mortality that has occurred on the substratum up to the time of the first census, i.e. it is the number of recently settled juveniles that survive for a period of time after settlement (Connell, 1985). Thus recruitment is a composite of larval and juvenile stages, while settlement involves only larval stages (Keough and Downes, 1982).

Keough and Downes (1982) and Connell (1985) stressed the importance of distinguishing between settlement and the processes that occur thereafter on the substratum. The implicit assumption of many studies is that settlement can be measured with sufficient accuracy by recruitment; if this is not the case, then a number of misleading conclusions may arise (Keough and Downes,

1982). The majority of studies measure recruitment; few have measured settlement and to do this requires censusing at very frequent intervals to avoid missing larvae that attach and then become rapidly lost. Ideally, each larva should be mapped as it attaches. Gaines and Roughgarden (1985), for example, monitored quadrats on consecutive low tides to detect any mortality that might affect barnacles within hours of settlement. Shanks (1986) made daily counts of barnacles during daytime low tides. However, the majority of studies census recruitment every 4-6 weeks (e.g. Harger and Tustin, 1973; Dean and Hurd, 1980; Harris and Irons, 1982; this study). The question then arises as to how much the observed pattern of recruitment reflects active larval choice, and how much it reflects mortality subsequent to settlement. Keough and Downes (1982) found that the period immediately following settlement and metamorphosis of sessile marine invertebrates may involve heavy mortality. Clearly, therefore, the relationship between settlement and recruitment may not be strong, nor is it necessarily constant between species. Caffey (1985) stressed the need to determine how, and under what circumstances, settlement and the early survival of juveniles varies, and what consequences this variation has for the populations and communities. He has shown that the proportional survival of settlers varied greatly on all the spatial and temporal scales he monitored, but with few distinct patterns or trends, indicating that settlement and recruitment may not be well related.

Connell (1985), however, concluded that it may be possible to use densities of recruits as indicators of the density of settlers, if the mortality between the 2 stages acts in a density independent way. He stressed that the current understanding of pre-settlement versus post-settlement processes in marine benthic communities is small. Osman (1982) suggested that if the omission of immigrations and extinctions of individuals on a substratum occurs suddenly in space and time, then the crudely measured rates can still be compared on a relative scale. It must be concluded, however, that until more is understood of the relationship between settlement and recruitment, studies such as the present one - concerned primarily with recruitment - must be interpreted with considerable caution if the conclusions drawn are to be related to overall assemblage processes.

2.3.4. **Bryozoan Competition**:- Two series of panels were immersed in the autumn/winter of 1983 and 1984, for approximately 1 year, until the following September or October, at sites on the west coast of Scotland. Ten panels were immersed at Clachan in 1983 and 8 in 1984, and at Cuan 8 panels were immersed in both 1983 and 1984. A further series of panels was immersed in the summer of 1984, for approximately 2 years, at both sites at St.Andrews (4 panels were immersed at the upper site and 6 at the lower site). The aim was to examine the competitive interactions among the bryozoans becoming established in the assemblages. The panels immersed at

the west coast sites were non-destructively sampled every 4-6 weeks. They were removed to the Scottish Marine Biological Laboratory at Dunstaffnage, Oban, where the panels were held overnight in aquaria with running seawater, prior to being returned on the next days low tide. Each panel was photographed using a Pentax 100mm macrolens (with Ilford PanF film, 50 ASA), and examined with a Wild M8 stereomicroscope to determine initial growth rates and the development of interactive contacts between individual colonies. The panels at the east coast sites were not censused regularly during the period of immersion, but were finally removed in April 1986 and were then photographed and examined.

All the data in the present analysis of bryozoan competition were derived from panels which were removed from their respective sites and returned to the laboratory at St.Andrews, where all the panels were examined microscopically for situations where pairs of bryozoan colonies interacted along common boundaries. The particular species were identified, and the outcome, nature and extent of the interaction were recorded (including the incidence of stolonal outgrowths, concentrations of pigments along the encounter zone etc., see, for example, Gordon (1972) and Osborne (1984)). Observations were made along the entire length of the colony margin. All the interaction zones were recorded diagrammatically using a camera lucida and supplemented with photographs taken with an Olympus OM2 (Ilford PanF film, 50 ASA) attached to a photomicrotube of a Wild M8 stereomicroscope.

In the competition for space between 2 encrusting bryozoan colonies, which occurs whenever the growing edges come into contact, either of 2 results may occur:-

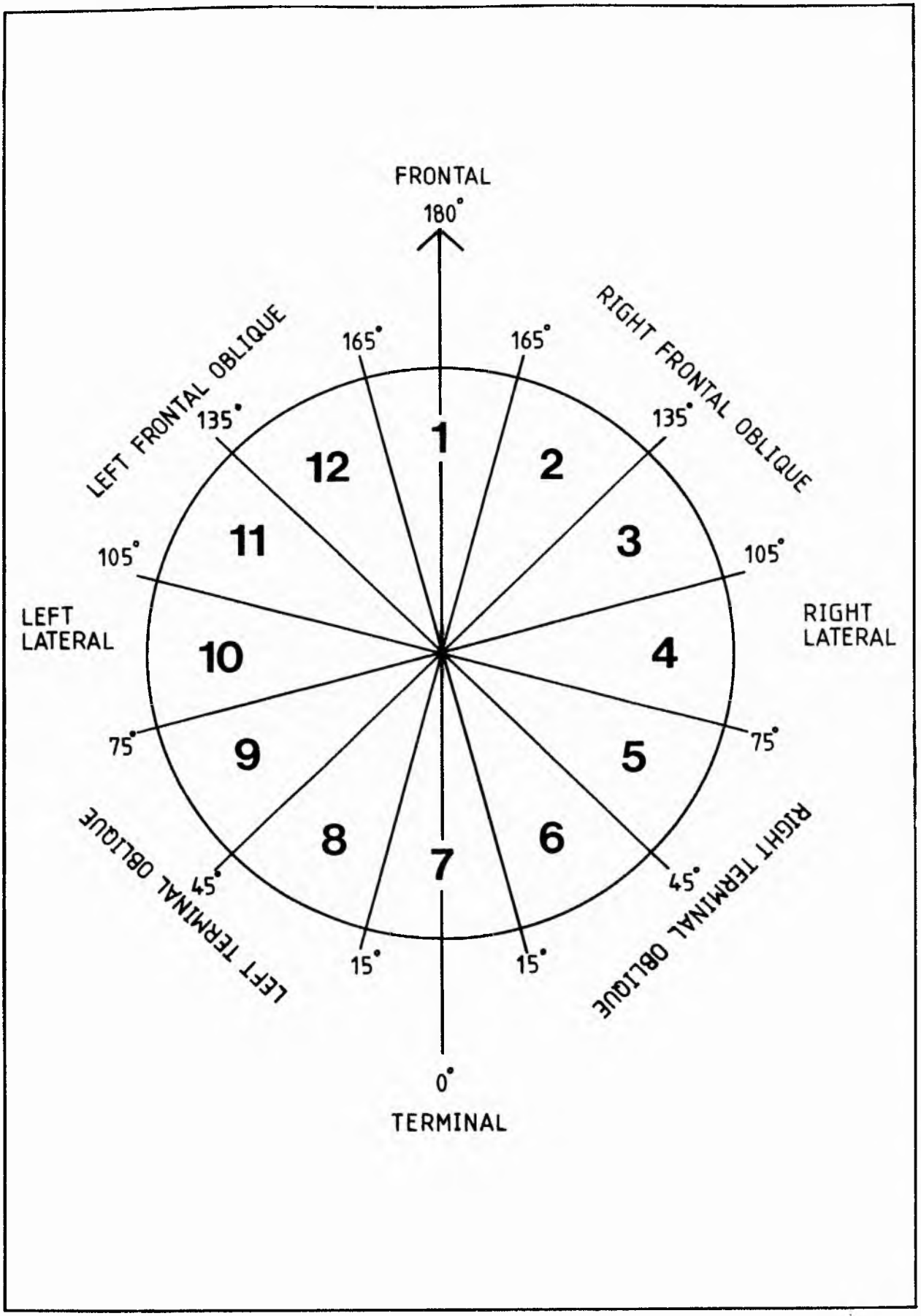
(i) OVERGROWTH: Whereby one colony expands by growth into the space occupied by the other. The practical definition of overgrowth encounters utilized in this study was based on that of Buss (1980) and Breitburg (1984) - i.e. "Overgrowth is defined as the elevation of the growing margin of one colony over that of another" (Buss 1980, p. 5355). This definition is less conservative than that utilized elsewhere. For example, Stebbing (1973a, p. 248) defined overgrowth "...as the elevation of the growing edge of one colony over the edge of another to the extent that it had covered the apertures of zooids". Quinn (1982) only recorded overgrowth when the loser was overtopped for at least 5mm. Russ (1982) recognized a "win" when 25% of the surface of the losing colony was overgrown. Although, in practice, because of the large variation in the extent of overgrowth exhibited by colonies, all these definitions were in fact recognized. Thus, overgrowth interactions ranged from instances where developing zooids were laid down on the adjacent colony, to those where zooids were completely overgrown at the contact zone with a corresponding loss of function, and in extreme instances a large proportion of, or even all, the colony was overgrown.

(ii) TIE: Where 2 colonies cease growth along the shared margin. This is the definition adopted, for example, by Jackson (1979a), Buss and Jackson (1979) and Buss (1980); Keough (1984b) recognized a "stand-off" or "static interface" when the interface between 2 colonies had not moved in 4 months. The present study included, within the tie category, any incidence where the outcome of an interaction changed along the encounter zone between 2 colonies, i.e. both colonies extended zooids over the other. This situation was observed to range from a nearly typical overgrowth interaction where along most of the contact zone the dominant species extended zooids over the other colony but a few zooids of the subordinate species were able to extend over its competitor, to an approximately equal degree of dominance, both species extensively overgrowing the other. Jackson (1979a) and Buss (1980) recorded such changes in outcome along the line of contact between 2 colonies as separate distinct encounters. In the present study definition of a tie was also extended to include instances where the 2 colonies exhibited redirection of growth, including situations where horizontal growth was replaced by vertical growth away from the substratum. Similar observations were referred to as "obstructing" or the "delaying of overgrowth" by Russ (1982). Extreme instances where 2 contact margins merged ("fusion" of Jackson (1979a)) were also occasionally noted.

It must be emphasized that such observations of bryozoan interactions provide only a static picture of

overgrowth relationships at a particular time and place (Jackson 1979a). Observations pertaining to competition may not, therefore, represent the ultimate outcome of all competitive encounters. This is likely to be of particular importance for tie situations which may prove to be reflections of the beginnings of the establishment of dominance by one species over another, or a reversal of an overgrowth interaction. Stebbing (1973a) assumed that once a colony had overgrown another to the extent of covering the others' zooids, then further overgrowth was possible, because once the growing edge of a colony is covered by another it can grow no further. Conversely, an overgrowing colony can usually continue to do so. However, Osborne (1984) has recorded the formation of secondary growth margins associated with frontal stolons, during bryozoan competitive interactions, illustrating that smothering of a growing edge does not always prevent subsequent growth. Osborne (1984) further emphasized the need for caution when interpreting data from instantaneous readings of interactions, suggesting that it is only after repeated observations that the dynamic nature of interactions is revealed. Similarly, Todd and Turner (1988) stressed the importance of repeated, as opposed to single instantaneous observations of overgrowth. Buss and Jackson (1979) and Jackson (1979a) suggested that due to the "point-in-time" nature of observations of competitive interactions it is not possible to produce generalizations regarding the

FIGURE 2.9. The sectors into which interactions between pairs of encrusting bryozoans were classified according to the encounter angle between the colonies.


FRONTAL
180°
RIGHT FRONTAL OBLIQUE
LEFT FRONTAL OBLIQUE
165°
165°
135°
135°
105°
105°
LEFT
LATERAL
RIGHT
LATERAL
75°
75°
RIGHT TERMINAL OBLIQUE
LEFT TERMINAL OBLIQUE
45°
45°
15°
15°
0°
TERMINAL
1
2
3
4
5
6
7
8
9
10
11
12

relative importance of competitive rankings of overgrowth ability which may vary considerably with the place and time of year.

The encounter angle represents the angle between the growth directions of the 2 interacting colonies. The bryozoan competitive interactions observed in this study were classified into one of twelve 30^{o} categories or sectors (see Figure 2.9.). Jackson (1979a) recognized only 4 such categories and Rubin (1982) 8, although he did not include the interactions which fell within his 4 "oblique sectors". Encounter angles were recorded by superimposing an acetate sheet marked out as in Figure 2.9. over the camera lucida drawings of the zooid orientations of both colonies, along the encounter margin. The central ($0-180^{o}$) axis was placed along the longitudinal axis of each zooid concerned, with the arrow pointing distally, and the orientation of the zooids contacted in the opposing colony could then be read off. Encounter angles were recorded along the entire common line of the encounter between the 2 colonies and the most frequently observed sector was taken as representative of the overall encounter angle for the particular interaction concerned. Often the encounter angles changed considerably along the encounter line between 2 colonies, thus one overgrowth interaction may have involved both frontal and lateral overgrowth along the same encounter line.

All the intra- and interspecific bryozoan interactions were analyzed in this manner, with the exception of cases where:

- there was evidence that the overgrown colony was dead before the overgrowth occurred;
- one colony was completely overgrown by another;
- much of the interaction zone had been lost; for example, as colonies of *Alcyonidium* spp. die, the colonies deteriorate and slough-off leaving small fragments attached to the substratum which may be subsequently overgrown;
- colonies interacted over very short distances, i.e. where only 5 or fewer encounter angles were recorded;
- one species recruited onto another rather than overgrowing it; for example, many ancestrulae were observed to recruit onto *Alcyonidium* spp..

2.4. STATISTICAL ANALYSIS

All the statistical analysis was carried out on the St.Andrews University VAX/VMS Version V4.5..

2.4.1. Analysis of the Recruitment and Grazing Experiments:- The following section discusses the statistical methods of data analysis for the recruitment and grazing experiments. Figure 2.8. shows the periods over which panels of different 'ages' were statistically compared in the recruitment experiment, the periods being chosen so as to maximize the information obtained while keeping to a minimum the degree of interpolation required. On occasions where not all the panels were sampled at the beginning and end of a period used in the analysis, recruitment was adjusted by linear interpolation. The majority of the analytical periods examined recruitment over 2 tidal cycles (i.e. approximately 1 month). However, if very few sets of panels were censused at a particular time then recruitment over longer periods was analysed (e.g. during the winter months). Very occasionally recruitment had to be analysed over shorter periods. Wherever possible recruitment was compared between sets of panels which had been immersed for 1, 2, 3, 4, 5 or 6 months, although where discrepancies arose between the dates of panel immersion and the periods of analysis, such an ideal 'age' distribution may not have been attainable. Furthermore, if the 'youngest' panels were not immersed for the whole of the analytical period, then the analysis was carried out including and excluding

the sets of panels which were not immersed for the full period. 'Older' panels which were terminated during an analytical period were not considered. For the grazing experiment no interpolation was necessary and all the data sets were analysed (but see below for instances of unequal replication).

All the sessile species recorded on the panels were used in the analyses, with the exception of the sponges in the grazing experiment (see above). Most species were grouped into 'taxa' for the analysis and description of trends in assemblage development. Each taxon consisted of a group of morphologically similar and taxonomically related species.

For a variety of logistic reasons - primarily because of a limited number of spaces available in the retaining frames - the number of replicates for the recruitment and grazing experiments were restricted to only 3 panels per 'treatment' (where the 'treatment' represents either the length of immersion, or 'age', of the panels, or the density of the grazing invertebrates). Consequently parametric methods of statistical analysis were the more appropriate (A.D. Gordon, personal communication). Underwood (1981) suggested that, because of the nature of most marine biological investigations, the analysis of variance is the most appropriate statistical technique available. However, suitable alternative non-parametric methods are briefly considered later.

The Minitab statistical package (Ryan *et al.*, 1982; Ryan *et al.*, 1985) was used to analyse the recruitment and grazing experiments. Programs inherent in the package were used, for example, AOVONEWAY for the analysis of variance, and supplemented with programs of my own.

Preliminary inspection of the data was through a single classification, fixed effects analysis of variance to compare the means of the several treatments. The null hypothesis that there was no added component due to treatment effects among the groups, i.e. the population means were all assumed to be equal, may be represented algebraically by:

$$Ho : \mu_1 = \mu_2 = \mu_3 = \ldots = \mu r$$

where r = number of populations under study,

μ_1 = mean of the 1st population,

μ_2 = mean of the 2nd population, etc.

The relevant formulae for the 3 sums of squares are, from Ryan *et al.* (1985):-

SOURCE	DEGREES OF FREEDOM	SUMS OF SQUARES	MEAN SQUARES
FACTOR	$r-1$	$\Sigma_i m_i(\bar{X}_i-\bar{X})^2$	$\Sigma_i m_i(\bar{X}_i-\bar{X})^2/r-1$
ERROR	$N-r$	$\Sigma_i\Sigma_j(X_{ij}-\bar{X}_i)^2$	$\Sigma_i\Sigma_j(X_{ij}-\bar{X}_i)^2/N-r$
TOTAL	$N-1$	$\Sigma_i\Sigma_j(X_{ij}-\bar{X})^2$	

where X_{ij} = j th observation in the sample from population i,

$\bar{X}_i$ = sample mean from population i,

m_i = sample size for population i - sample sizes need not be equal,

r = number of populations,

N = total number of observations

$\bar{X}$ = mean of all observations.

This gives rise to the variance ratio F :

$$F = \frac{\text{Factor Mean Square}}{\text{Error Mean Square}} = \frac{\text{Between Groups Mean Square}}{\text{Within Groups Mean Square}}$$

the distribution of which is known and can be used for a statistical test for departures from the null hypothesis. The hypothesis of equal means is rejected in favour of the hypothesis that means differ if:

$$F_{r-1, N-r} > F_{1-\alpha; r-1, N-r}$$

where α is the level of significance of the test (5% in this study), i.e. the probability level associated with a Type I error. Where a Type I error is the rejection of the null hypothesis when it is in fact true; and a Type II error is the retention of the null hypothesis when it is false (Underwood, 1981).

The validity of the analysis of variance techniques depends on the inherent assumptions that the treatment and environmental effects are additive; and that the experimental errors are independent in the probability sense, have equal variance and are normally distributed (Cochran, 1947). In practice, these assumptions may fail to hold simultaneously, however Cochran (1947), Box (1953) and Scheffé (1959), among others, have suggested that inferences from the analysis of variance are not

seriously invalidated by the violation of such assumptions, and concluded that the analysis of variance is robust to many types and magnitudes of non-normality and departures from homogeneity of the variances - especially with similar sample sizes. Cochran (1947) considered that the analysis of variance should be regarded as an approximative, rather than an exact, technique. Underwood (1981) suggested that one option is to proceed with the analysis of variance test, bearing in mind that a non-significant outcome of the *F*-ratio is still a reliable result, although significant results may be less reliable if there is evidence of violation of the assumptions. But more importantly, further information on the data may be gained from violation of these assumptions, for example from the heterogeneity of the variances (Underwood, 1981).

Since the analysis of variance is derived from the assumptions that include normality of the data and equality of the variances, it is often recommended that these assumptions first be tested. Cochran (1947), however, suggested that application of the standard tests for departure from normality would not be profitable, because for small sample sizes the tests would detect only very severe skewness or kurtosis. A number of tests are frequently used to detect homogeneity of the variances: for example, Bartlett's test (described in Snedecor and Cochran, 1967) which compares the log of the sample variance with the log of the mean variance of all

samples, and Cochran's test (in Guenther, 1965) which is the largest variance divided by the sum of the variances of all treatments. However, Bartlett's test is particularly sensitive to non-normality, and its application may lead to more erroneous conclusions than if its use is omitted (Box, 1953). In other words, the test may cause rejection of the assumption of homogeneity of the variances (even where the variances may in fact be equal) where the data are non-normal, in instances where the lack of normality may itself not have much effect on the reliability of the analysis of variance. Cochran's test is less sensitive but still subject to aspects of non-normality. Since Bartlett's test is also inadequate if most of the degrees of freedom are less than 5 (Snedecor and Cochran, 1967), Cochran's test was applied in this study. Nevertheless, instances where results for this test diverged from those for Bartlett's test have also been noted.

The analysis of variance is only the first step in evaluating the experimental results. It may lead to the conclusion that the means under consideration are not alike, but it fails to signify any arrangement of distinguishable groups among the means. It thus becomes necessary to examine all the means and determine which differences among them appear to be real; simultaneous multiple comparisons of the means' tests represent a set of procedures whereby a group of heterogeneous means may be separated into sub-groups of homogeneous means. Multiple comparisons procedures enable any number of

comparisons among a set of sample means to be made with the assurance that the probability of all the significance or confidence statements being correct will be equal to or greater than the specified α significance level. They involve more stringent criteria for declaring significance than the more powerful *t*-test, for the differences between 2 means must be larger to be identified as true differences.

As for the analysis of variance, many of the multiple comparisons tests assume at least approximately normal distributions and homogeneity of the variances (Seeger, 1966). One method, the Scheffé test, is known to be insensitive to violations of assumptions of normality and equality of variances (Scheffé, 1959), but Scheffé concluded that non-normality and inequality of the variances may have little effect on "inferences about means", which includes multiple comparisons tests.

The general procedure for multiple comparisons is:

MSD = (critical value) x *SE* (Sokal and Rohlf, 1981)

Where *MSD* = minimum significant difference;
critical value = reference to the statistical distribution appropriate to a given test;
SE = appropriate standard error of the mean in each treatment, and this varies from test to test.

A pair of means are declared significantly different only if the difference between sample means exceeds the minimum significant difference. There are many multiple comparisons procedures available (see, for example, Duncan (1955), Federer (1955) and Seeger (1966)). Duncan's (1955) classification suggests 3 basic characteristics of a test procedure:-

(i) Tests with constant minimum significant differences (e.g. Scheffé's method, Tukey's T-method), distinct from those with variable minimum significant differences (e.g. Student-Newman-Keuls (hereafter referred to as 'S-N-K') on range test, Duncan's new multiple range test).

(ii) Tests based on multiple ranges (e.g. 'S-N-K' test) compared to multiple *F*-tests (e.g. Fisher's test, Scheffé's test).

(iii) Tests distinguished on the basis of the type of protection levels, either constant values of $1-\alpha$ for protection levels (e.g. 'S-N-K' test) or tests based on degrees of freedom (e.g. Duncan's new multiple range test). The protection level of a test measures protection against finding erroneous significant differences; for example, if the significance level is 5% the protection level is 95% (Duncan, 1955).

A complete consensus of opinion has not yet been achieved on which method is the best to employ, each method having its own relative merits and disadvantages, and differing in power or sensitivity and the protection

levels provided. Duncan (1955) and Wine (1964) have tabulated comparisons of minimum significant differences for the various tests (Table VI and Table 10.11., respectively), and Federer (1955) has commented on their associated Type I and Type II errors.

The method adopted in this study was Hartley's (1955) sequential method based on studentized ranges and originally developed by Newman (1939) and Keuls (1952) in the 'S-N-K' multiple range test. The sequential method gives the same type of protection and is more powerful than the original method. The decision to utilize this test was based on an examination of the relevant literature, from which it was relatively easy to eliminate less appropriate methods. For example, tests based on a constant minimum significant difference suffer severely from reduced power, and thus cannot be recommended, compared to variable minimum significant difference tests. Scheffé's procedure is more efficient for comparisons involving groups of several means, however, at this stage in the analysis pair-wise comparisons between all the pairs of means were considered to be of more interest. Although Duncan's new multiple range test is more powerful than many other methods, Scheffé (1959) has criticized the original justification of the test. The sequential 'S-N-K' method would thus appear to be a satisfactory compromise - and indeed it is a common procedure in current use (Underwood, 1981).

The sequential 'S-N-K' multiple range test (see Hartley, 1955; David, 1962; and Snedecor and Cochran, 1967, for example) allows one to make comparisons between all the pairs of ranked means (number of possible pair-wise comparisons = $r(r-1)/2$), proceeding in a sequential manner. Here, the largest difference is tested first, and tests on means that are more similar in ranking are only made if the previous tests are significant. The minimum significant difference between 2 means, n means apart, is calculated as a product of the standard error of the mean (i.e. within-treatments or error mean square from the analysis of variance) and the tabulated value of q (at a given significance level). The value of q is dependent on n and the degrees of freedom of q which is that of the standard error (i.e. $N-r$); thus the minimum significant difference for each test of a pair of means is adjusted to reflect the size of the range of the means being tested, i.e. n. The difference between 2 means is said to be significant, at the α-level if it exceeds the minimum significant difference:

$$\bar{X}_{max} - \bar{X}_{min} \geq q_{\alpha(n,(N-r))}\ s/\sqrt{m}$$

$\bar{X}_{max}$ = the largest mean in the group under consideration;

$\bar{X}_{min}$ = the smallest mean in the group;

m = number of observations per treatment;

s = $\sqrt{}$ within treatments or error mean square;

n = size of range between 2 means ($\bar{X}_{max}$ and $\bar{X}_{min}$);

$N-r$ = within treatments or error mean square degrees of freedom.

The process stops when non-significant differences are found between 2 means, and they and all the intervening means are considered to represent a homogeneous group. The 'S-N-K' procedure is more conservative than the *F*-ratio and therefore it is possible to reject the overall null hypothesis of the analysis of variance, but to have no evidence of differences among means in the range test (Underwood, 1981).

Kramer (1956) extended the multiple range tests to unequal numbers of replicates. In terms of the sequential 'S-N-K' test:

$$(\bar{x}_{max} - \bar{x}_{min}) \sqrt{\frac{2m_{max}\, m_{min}}{m_{max} + m_{min}}} > Sq\alpha(r, (N-r))$$

Where m_{max} = sample size of the largest mean in the group under consideration;

m_{min} = sample size of the smallest mean in the group under consideration,

and the rest of the notation is as above. This extension to unequal replicates is, however, conservative. This test was applied when unequal replication arose in the grazing experiment.

The sequential 'S-N-K' test was applied to both the recruitment and grazing experiments. Dunnett (1955, 1964) has provided a procedure for multiple comparisons between several treatments and a control. However, because all the pair-wise comparisons between treatments

(i.e. varying grazer density) were of interest, as well as comparisons with the control (i.e. grazer exclusion) in the grazing experiment, this method was not adopted.

In the instances where there were only 2 treatment groups to be analysed (i.e. at the initiation and completion of the recruitment experiment) the homogeneity of the variances was tested using the *F*-test (Wardlaw, 1985); and a two-sample *t*-test was utilized to compare the 2 treatment means - the pooled *t*-test being applied when the *F*-test indicated homogeneity of the variances (see Ryan *et al.*, 1985).

NOTE: To examine the validity of the assumption of the robustness of the analysis of variance, several analyses were repeated using the relevant non-parametric procedures which are considered to have less rigorous assumptions. The Kruskal-Wallis test is one such non-parametric "analysis of variance" (Wardlaw, 1985). Underwood (1981) points out, however, that there are also restrictive underlying assumptions in this test, including that the distributions in each treatment are identical, except for their medians, which implies that the variances in each treatment are equal. This will be violated where the heterogeneity of the variances was the original basis for applying the non-parametric procedures.

2.4.2. Statistical Analysis of Competitive Interactions:- Results from the study of bryozoan overgrowth

interactions were analysed with the Generalized Linear Interactive Modelling System (GLIM release 3.77, Royal Statistical Society, 1986). GLIM is an interactive system for statistical analysis, enabling a class of models known as Generalized Linear Models (GLM) to be fitted to the data. In essence, models are applied to the data with the objective of explaining the variation in a response variable in terms of the variation in certain explanatory variables. The experimental data provided information on which effects had an important influence and which could be neglected. Since a smaller number of parameters leads to easier interpretation, the aim is to obtain the best trade-off between the numbers of parameters that must be included in the linear structure of the model (keeping numbers as small as possible) and the ability of the model to accurately represent the data (keeping the fit as good as possible). Thus a parsimonious model is required in which the number of parameters needed for an adequate fit is minimized.

There are 4 stages in fitting generalized linear models with GLIM (see Appendix 1):

(i) *Declaration of the Appropriate Data Structure:* A number of variables concerned with bryozoan competition were recorded in this study:

a) the colonies involved in the interaction, either those of 2 different species or of the same same species. 18 species were evaluated in this study and they were ranked alphabetically and each species

coded. For example, 1 = *Alcyonidium* spp., 2 = *Callopora aurita*,..., 18 = *Umbonula littoralis*.

b) 4 sites were examined: 1 = Clachan Seil, 2 = Cuan Ferry, 3 = St.Andrews lower site, 4 = St.Andrews upper site.

c) Panels were initiated in 2 years: 1 = 1983, 2 = 1984.

d) 12 sectors in which contact could occur were recognized.

e) the number of wins, losses and ties between 2 colonies of the same or different species, in each sector, at each site and in each year were counted.

These data can be tabulated to form a data matrix which is acceptable for data analysis by GLIM. The data matrix is a 2-dimensional structure indexed by units (=rows of data) and variables (= columns of data, e.g. SITE, SEASON, SECTOR). For example, it is possible to represent the appropriate data in the matrix below:

	SP1	SP2	SITE	SEASON	SECTOR	WIN	LOSE	TIE
1	17	10	1	1	6	1	0	0
2	17	7	2	1	1	1	0	0
3	17	4	2	1	1	0	0	1
4	17	4	2	1	12	0	1	0
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.
89	17	17	4	2	12	2	1	9
90	17	18	4	2	1	0	0	1
91	17	18	4	2	5	1	0	0
92	17	11	4	2	1	1	0	0

Row 1 represents results for an interaction between *Schizoporella unicornis* (= species 17) and *Escharoides coccinea* (= species 10) at Clachan Seil (= site 1) in 1983 (= season 1) in sector 6, where only 1 win was recorded with no losses or ties. Similarly row 89 represents results for an intraspecific *S.unicornis* interaction, at the St.Andrews upper site (= site 4) in 1984 (= season 2), in sector 12, where 2 wins, 1 loss and 9 ties were observed.

Thus the data create a matrix of the variable outcome (i.e. win, lose or tie) indexed by the parameters of SITE, SEASON, SECTOR etc.. Note that although the parameters are read in as integers (for example site = 1, 2, 3, 4) they are recognized to be non-numeric by GLIM because of a specific declaration to this effect prior to the data input.

(ii) *Input of the Data:* The data was read in, row by row, from a data file external to the GLIM system.

(iii) *Definition and Fitting of the Model:* The generalized linear model has several components which can either be specified by the user or left to be given the default values by GLIM:

a) the dependent or y-variable, which is the observed response as given by the data; in the present case it represents the number of wins, losses and ties.

b) the required probability distribution (the error structure in GLIM) for each element of the y-variate. The simplest approach to the analysis of competition is to consider 2 possible outcomes: win (or more precisely the probability of not losing, so that ties may be included as wins) and lose. This is represented by the binomial error structure in GLIM. Ideally, however, 3 independent outcomes should be recognized: *viz.* win, lose, tie, represented by a trinomial distribution or the Poisson error structure in GLIM. Both the binomial and Poisson distributions are available as system defined error structures in GLIM.

c) the role played by the explanatory variables in the structure of each observation is expressed as the linear sum of their effects for the observation, which is known as the linear predictor, η . $\eta = \sum \beta_j x_j$ where $\sum \beta_j x_j$ is the linear combination of the known explanatory variables x_j with the (usually unknown) parameters β_j.

d) the link function defines the functional relationship between the linear predictor, η , from the linear model and μ the assumed mean of the y-variate. Thus $\eta = g(\mu)$. The default settings for the binomial and Poisson distributions were used (the link function for the binomial distribution is the logit link, and for the Poisson, the log link).

e) if an *a priori* value for the scale parameter of the exponential family is available then this is set. The binomial and Poisson distributions have variance-mean

relationships which are known completely, therefore there is no adjustable scale parameter so that the scaled deviance can be calculated with the default scale parameter of 1.

f) it may be desirable to analyse the data excluding particular subsets of the data from the calculations. This is possible by declaring a weight variate, so that individuals with a weight value 0 will be omitted from all the subsequent analyses, while those with a weight value of 1 will be included.

Having defined the sampling or error distribution, the dependent variable and possibly a prior weight variate, it is then necessary to describe the form of the linear predictor. The linear component is defined and fitted using the $ FIT directive, and any number of different models may be fitted by issuing the appropriate $ FIT directive. The simplest, or null model, implies fitting of only the "grand mean" which is constant over all the data and indicates the overall variance about the overall mean. In most cases this model will not adequately represent the structure of the data. In the binomial model this fit indicates the overall probability of, for example, winning; in the Poisson model this fit is of no informative value. It was therefore necessary to fit the minimal model which incorporated the parameter OUTCOME, to arrive at overall probabilities of the 3 possible outcomes (win, lose, tie).

The model specification resembles an algebraic expression in appearance, having operators and operands; the model formulae of particular interest in this study were the crossed (or factorial) models utilizing the '*' crossing operator, which indicates that separate and interaction effects among the specified parameters are to be considered in the model. For example:-

OUTCOME*SECTOR=>OUTCOME+SECTOR+OUTCOME.SECTOR

and

OUTCOME*SECTOR*SITE=>OUTCOME+SECTOR+SITE+

OUTCOME.SECTOR+OUTCOME.SITE+SECTOR.SITE+

OUTCOME.SECTOR.SITE

Where OUTCOME.SECTOR can be interpreted as the 'OUTCOME X SECTOR' interaction, and similarly OUTCOME.SECTOR.SITE indicates a 3-factor interaction. If all the parameters are added into the model, it produces the complete or full model, in which the data are reproduced exactly, but without any simplification of interpretation. It must be noted that the order in which parameters are included in the model may be important.

(iv) *Examination of the Results:* The $FIT directive produces output in the form of the scaled deviance and its degrees of freedom, for the fitted model. If the model is identified as a modification of a previous model then GLIM also outputs changes in the scaled deviance and its degrees of freedom. If some of the observations have been weighted out of the analysis then the number of

effective observations is also printed. For binomial and Poisson distributions, the model is fitted iteratively, the process may therefore require several cycles, the number of which is indicated in the output. The algorithm underlying the fitting of the models is generally robust and convergence occurs quite rapidly; if, however, convergence is not achieved after the maximum number of cycles (the default is 10 cycles) then an error message to this effect is printed. These results are, however, approximately correct (personal observations).

The problem is to determine the usefulness of a parameter or set of parameters to the current model (i.e. the model under consideration) or conversely, the lack of fit induced by omitting that parameter. A measure of the reasonableness of a model is the likelihood of the model given the data. By comparing the likelihood of the current model (1_c) to the likelihood of the full model (1_f) it is possible to obtain a measure of the acceptability of the current model relative to that of the full model. This is represented by the scaled deviance, S, where

$$S\ (c,f) = -2\ \log\ (1_c/1_f),$$

the arguments of S representing the models under comparison. Large values of the scaled deviance indicate low values of the likelihood of the current model relative to the likelihood of the full model, i.e. an

increasing lack of fit. For linear models with binomial and Poisson error structures, comparisons between models to allow assessment of the goodness-of-fit are facilitated because it is known that the scaled deviances are distributed approximately as χ^2, at least for large samples. Less, however, is known about how good the approximation is for small samples. The approximation is better for the difference between 2 scaled deviances, which expresses the effect of adding a term to the model, than for an absolute scaled deviance expressing the goodness-of-fit of a single model. Thus to determine the influences of the different parameters on the model it is necessary to examine the changes in scaled deviances and associated degrees of freedom as more complex models are fitted. The model considering only the overall "grand mean" is unlikely to fit the data closely; but as parameters are added to the model, a reduction in the scaled deviances and degrees of freedom can be expected, until sufficient parameters have been added to adequately explain the data. When the scaled deviance is not significant when compared to the tabulated χ^2 values at the chosen level of probability then the model can be concluded to fit the data. "Exact" probability levels should not, however, be attached to the scaled deviances, and the corresponding χ^2 values should be regarded only as a general indication in the assessment of the goodness-of-fit of a model.

After fitting a model to the data, one may often require more than one measure of the goodness-of-fit than

that given by the scaled deviances. The $DISPLAY directive allows various quantities associated with the fitted model to be output. Two of the possible options were of particular interest here:

a) the estimates of the parameters:- the parameter estimates are listed with their standard errors and parameter names. The estimate of "parameter 1" represents that of the "grand mean" and all the other parameter estimates represent the differences between the parameter means and the "grand mean". Thus the estimates represent the "effects" of the different parameters compared to that of the "grand mean". The extra information gained from a fit resides within the standard errors of the estimates. It is possible to perform tests equivalent to the t-test, accepting those estimates which have significant t-ratios. The standard errors can be regarded only as a guide to the reliability of the estimates, because they do not provide "exact" values for the significance tests. Parameter estimates less than the standard error are therefore usually considered to be insignificant while those greater than twice the standard error are usually considered significant, i.e.:-
estimate/standard error $> \pm 2$ statistically significant at the 5% level,
estimate/standard error $< \pm 2$ shows little evidence of a significant difference at the 5% level.
These t-tests are, however, inadequate substitutes for the information from the scaled deviances obtained by fitting various models.

b) the standardized residuals and fitted values:- this display lists the fitted values from the model and the standardized residuals. For the Poisson error model the "fitted values" represent the probabilities of winning, losing and tying, under the assumptions incorporated in the model. These probabilities are of particular interest in this study. Similar probabilities may be obtained for the binomial error model from the "observed" and "out of" values output with this directive.

Stages (iii) and (iv) can be repeated as required. It is therefore possible to examine a range of compound and nested models in an attempt to achieve a statistically significant reduction in the scaled deviances between models, i.e. a statistically significant improvement in the fit. This analysis may be supplemented with an examination of the t-ratios of estimates obtained from these fits. It is therefore possible to arrive at the most efficient and parsimonious model of the data, taking into account the overall fit as measured by the scaled deviance and the statistical significance of the individual parameters and their interaction terms.

3. THE INFLUENCE OF PANEL 'AGE' ON LARVAL RECRUITMENT

3.1. INTRODUCTION

Sessile marine invertebrates almost invariably have a free-swimming larval stage, and for many this putatively represents the only mode of genetic dispersal, enabling otherwise immobile organisms to exploit a spatially or temporally scattered or transient ecological niche. However, not all sessile marine invertebrates disseminate by planktonic larvae; e.g. species in the ascidian family Molgulidae have direct development without a swimming larva (Cloney and Torrence, 1984). In many species propagation by planktonic larvae is accompanied by asexual multiplication over shorter distances; thus, the successful genotype monopolizes a favourable habitat but retains the possibility of propagule dispersal (Crisp, 1984). Jackson (1986) has suggested that for clonal organisms dispersal of the "sessile" stage through growth, active movement, passive transport of detached organisms or fragments, and "rafting" may be more important in long-distance dispersal than that mediated by larval dispersal.

The activities of most marine invertebrate larvae consist of basically 3 phases: active moving, settlement and metamorphosis (Chia, 1978). Initially the larva undergoes either an active feeding-differentiation-growth period in planktotrophic development, or a differentiation period alone in lecithotrophic development - this is essentially a preparatory period for eventual settlement and metamorphosis (Chia, 1978).

In general, non-feeding lecithotrophic larvae (e.g. ascidian larvae (Cloney and Torrence, 1984); and most bryozoan larvae (Ryland, 1976)) have greatly shortened obligatory planktonic phases and hence the dispersal distances are markedly reduced. The settlement and metamorphosis stages transform the larva into a juvenile. Settlement, often including attachment, refers to general behavioural and habitat changes, whereas metamorphosis denotes morphological and physiological changes (Scheltema, 1974; Chia, 1978; Burke, 1983). A larva is said to be "competent" when it has entered a physiological state in which it is capable of metamorphosis when encountering the prerequisite environmental conditions (Chia, 1978).

Although initially larvae were considered to settle at random over the sea floor, surviving where conditions were favourable and dying where conditions were not (see for example, Nelson, 1928), there is increasing evidence that the larvae of many marine invertebrates have relatively sophisticated discriminatory capabilities, and frequently test for, and only metamorphose after finding, a suitable substratum. The suitability of its choice will ultimately be reflected in the survival and reproductive success of the adult. Davis (1987), for example. found that cues eliciting settlement of the larvae of the ascidian *Podoclavella cylindrica* concentrated larvae on substrata where survival was enhanced; *viz*. significantly more larvae settled on bare space (63-78% survivorship after 30 days) than upon the

sponges *Dendrocia* sp. and *Mycale* sp. (29% and 11% survivorship respectively). Strathmann and Branscomb (1979) predicted that the adequacy of available cues regarding site suitability was probably dependent on both the scale of dispersal and the causes of adult mortality. Specialization on cues most suitable for a particular locality was likely to decrease as the scale of dispersal increased, because the favourability of sites varied greatly within a wide range of dispersal scales and there was a low probability of finding adequate cues applicable to all sites. When mortality or reproductive failure was due to predation or parasitism, rather than directly from physical factors, the available cues were likely to be less adequate.

At release the majority of larvae swim upwards, thereby apparently escaping from benthic filter-feeders, to reach the surface where currents are generally maximal. At the end of larval life, after a few hours or days, many larvae react negatively to light and/or positively to gravity (e.g. *Spirorbis borealis* (Knight-Jones, 1951, 1953) and most bryozoan larvae (Ryland, 1960, 1977)). Such behavioural patterns facilitate an initial period of dispersal followed by a period of contact with a potentially suitable surface. However, for most species it is uneconomical to produce larvae which fix permanently as soon as they touch a surface by chance and thus the final choice of a suitable site is identified by means of more specific indicators. Larvae

periodically alight and explore different surfaces and Woollacott (1984) has suggested that the ability to disengage from a substratum and continue exploring is indicative of a high capacity for discrimination in the selection of a suitable substratum. Exploratory behaviour, which proceeds through phases of "broad exploration", "close exploration" and detailed "inspection", prior to the larva attaching permanently and commencing metamorphosis (Crisp, 1974, cited in Ryland, 1976), is exhibited by the larvae of many invertebrate species studied, e.g. *Spirorbis borealis* (Knight-Jones, 1951), *Bugula* spp. (Woollacott, 1984) and *Semibalanus balanoides* (Le Tourneux and Bourget, 1988).

Many marine invertebrate larvae react to their physical environment at settlement, responding to, for example, light (e.g. Grave, 1930; Cloney and Torrence, 1984), physical surface properties (e.g. Müller *et al.*, 1976; Mihm *et al.*, 1981), surface texture and contour (e.g. Pomerat and Weiss, 1946; Ryland, 1959), or current velocity (e.g. Crisp, 1984). However, Scheltema (1974) concluded that although the physical properties and attributes of submerged surfaces influence larval settlement, biological interactions have proven to be more subtle and important than nonbiological in determining the settlement of marine larvae. The presence of established adults of the same species, for example, is an appropriate indication of the 'suitability' of the local habitat and many marine larvae settle preferentially near adults of their own species,

e.g. hydroids (Pyefinch and Downing, 1949), polychaetes (Knight-Jones, 1951; Jensen and Morse, 1984), barnacles (see review in Newell, 1970), bryozoans (Wisely, 1958; Buss, 1981; Mihm *et al.*, 1981) and ascidians (Schmidt, 1982; Svane *at al.*, 1987). Keough (1984c) observed that the larvae of *Bugula neritina* settled in aggregations of closely related juveniles, but that the larvae did not respond to the presence of conspecific adults; similarly, Grosberg and Quinn (1986) found that sibling larvae of the ascidian *Botryllus schlosseri* settled in aggregations. As well as these intraspecific associations, the planktonic larvae of many marine invertebrates have been shown to settle in response to specific materials or to the presence of other animals or plants in the typical habitat. For example, many species are found associated exclusively with one or a few species of algae, and there is increasing evidence that their localized distribution arises through larval choice at settlement, e.g. the spirorbids, *Spirorbis rupestris* (Gee, 1965), *S.spirorbis* (Knight-Jones *et al.*, 1971), *S.inornatus* (Al-Ogily, 1985), and the bryozoans *Alcyonidium* spp., *Flustrellidra hispida* and *Celleporella hyalina* (Ryland, 1959, 1962a). Gregarious and associative settlement are generally considered to be responses to chemicals present in, or released by, the larvae or metamorphosed adults, or the settlement surface. Both the response and the chemicals eliciting it are generally species-specific.

Preceding the attachment and growth of macrofouling organisms is the formation of microfouling layers which are supported by earlier biopolymeric or "conditioning" films. Baier (1984) found that the first discernible event at the interface between an immersed solid surface and the seawater was the spontaneous adsorption of biological molecules or their oxidized end-products e.g. humic matter and "gelbstoffe", originally in solution or suspension in seawater. This "molecular fouling" alters the physical and chemical characteristics of a surface (Marszalek *et al.*, 1979), and in particular, Mitchell and Kirchman (1984) suggested that the deposition of a polymeric layer lowers the critical surface tension at the surface interface thus facilitating the attachment of a primary bacterial film. There is experimental evidence that organic films alone will not induce larval settlement. Mihm *et al.* (1981), for example, found that organically filmed glass surfaces had no measurable effect on *Bugula neritina* settlement, but bacterial-organic films increased the percent settlement from zero to over 70%. Similarly Kirchman *et al.* (1982), and Mitchell and Kirchman (1984), found that a non-specific organic film (gum arabic) did not induce settlement and metamorphosis of the spirorbid *Janua (Dexiospira) brasiliensis*. Bacteria are attracted to the wide range of organic chemicals that accumulate on submerged surfaces. However, Zobell and Allen (1935) and Zobell (1943) observed that it required 2 to 4 hours for appreciable numbers of bacteria to become attached to submerged

surfaces, and that regardless of their density, more attached during the early logarithmic phase of growth than during later growth phases. The establishment of bacteria, according to Marshall *et al.* (1971), involves 2 distinct phases: the initial attraction of bacteria to a surface, or reversible adsorption, and irreversible sorption which involves firm adhesion of the bacteria and which is probably dependent on the production of bacterial extracellular bridging polymers.

The bacteria and their organic secretions form the main constituents of the primary film. This stage is followed rapidly by the proliferation of the secondary colonizers, principally stalked and filamentous bacteria. Marshall *et al.* (1971) have suggested that this apparent succession of bacterial types may arise through alterations of the surface by the initially sorbed bacteria, which could result from the release of nutrients, surface active agents or extracellular polymeric materials. The appearance of diatoms, microalgae and protozoa usually occurs after the development of the bacterial film (see, for example, Zobell and Allen, 1935; Marshall *et al.*, 1971; Marszalek *et al.*, 1979; Little, 1984; see also Niell and Varela, 1984).

Zobell and Allen (1935) and Zobell (1939) concluded that many fouling organisms attached to submerged surfaces coated with films of bacteria more readily than to bacteria-free surfaces. They suggested that bacteria

might promote the fouling of surfaces by altering the chemical or physical properties of the surface, by mechanically facilitating the attachment of larval forms, or by providing a source of nutrients. Since the work of Zobell it has been reported that microbial films promote the settlement and metamorphosis of the larvae of a variety of marine invertebrates, e.g. the hydroids *Tubularia larynx* (Pyefinch and Downing, 1949) and *Hydractinia echinata* (Müller *et al.*, 1976); the spirorbids *Spirorbis borealis* (Knight-Jones, 1951; Meadows and Williams, 1963) and *S.rupestris* (Gee, 1965); and the bryozoans *Watersipora cucullata* (Wisely, 1958), *Bugula neritina* (Miller *et al.*, 1948; Mihm *et al.*, 1981), *B.simplex*, *B.turrita* and *B.stolonifera* (Brancato and Woollacott, 1982). Several studies have proposed mechanisms to explain the induction of settlement and metamorphosis of invertebrate larvae by bacterial films. Kirchman *et al.* (1982) and Mitchell and Kirchman (1984) have suggested that larval settlement and metamorphosis of *Janua* (D.) *brasiliensis* is induced by the binding of lectins (proteins or glycoproteins) of the larvae to extracellular lectin receptors (probably a polymer of glucose) produced by specific bacterial populations on surfaces. Coon *et al.* (1985) have found that selected neuroactive compounds and their structural analogs induce settlement and metamorphosis in the larvae of *Crassostrea gigas*, and have suggested that the natural sources of these molecules could be bacterial films.

Scheer (1945) and Wood (1950) found that some bryozoan and ascidian larvae were not influenced by the presence of a bacterial film, but suggested that the important change favouring settlement was the growth of diatoms. Other studies have suggested that the filming of surfaces is not an essential prerequisite to the attachment of all marine larvae. Crisp and Ryland (1960) found that although the majority of larvae appeared to selectively settle on filmed surfaces, those of at least one species, *Bugula flabellata*, settled more readily on a clean unfilmed surface than on a filmed one. Similarly, Crisp and Williams (1960) found that the larvae of *Alcyonidium polyoum* tended to avoid filmed surfaces, although they did not settle very readily on unfilmed surfaces either. Thus a considerable diversity of behaviour towards microbial films exists among marine invertebrate larvae.

The evidence suggests that in the development of microbial films a series of biological and chemical events occur on submerged surfaces (see, for example, Scheer, 1945; Marshall *et al.*, 1971; Marszalek *et al.*, 1979; Little, 1984). Thus there may be quantitative and qualitative differences in the microbial assemblages over time. Crisp and Williams (1960) have suggested that the larvae of some invertebrates may respond to qualitative differences in the microbial films formed on immersed surfaces, i.e. different film-forming microorganisms may vary in their ability to promote settlement. Recent studies using single-species bacterial films have

indicated that this might be the case. The larvae of *Janua (D.) brasiliensis*, for example, settled and metamorphosed in significantly different numbers in the presence of different bacterial films of single-species cultured from *Ulva lobata*, the common substratum of the adults; some bacterial strains failed to induce settlement, while others induced as much as 90% metamorphosis (Kirchman *et al.*, 1982; Mitchell and Kirchman, 1984). Similarly, Maki *et al.* (1988) tested the attachment responses of *Balanus amphitrite* cyprids on single-species bacterial films, cultured from 18 species of marine bacteria, and found that 7 species were inhibitory, 10 species showed no effect and 1 was stimulatory. Maki *et al.* (1988) concluded that the presence or absence of a certain species of bacteria and its extracellular products in a film, can influence the settlement behaviour and subsequent attachment of competent larvae, and thus may explain the variety of effects of microbial films observed on larval attachment. Microalgae are also often important components of microbial films and several studies have examined the effects of single-species microalgal films on larval settlement. Knight-Jones (1951) found that larvae of *Spirorbis borealis* readily settled on microbial films developed in seawater to which algal cultures of *Chlamydomonas* or *Synechococcus* were added: 78-100% of the larvae metamorphosed after 24 hours on filmed surfaces with *Chlamydomonas* and 92% with *Synechococcus*, compared to 0-30% on unfilmed surfaces. Meadows and

Williams (1963) examined the effect on settlement of *S.borealis* larvae of some of the microalgal constituents occurring in natural films. The results showed that the larvae settled on films previously developed in the presence of mixed diatoms (including *Ceratium*, *Chaetoceros*, *Navicula*, *Nitzchia* and *Skeletonema* species), and the diatom *Navicula*, but avoided those of the green flagellate *Dunaliella galbana*. They concluded that similar variations in the constituents of the microbial films would affect the settlement of *S.borealis* under natural conditions. Kirchman *et al*. (1982) and Mitchell and Kirchman (1984) found that only low numbers of *J.(D.) brasiliensis* settled and metamorphosed on films of the diatom *Nitzchia* sp. compared to multi-species bacterial films.

The 'attractiveness', or otherwise, of the microbial films may also vary as a function of the environmental conditions, physiology and 'age' of the films concerned. Mitchell and Kirchman (1984) and Maki *et al*. (1988) have suggested that chemical factors in the bacterial exopolymers may be involved, the quantity and quality of which may change with the growth stage of the bacteria and/or their physiological state. Mitchell and Kirchman (1984), for example, found that metamorphosis of *Janua (D.) brasiliensis* larvae was consistently higher on older films of *Pseudomonas marina*; and for multi-species films, Kirchman *et al*. (1982) found that, after 4 hours, more than 90% of the larvae exposed to a 7-day-old bacterial

film had metamorphosed, compared to only 60% on the 3-day-old films. They suggested that the increased attractiveness of the films with age arose because more polymer per cell was produced as the film aged. Maki *et al.* (1988) also demonstrated that the age of the bacterial film influenced the attachment response of *Balanus amphitrite* cyprids. However, they found that aged films of *Deleya marina* were more inhibitory to cyprid attachment; approximately 5% of 4-day-old cyprids attached after 22 hours on 5-day-old films compared to approximately 22% on 1-day-old films. Similarly, with mixed films of bacteria of different ages, 36.6% of 4-day-old cyprids attached to 24-hour-old films compared to 19.3% on 120 hour films. Maki *et al.* (1988) suggested that the response of cyprids to the different bacterial and multi-species films could arise if the cyprid antennular proteinaceous adhesive cannot bind strongly to the extracellular bacterial polymers. If a particular extracellular polymer allowed strong binding with the antennular cement, the cyprids may settle and permanently attach in greater numbers. Evidence that bacteria may produce the stimulatory effect on larval settlement only when they are at a certain growth stage was produced by Schmahl (1985a,b), who studied the settlement of stolons of the scyphopolyps of *Aurelia aurita*. He found that a species isolated from *Caulerpa* thalli was particularly effective in inducing the initiation of settlement. Bacteria which had entered the log-phase, and were on the verge of the stationary

phase, of growth showed the highest incidence of stolon settlement; bacteria from the earliest and stationary growth phases were less effective, and those from the decay phase only produced sporadic settlement (Schmahl, 1985a). Furthermore, Schmahl (1985b) found that crude lipid extracts from bacteria in the late phase of logarithmic growth resulted in the highest numbers of settled polyps; extracts from bacteria in the early and medium log-phases were significantly less effective.

The influence of variable quantities of bacteria in inducing larval attachment has also been examined. Schmahl (1985a) found that the numbers of settled stolons of the scyphopolyps of *Aurelia aurita* increased in direct proportion to the quantity of bacteria, although at high concentrations the percentage of settled stolons declined. Maki *et al.* (1988) found no significant differences between treatments in the attachment of either 2- or 4-day-old *Balanus amphitrite* cyprids, with varying densities of *Deleya marina*, once the bacterial densities were above 10^6 cells.cm^{-2}. Furthermore, Kirchman *et al.* (1982) found that the numbers of bacteria in films which were ineffectual in inducing the settlement and metamorphosis of *Janua (D.) brasiliensis* larvae were comparable to those in films which were effective inducers.

Superimposed on qualitative and quantitative variations in the microbial film, which may potentially produce differences in the effectiveness of films in

inducing larval settlement and metamorphosis, the composition of the microbial film may vary seasonally and/or spatially with concomitant effects on larval settlement. Zobell and Allen (1935), for example, recorded a change in the number of bacteria attaching to glass slides submerged in the sea for short-time intervals at different times of the year. Marszalek *et al.* (1979) found that the species involved in marine microfouling varied both with the season and site of exposure. Similarly, Castenholz (1963) recorded marked seasonal and spatial differences in the quantitative and qualitative development of diatom films on intertidal rocky substrata. He found that the species composition, distribution and density of the diatom cover on a shore depended principally on the period of exposure to direct solar radiation during emergence at low tide; high-temperature, desiccation, high light intensity and ultra-violet radiation being the principal adverse factors of exposure. That such temporal and spatial variations in microbial film constituents may influence larval settlement and metamorphosis has been illustrated by a study on the settlement of *Balanus cariosus* and *B.glandula* cyprids by Strathmann and Branscomb (1979) and Strathmann *et al.* (1981). They found that cyprids of *B.cariosus* readily settled on panels bearing "lower intertidal microflora", but avoided panels colonized by "upper intertidal microflora". Strathmann and Branscomb (1979) suggested that the physical factors which killed the components of the microflora were also likely to

affect settling marine invertebrates and that the microflora species may therefore be good indicators of intertidal physical conditions affecting post-settlement survival. They observed that *B.cariosus* cyprids settling in the upper intertidal occupied surfaces which remained moist at low tide, but not adjacent drier surfaces. They suggested that the cyprids were able to detect differences, when the rocks were immersed, between those which were damp or dry at low tide, and that the possible cue to dampness at low tide was the microflora on the rocks.

There is, therefore, abundant evidence suggesting that the microbial films which rapidly develop on surfaces in the marine environment may influence larval settlement. It should be noted that such 'bare' space may arise either through the introduction of 'new' surfaces into the habitat, for example, in the form of volcanic flows (e.g. Gulliksen *et al.*, 1980), pilings and other man-made structures (e.g. Karlson, 1978; Keough and Butler, 1979; Keough, 1984a), and a miscellany of experimental substrata utilized in the study of fouling assemblages (e.g. Sutherland and Karlson, 1977; Dean and Hurd, 1980; Breitburg, 1985; this study). Alternatively, 'free' space may be generated by the clearing of previously occupied substrata, for example through predation (e.g. Paine, 1974; Smedes and Hurd, 1981), wave or current action (e.g. Osman, 1977; Sousa, 1979, 1980; Davis and Wilce, 1987), or by the senescence and death of individuals or colonies of the resident assemblage (e.g.

Sutherland and Karlson, 1977; Keen and Neill, 1980). The effect of the microbial film in inducing or inhibiting the settlement and metamorphosis of invertebrate larvae may vary with the stage of development of the microbial film (i.e. its 'age'), due to either qualitative or quantitative differences in the film constituents. The principal aim of the present study was to examine the influence of the duration of substratum immersion, or the 'age' of the microbial film, on the induction of settlement and metamorphosis in invertebrate larvae. Sets of panels were examined over periods of 5 to 6 months, for the incidence of new recruits. Furthermore, since there is evidence that qualitative and quantitative differences may arise in the microbial films because of seasonal and spatial variations in the film constituents, substrata were initiated every month over a period of 18 months and at 2 intertidal sites. The 2 sites differed markedly in their duration of emergence at low tide. Thus, differences in the developing assemblages may be attributable to variation in the length of time the panels were immersed during the tidal cycle and consequently available for larval settlement; or because of differences in their physical regimes (e.g. desiccation and exposure to high and low temperatures) which may influence the 'attractiveness' of a surface to settling larvae (cf. Strathmann and Branscomb, 1979) or may directly influence their post-settlement survival.

This study has, thus, been concerned with the cumulative effects of substratum 'age', time and site of immersion on invertebrate larval recruitment.

FIGURE 3.1. (a) The mean (+1 standard error) total number of recruits and post-settlement mortalities recorded on the panels initiated each month between April 1984 and October 1985 at the upper intertidal site, after approximately 1 month immersion.
(b) The mean (+1 standard error) total number of recruits and post-settlement mortalities recorded on the panels immersed at the upper intertidal site, at each sampling date during the 5 month total immersion period.

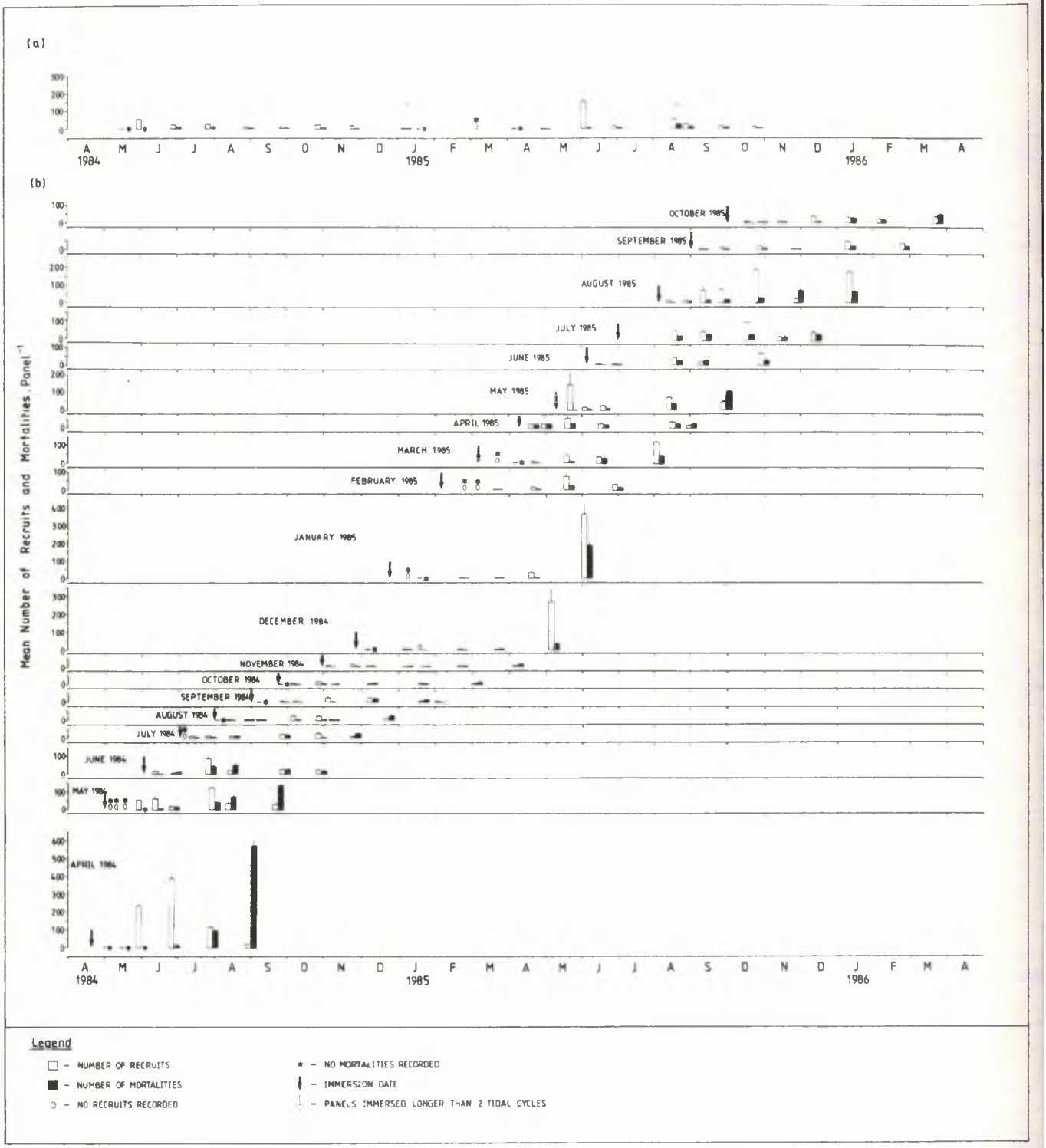
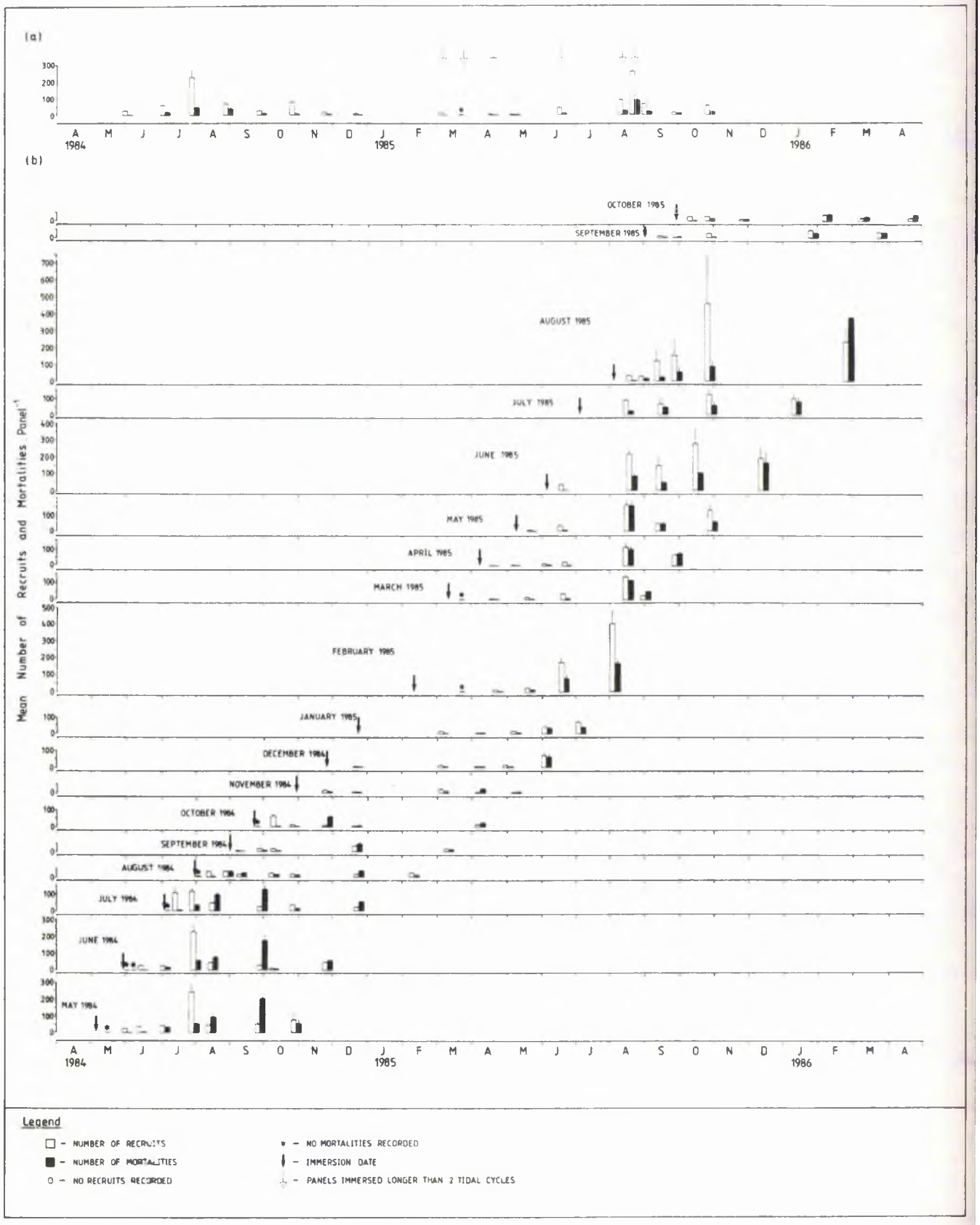

(a)
(b)
Mean Number of Recruits and Mortalities. Panel⁻¹
A M J J A S O N D J F M A M J J A S O N D J F M A
1984
1985
1986
OCTOBER 1985
SEPTEMBER 1985
AUGUST 1985
JULY 1985
JUNE 1985
MAY 1985
APRIL 1985
MARCH 1985
FEBRUARY 1985
JANUARY 1985
DECEMBER 1984
NOVEMBER 1984
OCTOBER 1984
SEPTEMBER 1984
AUGUST 1984
JULY 1984
JUNE 1984
MAY 1984
APRIL 1984
Legend
□ – NUMBER OF RECRUITS
■ – NUMBER OF MORTALITIES
○ – NO RECRUITS RECORDED
* – NO MORTALITIES RECORDED
– IMMERSION DATE
– PANELS IMMERSED LONGER THAN 2 TIDAL CYCLES

FIGURE 3.2. (a) The mean (+1 standard error) total number of recruits and post-settlement mortalities recorded on the panels initiated each month between May 1984 and October 1985 at the lower intertidal site, after approximately 1 month immersion.
(b) The mean (+1 standard error) total number of recruits and post-settlement mortalities recorded on the panels immersed at the lower intertidal site, at each sampling date during the 6 month total immersion period.


(a)
(b)
Mean Number of Recruits and Mortalities Panel⁻¹
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
1984
1985
1986
OCTOBER 1985
SEPTEMBER 1985
AUGUST 1985
JULY 1985
JUNE 1985
MAY 1985
APRIL 1985
MARCH 1985
FEBRUARY 1985
JANUARY 1985
DECEMBER 1984
NOVEMBER 1984
OCTOBER 1984
SEPTEMBER 1984
AUGUST 1984
JULY 1984
JUNE 1984
MAY 1984
Legend
□ – NUMBER OF RECRUITS
■ – NUMBER OF MORTALITIES
0 – NO RECRUITS RECORDED
* – NO MORTALITIES RECORDED
– IMMERSION DATE
– PANELS IMMERSED LONGER THAN 2 TIDAL CYCLES

3.2. RESULTS

The mean total number of larval recruits and post-settlement mortalities recorded at each sampling date (see Figure 2.8.) for the sets of panels immersed each month between April/May 1984 and October 1985 at the 2 intertidal sites at St.Andrews are represented diagrammatically in Figures 3.1. and 3.2.. Figures 3.1.a. and 3.2.a. indicate the mean monthly abundances of recruits and post-settlement mortalities during the first month (or exceptionally 6 weeks) of panel immersion. There was a marked seasonality evident in larval recruitment, the greatest numbers of recruits occurred in the spring and summer, and recruitment declined to low levels during the winter months. Periods of high recruitment were generally followed by periods of high mortality, therefore any pattern evident in mortality levels was dependent initially on previous recent recruitment. Although this pattern of recruitment was evident at both sites, there were a number of between-site differences. Principally, there were fewer recruits recorded overall at the upper site, where the greatest numbers occurred in the spring/early summer, somewhat earlier than the late summer peak in recruitment which occurred at the lower site. These differences were reflected in the daily recruitment rates (i.e. the numbers of recruits standardized for the length of the immersion period between sampling dates). For example, the mean daily recruitment rates for the first 3 tidal cycles of immersion for panels initiated in May 1985 were

TABLE 3.1 - Mean number of each species, or 'species group', recorded on the panels every month throughout the study at the upper site.

SPECIES	MAY 1984	JUNE 1984	JULY 1984	AUG. 1984	SEPT. 1984	OCT. 1984	NOV. 1984	DEC. 1984	JAN. 198
- PORIFERA									
Sheet sponges	-	-	-	0.06	-	0.10	-	-	-
Leucosolenia spp.	-	-	1.76	2.00	0.29	0.33	-	-	-
- CNIDARIA									
Hydroids	1.62	8.27	0.76	0.50	0.24	0.14	0.33	-	-
Scyphistoma (*Aurelia aurita* (L.))	-	-	-	0.11	0.05	-	-	-	-
- ANNELIDA									
Spirorbis spp.	-	1.27	1.19	1.67	7.57	11.33	5.28	2.73	0.29
Pomatoceros triqueter (L.)	-	0.13	36.14	1.22	1.76	2.71	0.56	0.13	-
- ARTHROPODA									
Semibalanus spp.	38.91	84.60	0.14	1.56	-	0.05	0.06	-	-
Elminius modestus (Darwin)	-	-	0.14	0.78	-	0.10	-	-	-
Verruca stroema (O.F. Müller)	-	-	-	-	-	-	0.06	-	0.04
- MOLLUSCA									
Anomia spp.	-	-	-	-	-	0.05	-	0.33	-
- ENTOPROCTA									
Pedicellina spp.	-	-	-	-	-	-	-	-	-
- BRYOZOA									
Bowerbankia spp.	-	-	0.05	-	-	-	-	-	-
Ctenostome ancestrula	-	-	-	-	-	-	-	2.13	0.21
Alcyonidium spp.	-	-	-	-	-	-	0.06	1.53	0.96
Flustrellidra hispida (Fabricius)	0.38	2.87	0.14	0.06	-	-	-	-	-
Cheilostome ancestrula	-	-	0.95	0.72	0.95	0.95	1.22	2.00	1.00
Callopora spp.	-	-	0.05	0.11	0.10	0.38	0.06	-	-
Celleporella hyalina (L.)	-	-	-	0.06	0.05	0.10	0.11	0.07	-
Conopeum reticulum (L.)	-	-	0.05	-	-	-	-	-	-
Cribrilina spp.	-	-	-	-	-	-	0.11	0.07	0.08
Escharella immersa (Fleming)	-	-	-	-	-	-	-	-	-
Electra pilosa (L.)	-	-	-	-	0.14	0.14	0.44	0.20	0.29
Phaeostachys spinifera (Johnston)	-	-	-	-	-	-	-	-	-
Schizoporella unicornis (Johnston)	-	0.07	1.76	1.11	0.86	0.24	0.33	-	0.04
Umbonula littoralis Hastings	-	-	-	-	-	-	-	-	0.04
- CHORDATA									
Unidentified Ascidians	-	-	0.86	1.22	0.33	-	-	-	-
Dendrodoa grossularia (van Beneden)	-	0.80	3.71	3.72	0.91	0.95	1.50	0.93	0.04
Molgula manhattensis (De Kay)	-	-	-	-	-	-	-	-	-
Botryllus schlosseri (Pallas)/ *Botrylloides leachi* (Savigny)	-	-	0.57	0.17	0.10	-	-	-	-
Trididemnum tenerum Verrill	-	-	2.19	0.44	-	-	-	-	-
NUMBER OF SPECIES RECORDED	3	7	16	17	13	14	13	10	10
TOTAL NUMBER OF ORGANISMS	859	1470	1060	279	280	369	182	152	72
TOTAL MEAN NUMBER OF ORGANISMS. PANEL^{-1}	40.91	98.00	50.48	15.50	13.33	17.57	10.11	10.13	3.00
NUMBER OF PANELS EXAMINED	21	15	21	18	21	21	18	15	24

5	FEB. 1985	MARCH 1985	APRIL 1985	MAY 1985	JUNE 1985	AUG. 1985	SEPT. 1985	OCT. 1985	NOV. 1985	DEC. 1985	JAN. 1986	FEB. 1986	MARCH 1986
-	-	-	-	-	0.29	2.29	0.46	0.33	-	-	-	-	-
-	-	-	-	-	0.13	3.91	0.33	0.33	-	-	-	-	-
-	-	-	-	1.78	6.17	1.05	0.38	0.72	0.08	0.17	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	0.06	1.22	11.17	10.05	17.25	28.44	3.58	7.00	4.33	-	0.33
-	-	-	-	-	0.17	10.19	0.29	-	-	-	-	-	-
-	-	-	4.22	87.94	41.96	1.00	0.42	0.06	-	-	-	-	-
-	-	-	-	0.11	0.08	0.38	0.46	0.06	-	-	-	-	-
-	-	-	-	0.06	-	-	-	0.06	-	-	-	-	-
-	-	-	-	-	-	0.81	1.92	9.56	0.50	-	-	-	-
-	-	-	-	-	-	-	-	0.06	-	-	-	-	-
-	-	-	-	-	0.04	0.71	0.58	0.56	0.08	-	-	-	-
1.33	0.28	2.06	0.56	0.29	0.10	-	-	0.06	1.17	14.00	11.67	5.33	9.33
0.87	0.22	1.06	1.50	0.08	0.05	-	-	0.11	2.25	3.17	32.22	8.17	2.67
-	-	-	-	-	0.67	0.71	0.04	-	-	-	-	-	-
2.07	1.17	2.00	0.78	0.92	6.91	5.67	5.11	4.75	16.33	32.00	12.33	26.67	
-	-	-	-	-	0.08	1.76	5.67	11.11	1.33	-	0.44	0.50	-
-	-	-	-	0.08	0.08	0.14	0.21	0.83	1.00	0.17	1.00	0.67	-
-	-	-	-	-	-	0.19	-	-	-	-	-	-	-
-	-	-	-	0.06	-	0.10	0.04	0.11	0.33	-	0.33	0.17	0.33
-	-	-	0.06	-	-	-	-	-	-	-	-	-	-
0.13	0.56	0.83	0.50	0.08	0.10	0.13	0.11	0.25	0.83	0.78	0.50	-	
-	-	-	-	0.06	0.08	-	-	-	-	-	-	-	-
-	-	-	-	-	0.13	3.62	1.42	3.00	0.17	-	-	-	-
0.53	0.11	0.11	0.06	0.04	-	-	-	-	-	-	-	-	0.33
-	-	-	-	-	0.71	0.91	0.13	0.06	-	-	-	-	-
-	-	-	-	-	0.38	2.19	0.96	2.89	0.83	0.33	0.33	-	-
-	-	-	-	-	0.13	-	0.04	0.28	-	-	-	-	-
-	-	-	-	-	-	0.38	-	-	-	-	-	-	-
-	-	-	-	-	-	2.62	0.17	-	-	-	-	-	-
5		5	8	13	21	23	20	21	13	8	9	7	6
74		42	187	1704	1528	1053	877	1149	196	252	748	166	119
4.93		2.33	10.39	94.67	63.67	50.14	36.54	63.83	16.33	42.00	83.11	27.67	39.67
15		18	18	18	24	21	24	18	12	6	9	6	3

TABLE 3.2 - Mean number of each species, or species group, recorded on the panels every month throughout the study at the lower site.

SPECIES	MAY 1984	JUNE 1984	JULY 1984	AUG. 1984	SEPT. 1984	OCT. 1984	NOV. 1984	DEC. 1984	FEB. 1985	MARCH 1985	APRIL 1985	MAY 1985	JUNE 1985	JULY 1985	AUG.1985	SEPT.1985	OCT.1985	NOV.1985	DEC.1985	JAN.1986	FEB.1986	MARCH 1986	APRIL 19
- PORIFERA																							
Sheet sponges	-	-	1.29	1.47	-	-	-	-	-	0.11	-	0.05	7.63	3.00	5.38	0.48	0.24	0.33	1.00	0.17	-	0.33	-
Leucosolenia spp.	-	-	0.38	0.80	-	0.04	0.11	-	-	-	-	-	0.71	0.33	0.50	0.26	0.10	-	-	-	-	-	-
- CNIDARIA																							
Hydroids	0.17	6.00	2.04	0.47	0.19	0.04	0.11	-	0.33	-	0.14	3.76	4.25	1.67	0.63	0.07	0.43	-	0.33	-	-	-	-
Scyphistoma (*Aurelia aurita* (L.))	-	-	-	-	0.10	-	-	-	-	-	0.05	-	-	-	-	-	0.05	-	-	-	-	-	-
- ANNELIDA																							
Spirorbis spp.	-	8.50	9.00	7.00	16.24	27.38	17.11	9.39	1.00	0.89	0.19	0.48	26.00	30.67	55.25	52.07	128.10	6.67	109.00	12.33	13.33	0.17	-
Pomatoceros triqueter (L.)	-	-	47.63	1.53	1.48	2.33	0.67	0.39	-	0.11	-	-	0.04	14.00	39.33	1.00	0.05	0.33	1.00	0.50	-	-	-
- ARTHROPODA																							
Semibalanus spp.	0.17	1.33	0.13	0.07	-	-	-	-	-	-	0.62	3.33	2.25	0.67	0.38	0.26	0.14	-	-	-	-	-	-
Elminius modestus (Darwin)	-	-	-	-	-	-	-	-	-	-	-	-	0.13	-	0.17	0.04	-	-	-	-	-	-	-
Verruca stroemia (O.F. Müller)	-	-	-	-	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-	-	-
- MOLLUSCA																							
Anomia spp.	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	0.25	2.30	2.43	-	0.67	0.67	-	-	-
- ENTOPROCTA																							
Pedicellina spp.	-	-	-	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
- BRYOZOA																							
Bowerbankia spp.	-	-	-	-	-	-	-	-	-	-	-	-	0.13	-	0.46	0.11	0.10	-	-	-	-	-	-
Ctenostome ancestrula	-	-	-	-	-	-	-	2.39	7.00	0.72	0.29	0.57	0.04	-	-	0.07	0.38	1.67	30.00	15.33	10.67	3.83	-
Alcyonidium spp.	-	-	-	-	-	-	0.56	1.06	4.33	3.17	0.71	1.71	0.25	0.33	0.04	-	0.10	0.33	11.33	10.83	24.00	2.83	0.33
Flustrellidra hispida (Fabricius)	0.17	6.17	3.79	-	-	-	-	-	-	-	-	-	3.75	4.33	1.42	-	-	-	-	-	-	-	-
Cheilostome ancestrula	-	0.58	1.83	2.33	0.86	0.54	1.89	0.78	7.67	3.61	3.24	0.86	1.25	3.67	7.46	4.30	7.10	0.33	22.67	20.67	71.50	14.67	13.00
Callopora spp.	-	-	-	-	-	0.04	-	-	-	-	-	0.05	0.04	-	1.83	4.44	5.86	-	7.33	1.83	3.17	0.17	-
Celleporella hyalina (L.)	-	0.08	0.50	0.33	0.19	0.21	0.22	0.17	-	-	-	0.10	0.13	0.33	2.46	0.74	2.29	-	2.00	2.33	4.17	0.33	-
Conopeum reticulum (L.)	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-	0.04	0.04	-	-	-	-	-	-	-
Cribrilina spp.	-	-	-	-	-	-	0.11	0.11	-	0.78	0.95	0.05	0.08	-	0.13	0.07	0.14	-	-	2.83	3.00	0.50	1.67
Escharella immersa (Fleming)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	-	0.19	-	-	-	0.17	-	-
Escharoides coccinea (Abildgaard)	-	-	-	-	-	-	-	-	-	0.06	-	-	-	-	0.04	-	-	-	-	-	-	-	-
Electra pilosa (L.)	-	-	0.13	0.07	0.05	0.13	0.78	0.50	-	0.78	1.33	0.81	0.25	-	0.17	0.19	0.19	0.33	1.00	2.50	2.50	0.33	0.33
Hapiopora spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-
Microporella ciliata (Pallas)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	0.04	-	-	-	-	-	-	-
Phaeostachys spinifera (Johnston)	0.17	-	0.08	-	-	-	-	-	-	-	0.05	0.43	1.46	0.33	1.25	-	0.05	-	-	-	-	-	-
Schizomavella linearis (Hassall)	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	-	0.04	0.05	-	-	-	-	-	-
Schizoporella unicornis (Johnston)	-	-	8.25	2.53	0.43	0.08	-	-	-	-	-	-	0.21	0.67	3.21	0.37	0.29	-	-	-	-	-	-
Umbonula littoralis Hastings	-	-	-	-	-	-	-	-	2.00	0.89	0.05	0.10	-	-	-	-	-	-	-	-	-	0.50	0.33
- CHORDATA																							
Unidentified Ascidians	-	-	1.50	6.87	0.48	0.04	0.11	-	-	-	-	-	1.75	0.67	0.50	0.67	0.38	-	0.33	-	-	-	-
Dendrodoa grossularia (van Beneden)	-	-	5.42	6.07	0.62	1.17	1.44	0.83	-	-	-	-	2.04	6.00	3.88	1.63	2.48	-	2.33	1.00	0.17	-	-
Molgula manhattensis (De Kay)	-	-	-	-	-	-	-	-	-	-	-	-	1.05	1.08	-	0.13	0.19	0.05	-	-	-	-	-
Botryllus schlosseri (Pallas)/ *Botrylloides leachii* (Savigny)	-	-	9.08	7.47	0.29	0.04	-	-	-	-	-	-	-	2.00	18.00	0.82	0.10	-	-	-	-	-	-
Trididemnum tenerum Verrill	-	-	4.96	3.13	0.10	0.04	-	-	-	-	-	-	-	-	1.63	0.26	-	-	0.33	-	-	-	-
NUMBER OF SPECIES RECORDED	4	6	16	15	13	14	11	9	6	10	11	15	21	16	27	24	25	7	14	12	10	10	5
TOTAL NUMBER OF ORGANISMS	4	272	2304	600	442	771	208	281	67	200	160	360	1259	207	3511	1902	3177	30	568	426	796	142	47
TOTAL MEAN NUMBER OF ORGANISMS. PANEL^{-1}	0.67	22.67	96.00	40.00	21.05	32.13	23.11	15.61	22.33	11.11	7.62	12.38	52.46	69.00	146.29	70.44	151.29	10.00	189.33	71.00	132.67	23.67	15.67
NUMBER OF PANELS EXAMINED	6	12	24	15	21	24	9	18	3	18	21	21	24	3	24	27	21	3	3	6	6	6	3

4.085 larvae. panel^{-1} at the upper site and 0.960.panel^{-1} at the lower site; for panels initiated in August 1985 the mean daily recruitment rates over the first 2 tidal cylces were 1.188 larvae.panel^{-1} and 2.667.panel^{-1} at the upper and lower sites respectively.

Tables 3.1. and 3.2. list the species recorded on the panels at both sites throughout the 2-year study period. An estimate of the mean monthly abundance of each species was calculated from the numbers of each recorded on all the panels examined in each month (some panels may have been examined more than once in any particular month), but taking no account of the total duration of panel immersion at the time of examination (i.e. panel 'age'), or the time since the previous examination of the panels concerned. Recently settled bryozoan ancestrulae and ascidian tadpole larvae, for example, were not readily identifiable to species and were therefore classified into 'species groups'. Thirty-four species or 'species groups' were identified overall. Thirty of these occurred at both sites; none were unique to the upper site, but 4 cheilostome bryozoans (*Escharoides coccinea* (Abildgaard), *Haplopoma* spp., *Microporella ciliata* (Pallas) and *Schizomavella linearis* (Hassall)) were observed occasionally at the lower site only. The majority of the species recruited in greatest abundance to the lower site, although there were a number of exceptions, e.g. *Leucosolenia* spp., hydroids and barnacles (principally *Semibalanus balanoides* (L.) and

S.crenatus (Bruguière)). Differences in the abundance of the species at each site accounted for the disparities in the overall seasonal pattern of recruitment already noted; *viz.* the abundance of barnacle recruits at the upper site was primarily responsible for the earlier peak of larval recruitment recorded at the upper site compared to the lower site.

None of the species were recorded on panels throughout the study period and most showed marked seasonality in recruitment, the principal exceptions being the 'species groups' (e.g. spirorbids and cheilostome ancestrulae) which comprised a number of species, thus there were more prolonged periods of recruitment evident for each 'group'. Most species had peaks of recruitment in the summer and were absent, or present only in low numbers, during the winter months. Correspondingly, there were marked differences in the numbers of species recorded on panels at different times of the year: 5 species were recorded on panels at the upper site in March 1985 and 6 in March 1986, there were 10 in the same months at the lower site, whereas in August 1984 17 species were recorded at the upper site and 23 in August 1985, compared to 15 and 27 respectively, in August 1984 and 1985 at the lower site.

Although recruitment was only studied over a period of 2 years (April 1984 - April 1986) there was evidence of between-year differences in recruitment. For example, fewer *Flustrellidra hispida* (Fabricius) and *Tridemnum*

tenerum Verrill and more spirorbids and cheilostomes were recorded in 1985. There was, therefore, considerable qualitative and quantitative variation in larval recruitment onto panels immersed at different sites, in different seasons and in different years.

For the detailed analysis of the influence of the duration of panel immersion, or panel 'age', on recruitment and mortality, the 34 species were classified into 8 taxonomic groups (*viz.* sponges, serpulids, barnacles, anomiids, hydroids, cheilostome and ctenostome bryozoans, and ascidians). The mean number of recruits and mortalities recorded for each taxonomic group, at each sampling date, for each set of panels immersed are tabulated in Appendix 2. The results from the ANOVA and the tests for the homogeneity of the variances are given in Tables 3.4. - 3.39.. Also the sets of panels of varying periods of immersion are ranked in increasing order of the mean numbers of recruits or mortalities recorded; groups under-scored by the same line are considered to be significantly homogeneous, whereas those not underscored by the same line are significantly heterogeneous on the basis of the Student-Newman-Keuls test (hereafter referred to as 'S-N-K') at the 5% level. The 'S-N-K' test is more conservative than the ANOVA and therefore it is possible to reject the overall null hypothesis of the original analysis, leading to the conclusion that the means differ, but to have no evidence of differences among the means in the 'S-N-K' tests (Underwood, 1981). The results of the analyses excluding

TABLE 3.3 - A comparison of the non-parametric and parametric analysis of variance for selected data sets where both Cochran's and Bartlett's test of the homogeneity of the variances were significant.

SITE	DATE	TAXONOMIC GROUP	RECRUITMENT /MORTALITY	F-TEST (ANOVA)	BARTLETT'S TEST	BARTLETT'S TEST (CORRECTED)	COCHRAN'S TEST	KRUSKAL-WALLIS TEST	KRUSKAL-WALLIS TEST (CORRECTED)
LOWER	END SEPT. 1984	TOTAL	RECRUITMENT	0.67 ns	14.748*	12.290*	0.887*	4.233 ns	4.263 ns
LOWER	MID JUNE 1985	TOTAL	RECRUITMENT	13.96*	22.852*	19.132*	0.855*	13.439*	13.453*
LOWER	END OCT. 1985	SERPULIDS	MORTALITY	3.26*	27.610*	23.115*	0.832*	13.632*	13.689*
LOWER	END OCT. 1985	CHEILOSTOMES	MORTALITY	7.51*	13.991*	11.713*	0.762*	13.146*	13.367*
UPPER	MID APRIL 1985	TOTAL	RECRUITMENT	12.08*	39.462*	32.885*	0.992*	13.358*	13.406*
UPPER	MID MAY 1985	TOTAL	MORTALITY	74.65*	12.632*	10.526*	0.772*	12.258*	12.280*
UPPER	MID MAY 1985	SERPULIDS	RECRUITMENT	24.92*	22.443*	18.702*	0.954*	10.917*	11.363*
UPPER	END OCT. 1985	ANOMIIDS	MORTALITY	1.14 ns	14.852*	12.377*	0.851*	3.000 ns	3.854 ns

* = significant at the 5% level i.e. $P<0.05$; ns = not significant.

those sets of panels which were not immersed for the whole of the period analysed (i.e. those panels which were initiated at the spring tide falling in the middle of the period of analysis) are also given in Tables 3.4. - 3.39..

Results from a comparison of the ANOVA test and the non-parametric Kruskal-Wallis "analysis of variance", for examples where both tests of the homogeneity of the variances were significant, are given in Table 3.3.. The results suggest that, provided the outcomes of the ANOVA are interpreted with caution, the ANOVA may be a suitable test despite the heterogeneity of the sample variances.

No correction was made in this study for the effects of pre-emption of space by previously recruited individuals and colonies on the rates of subsequent larval attachment. This was because, in general, the recruitment and growth of organisms on the panels did not combine to greatly reduce the surface area available for further settlement; even on the 'oldest' panels, and during periods of greatest larval recruitment, recruits rarely occupied more than approximately 15-20% of the space, and in winter less than 5% of the space was occupied. The principal exception was during the periods of greatest barnacle recruitment at the upper site, when approximately 50-60% of the primary surface area may have been occupied. Connell (1985), from his own work and a review of the literature, principally on barnacle settlement, concluded that during periods of high larval

TABLE 3.4 - Analysis of the total number of larval recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site.

(a) all the panels are included in the analysis;
(b) the analysis repeated to exclude the panels which were not immersed for the whole duration of the period under analysis.

(1) small data set, i.e. only 1-2 recruits observed on 1-2 panels;
(2) the result for Bartlett's test of the homogeneity of the variances differs in significance, at the 5% level, from the result for Cochran's test;
(3) the only recruits recorded occurred in equal numbers on the 3 replicates of one panel set, no other recruits were recorded. Such a data structure produces anomalous results in the analysis.

In the 'S-N-K' test the panel means are ranked in order of increasing size from left to right; means underscored by the same line are assumed to be homogeneous, and means not underscored by the same line are heterogeneous.

Months of panel initiation (Tables 3.4 and 3.6): Ja = January; F = February; Ma = March; Ap = April; My = May; Jn = June; Jl = July; Ag = August; S = September; O = October; N = November; D = December.

Approximate 'age' of panels (in months) at the time of analysis: 0.5, 1.0, ..., 6.0, 6.5.

* = $P < 0.05$; ns = not significant.

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	197.69*	ns	1.0 1.5 My Ap	-	-	-
JUNE	85.75*	ns	1.0 2.0 2.5 Jn My Ap	-	-	-
JULY	31.26*	ns	1.0 2.0 3.5 3.0 Jl Jn Ap My	-	-	-
AUG.	8.43*	ns	1.0 4.5 2.0 3.0 4.0 Ag Ap Jl Jn My	-	-	-
SEPT.	0.75ns	ns	1.0 3.0 4.0 2.0 5.0 S Jl Jn Ag My	-	-	-
OCT.	0.26ns	ns	2.0 5.0 1.0 4.0 3.0 S Jn O Jl Ag	-	-	-
NOV.	2.63ns	0.91*	1.5 0.5 3.5 4.5 2.5 O N Ag Jl S	-	-	-
DEC.	5.08*	0.84*	0.5 2.5 4.5 1.5 3.5 D O Ag N S	3.16ns	0.84*	2.5 4.5 1.5 3.5 O Ag N S
1985 JAN.	4.24*	ns	1.0 2.0 3.0 5.0 4.0 Ja D N S O	-	-	-
FEB.	12.11*	ns	0.5 2.0 5.0 3.0 4.0 F Ja O D N	3.04ns	ns	2.0 5.0 3.0 4.0 Ja O D N
MARCH	2.97ns	0.69*(2)	0.5 1.5 3.0 4.0 5.0 Ma F Ja D N	1.74ns	ns	1.5 3.0 4.0 5.0 F Ja D N
APRIL	12.08*	0.99*	0.5 1.5 2.5 4.0 5.0 Ap Ma F Ja D	11.44*	0.99*	1.5 2.5 4.0 5.0 Ma F Ja D
MAY	6.18*	ns(2)	1.5 2.5 3.5 0.5 5.0 Ap Ma F My Ja	18.26*	0.82*	1.5 2.5 3.5 5.0 Ap Ma F Ja
JUNE	2.79ns	0.70*(2)	0.5 4.5 2.5 1.5 3.5 Jn F Ap My Ma	1.05ns	ns	4.5 2.5 1.5 3.5 F Ap My Ma
AUG.	15.52*	ns	0.5 4.5 2.5 1.5 3.5 Ag Ap Jn Jl My	5.92*	ns	4.5 2.5 1.5 3.5 Ap Jn Jl My
SEPT. (middle)	3.77*	ns(2)	0.5 3.5 4.5 2.5 1.5 S Jn My Jl Ag	2.52ns	ns	3.5 4.5 2.5 1.5 Jn My Jl Ag
SEPT. (end)	3.82*	ns(2)	1.0 5.0 4.0 3.0 2.0 S My Jn Jl Ag	-	-	-
OCT.	19.37*	ns	1.0 2.0 5.0 4.0 3.0 O S Jn Jl Ag	-	-	-
NOV.	3.60ns	ns	3.0 4.0 2.0 5.0 S Ag O Jl	-	-	-
1986 JAN.	101.37*	ns	4.5 3.5 5.5 S O Ag	-	-	-
FEB.	0 ns	ns	5.5 4.5 S O	-	-	-

TABLE 3.5 - Analysis of the total number of recruit mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	9.59*	ns	1.0 2.5 2.0	-	-	-
JULY	8.64*	ns(2)	1.0 3.0 2.0 3.5	-	-	-
AUG.	175.41*	0.73*	1.0 2.0 3.0 4.0 4.5	-	-	-
SEPT.	203.97*	ns	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.	5.34*	0.75*(2)	2.0 1.0 4.0 3.0 5.0	-	-	-
NOV.	2.65ns	0.96*	0.5 2.5 3.5 1.5 4.5	-	-	-
DEC.	4.46*	ns(2)	0.5 1.5 2.5 4.5 3.5	2.50ns	ns	1.5 2.5 4.5 3.5
1985 JAN.	9.40*	ns	1.0 2.0 4.0 3.0 5.0	-	-	-
FEB.	4.39*	0.90*	0.5 2.0 3.0 4.0 5.0	3.70ns	0.90*	2.0 3.0 4.0 5.0
MARCH	11.38*	ns	0.5 1.5 3.0 4.0 5.0	9.17*	ns	1.5 3.0 4.0 5.0
APRIL	198.25*	ns	0.5 1.5 2.5 4.0 5.0	194.67*	ns	1.5 2.5 4.0 5.0
MAY	74.65*	0.77*	0.5 1.5 2.5 3.5 5.0	71.29*	0.78*(2)	1.5 2.5 3.5 5.0
JUNE	7.11*	ns(2)	0.5 4.5 1.5 2.5 3.5	3.30ns	ns	4.5 1.5 2.5 3.5
AUG.	8.71*	0.71*(2)	0.5 4.5 1.5 2.5 3.5	0.85ns	ns	4.5 1.5 2.5 3.5
SEPT. (middle)	2.78ns	0.89*	0.5 1.5 3.5 2.5 4.5	1.67ns	0.89*	1.5 3.5 2.5 4.5
SEPT. (end)	1.92ns	ns(2)	1.0 4.0 3.0 2.0 5.0	-	-	-
OCT.	3.63*	ns	1.0 2.0 5.0 4.0 3.0	-	-	-
NOV.	8.16*	0.81*	3.0 2.0 5.0 4.0	-	-	-
1986 JAN.	10.72*	ns	4.5 3.5 5.5	-	-	-
FEB.	0.66ns	ns	4.5 5.5	-	-	-

TABLE 3.6 - Analysis of the total number of larval recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Table 3.4 for details).

	(a)				(b)			
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K		ANOVA	COCHRAN'S TEST	S-N-K	
1984 JUNE	6.45ns	ns	1.0 2.0 Jn My		-	-	-	
JULY	0.03ns	ns	1.0 2.0 3.0 Jl Jn My		-	-	-	
AUG.	0.47ns	ns(2)	3.0 2.0 4.0 1.0 Jn Jl My Ag		-	-	-	
SEPT.	0.67ns	0.89*	3.0 4.0 1.0 2.0 5.0 Jl Jn S Ag My		-	-	-	
OCT.	2.53ns	0.92*	2.0 5.0 3.0 4.0 6.0 1.0 S Jn Ag Jl My O		-	-	-	
NOV.	16.12*	ns	4.0 2.0 5.0 3.0 1.0 6.0 Ag O Jl S N Jn		-	-	-	
DEC.	1.76ns	ns	2.0 3.0 5.0 1.0 6.0 4.0 N O Ag D Jl S		-	-	-	
1985 MARCH	1.66ns	0.67*	1.0 5.5 2.5 3.5 6.5 4.5 F O Ja D S N		0.41ns	ns	5.5 2.5 3.5 6.5 4.5 O Ja D S N	
APRIL	1.21ns	0.79*(2)	1.0 3.5 6.5 5.5 2.0 4.5 Ma Ja O N F D		-	-	-	
MAY	2.47ns	0.64*(2)	6.5 1.0 2.0 4.5 5.5 3.0 N Ap Ma Ja D F		-	-	-	
JUNE	13.96*	0.86*	2.5 0.5 1.5 3.5 6.0 4.5 Ap Jn My Ma Ja F		13.51*	0.87*	2.5 1.5 3.5 6.0 4.5 Ap My Ma Ja F	
AUG.	13.03*	ns	0.5 1.5 4.5 5.5 3.5 2.5 Ag Jl Ap Ma My Jn		6.87*	ns	1.5 4.5 5.5 3.5 2.5 Jl Ap Ma My Jn	
SEPT.	2.20ns	0.65*	0.5 5.5 4.5 2.5 3.5 1.5 S Ap My Jl Jn Ag		1.58ns	ns(2)	5.5 4.5 2.5 3.5 1.5 Ap My Jl Jn Ag	
OCT.	1.85ns	0.91*	2.0 1.0 4.0 6.0 5.0 3.0 S O Jl My Jn Ag		1.70ns	0.91*	2.0 4.0 6.0 5.0 3.0 S Jl My Jn Ag	
1986 JAN.	3.33ns	0.79*(2)	3.5 4.5 6.5 5.5 O S Jl Ag		-	-	-	
FEB.	4.33ns	0.96*	4.5 5.5 6.5 O S Ag		-	-	-	
MARCH	0.20ns	ns	6.5 5.5 S O		-	-	-	

TABLE 3.7 - Analysis of the total number of recruit mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	19.41*	ns	1.0 2.0	-	-	-
JULY	1.54ns	ns	1.0 3.0 2.0	-	-	-
AUG.	4.96*	ns	1.0 3.0 2.0 4.0	-	-	-
SEPT.	11.42*	ns(2)	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.	1.57ns	0.98*	1.0 2.0 4.0 3.0 5.0 6.0	-	-	-
NOV.	16.75*	0.71*(2)	1.0 4.0 3.0 5.0 6.0 2.0	-	-	-
DEC.	11.11*	ns	1.0 2.0 3.0 5.0 4.0 6.0	-	-	-
1985 MARCH	10.86*	ns	1.0 2.5 3.5 4.5 6.5 5.5	7.92*	ns	2.5 3.5 4.5 6.5 5.5
APRIL	2.87ns	0.95*	1.0 2.0 6.5 3.5 4.5 5.5	-	-	-
MAY	2.53ns	0.71*(2)	1.0 2.0 4.5 3.0 5.5 6.5	-	-	-
JUNE	7.57*	0.97*	0.5 1.5 2.5 3.5 6.0 4.5	6.60*	0.97*	1.5 2.5 3.5 6.0 4.5
AUG.	9.40*	0.67*	0.5 1.5 2.5 4.5 5.5 3.5	5.56*	ns	1.5 2.5 4.5 5.5 3.5
SEPT.	9.85*	ns	0.5 1.5 2.5 4.5 5.5 3.5	0.46ns	ns	1.5 2.5 4.5 5.5 3.5
OCT.	3.94*	0.80*	2.0 1.0 4.0 6.0 3.0 5.0	3.22ns	0.80*	2.0 4.0 6.0 3.0 5.0
1986 JAN.	2.27ns	0.96*	4.5 3.5 6.5 5.5	-	-	-
FEB.	2.47ns	0.99*	5.5 4.5 6.5	-	-	-
MARCH	0.75ns	ns	6.5 5.5	-	-	-

settlement there was an oversupply of larvae available and able to settle, and that the rates of settlement were limited by a pre-emption of surface space rather than by events in the water column or physical conditions. However, when the settled densities were low he suggested that other processes, for example larval supply, may have more influence on the rates of attachment. Similarly, Gaines and Roughgarden (1985) found that the settlement rate of *Balanus glandula* cyprids was directly proportional to the amount of unoccupied space - provided the free space was distributed around existing adults. However, in general, in the present study recruitment rates were such that recruits probably did not occupy sufficient space, during the 5 or 6 month sampling periods, to inhibit further recruitment.

(a) Total Recruitment and Mortality:- (Tables 3.4. - 3.7.)

At the upper intertidal site, the overall pattern evident in the ranking of the mean numbers of recruits recorded on panels differing in their length of immersion, was that more larvae recruited onto the longer-immersed panels than the lower-ranked, more recently-immersed, panels. Note that this was partially accounted for, in some instances, because the most recently-immersed panels were initiated half-way through the period under analysis. There were, however, exceptions to this generalization, for example, in

September 1985 when the recently initiated August 1985 panels were higher-ranked than panels which had been immersed for longer. There were a number of significant differences evident between panels differing in immersion period, the majority of which arose between the numbers of recruits recorded on the highest-ranked panels and one or more of the lower-ranked sets. For example, in May 1984 (F = 197.69, P<0.05), June 1984 (F = 85.75, P<0.05), April 1985 (F = 12.08 or 11.44, P<0.05 (Cochran and Bartlett's (hereafter referred to as 'C & B'), P<0.05)), October 1985 (F = 19.37, P<0.05) and January 1986 (F = 101.37, P<0.05), the highest-ranked set of panels, which in all cases except October 1985, were also the longest-immersed, had significantly more recruits than the other panels. Similarly, in August 1984 (F = 8.43, P<0.05) the highest-ranked panels had significantly more recruits than the other panel sets, and there was also a significant difference between the second highest-ranked panel set and the newly-immersed August 1984 panels. In May 1985 (F = 6.18 or 18.26, P<0.05 ('C & B', P<0.05, for the incomplete data set)) the highest-ranked, longest-immersed panels had significantly more recruits than the other panels, with the exception of the newly initiated May 1985 panels. In a number of the data sets the only significant differences were between the highest and lowest-ranked panel sets, for example, December 1984 (F = 5.08, P<0.05 ('C & B', P<0.05)), mid-September 1985 (F = 3.77, P<0.05), and November 1985 (F = 3.60, P>0.05; 'S-N-K',

$P<0.05$). Significantly fewer recruits were recorded on the newly-immersed panel sets in February 1985 (F = 12.11, $P<0.05$) and August 1985 (F = 15.52 or 5.92, $P<0.05$). There were also significant differences between the highest and second lowest-ranked panel sets, and in July 1984 (F = 31.26, $P<0.05$) there were significantly fewer recruits on the 2 most recently initiated panel sets. If the newly initiated panels were excluded from the analyses for December 1984, February 1985 and mid-September 1985 no significant differences were evident among the panels of different 'ages'.

Among the other sampling periods, September 1984, October 1984, November 1984, January 1985 (but note, F = 4.24, $P<0.05$; 'S-N-K', $P>0.05$), March 1985, June 1985, late-September 1985 (but note, F = 3.82, $P<0.05$; 'S-N-K', $P>0.05$) and February 1986, there were no detectable significant differences in the numbers of recruits recorded on the panels of different 'ages'. Thus there appeared to be no relationship between the presence of significant differences among the panels in terms of the numbers of recruits recorded, and the month of analysis; i.e. the incidence of significant 'S-N-K' tests appeared to be independent of the level of recruitment, which varied seasonally.

At the lower site, the overall pattern for the lower-ranked panel sets to be those which were immersed for shorter periods was not as consistent as at the upper site. There were several examples of an approximately

converse ranking of the panels, for example, August 1984 and September 1985. As with the upper site there was no consistent pattern among the ranking of the differently 'aged' panels in relation to the month of analysis.

Only in November 1984 (F = 16.12, P<0.05), June 1985 (F = 13.96 or 13.51, P<0.05 ('C & B', P<0.05)), and August 1985 (F = 13.03 or 6.87, P<0.05) were significant differences recorded among the numbers of recruits on the panels of different 'ages'. In all 3 instances the highest-ranked, and generally longer-immersed, set of panels had significantly more recruits than the other panels. In the August 1985 data set there were also significantly fewer recruits on the August 1985-initiated panels. In none of the other periods of analysis was there evidence of significant differences between the panels of different 'ages'.

Considering the numbers of post-settlement mortalities recorded, the characteristic pattern among all the sampling periods at both sites, was that the highest-ranked panels were generally the longest-immersed panels, and fewer post-settlement mortalities were recorded on the more recently-immersed panels. This partly arose because of the accumulation of recruits on the panels with time, i.e. after longer immersion periods there were generally more recruits potentially susceptible to agents of post-settlement mortality. It was probably also symptomatic of a general characteristic that became evident in this study: few recruits survived for more

than 1 or 2 sampling periods after recruitment. Thus these assemblages were characterized by high levels of post-settlement mortality. The results may be further confounded because, when a panel series was terminated after 5 or 6 months immersion, recruits were, if necessary, destructively examined to determine if they were alive. At sample dates prior to termination no recruits were damaged deliberately and thus mortality was probably slightly under-represented at these times. This pattern was not, however, absolute. For example, at the lower site in November 1984 (F = 16.75, P<0.05) the recently-immersed October 1984 panels had significantly more mortalities than were recorded on the 'older' panels.

At the upper site the majority of the statistically significant differences arose between the panels because significantly more mortalities were recorded on the longest-immersed set of panels than those which were more recently-immersed, for example, July 1984 (F = 8.64, P<0.05), October 1984 (F = 5.34, P<0.05), January 1985 (F = 9.40, P<0.05), February 1985 (F = 4.39, P<0.05 ('C & B', P<0.05), although if the February 1985-initiated panels were excluded from the analysis there were no significant differences between the panels), March 1985 (F = 11.38 or 9.17, P<0.05), May 1985 (F = 74.65 or 71.29, P<0.05 ('C & B', P<0.05, for the complete data set)), and January 1986 (F = 10.72, P<0.05). In June 1984 (F = 9.59, P<0.05) and November 1985 (F = 8.16, P<0.05 ('C & B', P<0.05)), significantly

more mortalities were recorded on the panel sets immersed for the second longest duration. In August 1984 (F = 175.41, P<0.05 ('C & B', P<0.05)) and April 1985 (F = 198.25 or 194.67, P<0.05) the 2 longest-immersed sets of panels had significantly more mortalities than were recorded on the other panels. Among the other significant differences, the patterns were less distinct, but essentially the same conclusions can be drawn. More mortalities were recorded on one or more of the longer-immersed panel sets than on those immersed for shorter periods in September 1984 (F = 203.97, P<0.05), December 1984 (F = 4.46, P<0.05), and June 1985 (F = 7.11 , P<0.05); although if the December 1984 and June 1985 newly initiated panels were excluded from the latter 2 data sets respectively, no significant differences were evident between the panels. Similarly, if the August 1985-initiated panels were excluded from the August 1985 (F = 8.71, P<0.05) data set, otherwise the August 1985 panels had significantly fewer mortalities than the other panel sets. No significant differences were evident in the November 1984, September 1985, October 1985 (but note, F = 3.63, P<0.05; 'S-N-K', P>0.05), and February 1986 data sets.

Although essentially the same patterns were evident in the results for the lower site, they were less consistent than those for the upper site. For example, in the December 1984 (F = 11.11, P<0.05), March 1985 (F = 10.86 or 7.92, P<0.05) and June 1985 (F = 7.57 or 6.60,

$P<0.05$ ('C & B', $P<0.05$)) data sets there were several significant differences among the panel sets. The highest-ranked, longest-immersed panel sets had significantly more mortalities than one or more of the lower-ranked, more recently-immersed sets. In June 1984 ($F = 19.41$, $P<0.05$), August 1984 ($F = 4.96$, $P<0.05$) and September 1985 ($F = 9.85$, $P<0.05$) significantly fewer mortalities were recorded on the most recently-immersed panels, and if the September 1985-initiated panels were excluded from the September 1985 analysis no significant differences were recorded between the panels. In September 1984 ($F = 11.42$, $P<0.05$) and August 1985 ($F = 9.40$ or 5.56, $P<0.05$ (' C & B ', $P<0.05$, for the complete data set)) the 2 most recently-immersed sets of panels had significantly fewer mortalities than the other panels; however, if the August 1985 panels were excluded from the August 1985 analysis, the lowest-ranked panels were significantly different from the 2 highest-ranked panel sets only. In the July 1984, October 1984, April 1985, May 1985, October 1985 (but note that for the complete data set, $F = 3.94$, $P<0.05$ ('C & B', $P<0.05$); 'S-N-K', $P>0.05$), January 1986, February 1986, and March 1986 data sets no significant differences were evident among the panels. Again, there appeared to be no relationship between the outcome of the statistical analysis and the month of the year.

TABLE 3.8 - Analysis of the number of sponge recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
JULY	3.78ns	ns	1.0 2.0 3.5 3.0	-	-	-
AUG.	6.66*	ns	4.5 3.0 1.0 2.0 4.0	-	-	-
SEPT.(1)	0.88ns	ns	1.0 3.0 5.0 2.0 4.0	-	-	-
OCT.	0.45ns	0.80* (2)	2.0 3.0 4.0 5.0 1.0	-	-	-
NOV.	-	-	-	-	-	-
DEC.	-	-	-	-	-	-
1985 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE(1)	(3)	(3)	0.5 1.5 2.5 3.5 4.5	(3)	(3)	1.5 2.5 3.5 4.5
AUG.	1.65ns	ns	4.5 1.5 2.5 0.5 3.5	3.13ns	ns	4.5 1.5 2.5 3.5
SEPT. (middle)	2.04ns	ns	4.5 0.5 2.5 3.5 1.5	2.20ns	ns	4.5 2.5 3.5 1.5
SEPT.(1) (end)	0.75ns	ns (2)	1.0 2.0 5.0 3.0 4.0	-	-	-
OCT.(1)	2.50ns	ns	2.0 1.0 4.0 5.0 3.0	-	-	-
NOV.	-	-	-	-	-	-
1986 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.9 - Analysis of the number of sponge mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
JULY	-	-	-	-	-	-
AUG.	4.36*	ns	3.0 1.0 2.0 4.5 4.0	-	-	-
SEPT.	6.78*	0.71* (2)	1.0 4.0 2.0 3.0 5.0	-	-	-
OCT.(1)	0.50ns	ns	1.0 2.0 3.0 4.0 5.0	-	-	-
NOV.(1)	0.80ns	0.80*	0.5 2.5 4.5 3.5 1.5	-	-	-
DEC.(1)	1.00ns	1.00*	0.5 1.5 3.5 4.5 2.5	1.00ns	1.00*	1.5 3.5 4.5 2.5
1985 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
AUG.(1)	6.25*	1.00*	0.5 1.5 3.5 4.5 2.5	6.25*	1.00*	1.5 3.5 4.5 2.5
SEPT. (middle)	7.46*	ns	0.5 2.5 3.5 4.5 1.5	4.59*	ns	2.5 3.5 4.5 1.5
SEPT. (end)	2.07ns	ns	3.0 4.0 1.0 2.0 5.0	-	-	-
OCT.(1)	1.64ns	ns (2)	2.0 3.0 1.0 4.0 5.0	-	-	-
NOV.(1)	1.00ns	ns (2)	2.0 3.0 4.0 5.0	-	-	-
1986 JAN.(1)	1.00ns	1.00*	3.5 4.5 5.5	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.10 - Analysis of the number of sponge recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	-	-	-	-	-	-
JULY	1.80ns	ns	2.0 3.0 1.0	-	-	-
AUG.	1.42ns	ns	1.0 4.0 2.0 3.0	-	-	-
SEPT.	-	-	-	-	-	-
OCT.(1)	1.00ns	1.00*	1.0 2.0 3.0 5.0 6.0 4.0	-	-	-
NOV.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 6.0	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH(1)	1.00ns	1.00*	1.0 2.5 4.5 5.5 6.5 3.5	1.00ns	1.00*	2.5 4.5 5.5 6.5 3.5
APRIL	-	-	-	-	-	-
MAY(1)	1.00ns	1.00*	1.0 2.0 3.0 4.5 6.5 5.5	-	-	-
JUNE	14.89*	0.72*	1.5 6.0 2.5 3.5 0.5 4.5	14.50*	0.87*	1.5 6.0 2.5 3.5 4.5
AUG.	0.90ns	ns(2)	5.5 3.5 2.5 0.5 1.5 4.5	1.06ns	ns(2)	5.5 3.5 2.5 1.5 4.5
SEPT.	20.46*	ns	0.5 4.5 5.5 2.5 3.5 1.5	17.29*	ns	4.5 5.5 2.5 3.5 1.5
OCT.(1)	2.60ns	0.78*	1.0 2.0 4.0 3.0 6.0 5.0	2.33ns	0.78*	2.0 4.0 3.0 6.0 5.0
1986 JAN.(1)	0.67ns	ns	4.5 5.5 3.5 6.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH(1)	1.00ns	ns	5.5 6.5	-	-	-

TABLE 3.11 - Analysis of the number of sponge mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	-	-	-	-	-	-
JULY	-	-	-	-	-	-
AUG.	2.74ns	ns(2)	1.0 3.0 4.0 2.0	-	-	-
SEPT.	3.75*	ns	1.0 2.0 3.0 5.0 4.0	-	-	-
OCT.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 6.0	-	-	-
NOV.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 5.0	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL(1)	1.00ns	1.00*	1.0 2.0 3.5 5.5 6.5 4.5	-	-	-
MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
AUG.	27.78*	0.67*(2)	0.5 1.5 3.5 4.5 5.5 2.5	25.90*	ns	1.5 3.5 4.5 5.5 2.5
SEPT.	1.33ns	ns	0.5 4.5 3.5 5.5 2.5 1.5	0.77ns	ns	4.5 3.5 5.5 2.5 1.5
OCT.(1)	6.97*	ns	1.0 2.0 4.0 6.0 5.0 3.0	6.08*	ns	2.0 4.0 6.0 5.0 3.0
1986 JAN.(1)	8.00*	1.00*	4.5 5.5 3.5 6.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

(b) Sponge Recruitment and Mortality:- (Tables 3.8. - 3.11.)

Sponge recruitment was more abundant between June and October, although at the lower site recruits were recorded in low numbers throughout much of the year. (See Tables 3.1. and 3.2.)

At neither site was there evidence of a marked overall pattern in the ranking of the panels in terms of the numbers of sponge recruits recorded. Instead there was considerable variability among the sampling periods, which was partly explained by the relatively low numbers of sponge recruits recorded during the study. During the periods of low recruitment, the smallest numbers of sponge recruits, if any, were generally recorded on the more recently-immersed panels. Furthermore, there were few incidences of significant differences in the numbers of sponge recruits recorded on the panels of different 'ages', and those that occurred were restricted to the periods of greater sponge recruitment. At the upper site, significant differences were only evident in the August 1984 (F = 6.66, P<0.05) and June 1985 (see Table 3.8.) data sets where the highest-ranked, longer-immersed panel sets had significantly more recruits than the others. Similarly, at the lower site during the periods of low sponge recruitment, none of the differences between the panels were significant. Differences were only observed during the periods of high recruitment, specifically in June 1985 (F = 14.89 or 14.50, P<0.05

('C & B', $P<0.05$)) and September 1985 (F = 20.46 or 17.29, $P<0.05$), where the 2 highest-ranked sets of panels, of differing immersion periods, had significantly more sponge recruits than the lower-ranked panel sets.

At both sites sponge mortalities were greatest during August and September (i.e. in the periods following peak sponge recruitment), fewer were recorded in winter and none in the spring/early summer months. Although there was no consistent pattern evident in the ranking of the mean number of sponge mortalities observed on the different panels, in general, the recently-immersed panels were lower-ranked than those immersed for longer periods; this pertained especially, but not exclusively, to the periods of low sponge mortality. At the upper site, significant differences among the panels were observed only in the months of greater sponge mortality. In September 1984 (F = 6.78, $P<0.05$) and August 1985 (F = 6.25, $P<0.05$ ('C & B', $P<0.05$)) the highest-ranked set of panels had significantly more sponge mortalities than were observed on the other panels. In the complete mid-September 1985 (F = 7.46, $P<0.05$) data set the highest-ranked sets of panels had significantly more mortalities than were observed on one or more of the lower-ranked sets, among which there were no significant differences; if, however, the recently initiated September 1985 panels were excluded from the analysis no significant differences were evident in the 'S-N-K' test, although a significant ANOVA F-value was obtained (F = 4.59, $P<0.05$). A similar situation occurred in August 1984 (F =

TABLE 3.12 - Analysis of the number of serpulid recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	9.60*	ns	1.0 2.5 2.0	-	-	-
JULY	15.12*	ns	1.0 2.0 3.0 3.5	-	-	-
AUG.	3.40ns	ns	1.0 4.5 2.0 3.0 4.0	-	-	-
SEPT.	0.64ns	ns	1.0 3.0 4.0 5.0 2.0	-	-	-
OCT.	0.55ns	ns	1.0 2.0 5.0 4.0 3.0	-	-	-
NOV.	4.37*	0.95*	0.5 1.5 4.5 3.5 2.5	-	-	-
DEC.	3.28ns	ns (2)	0.5 2.5 4.5 3.5 1.5	2.60ns	ns	2.5 4.5 3.5 1.5
1985 JAN.(1)	4.25*	ns (2)	1.0 3.0 4.0 2.0 5.0	-	-	-
FEB.	-	-	-	-	-	-
MARCH(1)	1.00ns	1.00*	0.5 1.5 3.0 4.0 5.0	1.00ns	1.00*	1.5 3.0 4.0 5.0
APRIL(1)	4.00*	1.00*	0.5 1.5 2.5 4.0 5.0	4.00ns	1.00*	1.5 2.5 4.0 5.0
MAY	24.92*	0.95*	0.5 1.5 3.5 2.5 5.0	24.15*	0.96*	1.5 3.5 2.5 5.0
JUNE	7.15*	0.82*	0.5 1.5 4.5 2.5 3.5	5.91*	0.82*	1.5 4.5 2.5 3.5
AUG.	23.13*	ns	0.5 4.5 1.5 2.5 3.5	4.77*	ns	4.5 1.5 2.5 3.5
SEPT. (middle)	1.40ns	0.81*	0.5 3.5 4.5 2.5 1.5	0.92ns	0.81*	3.5 4.5 2.5 1.5
SEPT. (end)	2.49ns	ns	1.0 5.0 4.0 3.0 2.0	-	-	-
OCT.	5.78*	0.74*	1.0 2.0 4.0 5.0 3.0	-	-	-
NOV.	4.07*	ns	3.0 2.0 4.0 5.0	-	-	-
1986 JAN.	1.21ns	0.95*	4.5 3.5 5.5	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.13 - Analysis of the number of serpulid mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE[1]	1.00ns	1.00*	1.0 2.5 2.0	-	-	-
JULY	1.52ns	ns	1.0 3.5 3.0 2.0	-	-	-
AUG.	19.11*	0.84*	1.0 2.0 4.0 3.0 4.5	-	-	-
SEPT.	40.40*	ns	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.	5.59*	0.90*	2.0 1.0 4.0 3.0 5.0	-	-	-
NOV.	3.19ns	0.98*	0.5 2.5 1.5 3.5 4.5	-	-	-
DEC.	4.49*	ns	0.5 1.5 2.5 3.5 4.5	3.19ns	ns	1.5 2.5 3.5 4.5
1985 JAN.	4.13*	0.78* [2]	1.0 2.0 4.0 3.0 5.0	-	-	-
FEB.[1]	2.22ns	0.78*	0.5 2.0 3.0 4.0 5.0	1.63ns	0.78*	2.0 3.0 4.0 5.0
MARCH[1]	6.75*	1.00*	0.5 1.5 3.0 4.0 5.0	6.75*	1.00*	1.5 3.0 4.0 5.0
APRIL	-	-	-	-	-	-
MAY	339.40*	0.70* [2]	0.5 1.5 2.5 3.5 5.0	336.40*	ns	1.5 2.5 3.5 5.0
JUNE	5.05*	0.85*	0.5 1.5 4.5 2.5 3.5	4.33*	0.86*	1.5 4.5 2.5 3.5
AUG.	12.22*	ns	0.5 3.5 4.5 2.5 1.5	3.20ns	ns	3.5 4.5 2.5 1.5
SEPT. (middle)	2.51ns	0.74* [2]	0.5 1.5 3.5 4.5 2.5	0.99ns	ns	1.5 3.5 4.5 2.5
SEPT. (end)	1.95ns	ns	1.0 2.0 4.0 5.0 3.0	-	-	-
OCT.	2.40ns	0.77*	1.0 2.0 4.0 5.0 3.0	-	-	-
NOV.	4.36*	0.80*	3.0 2.0 5.0 4.0	-	-	-
1986 JAN.	7.84*	ns	4.5 3.5 5.5	-	-	-
FEB.[1]	1.00ns	ns	5.5 4.5	-	-	-

TABLE 3.14 - Analysis of the number of serpulid recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	1.05ns	ns	2.0 1.0	-	-	-
JULY	0.04ns	ns	1.0 2.0 3.0	-	-	-
AUG.	1.01ns	0.83*	1.0 3.0 2.0 4.0	-	-	-
SEPT.	0.65ns	0.87*	3.0 4.0 1.0 2.0 5.0	-	-	-
OCT.	2.52ns	0.90*	2.0 5.0 3.0 4.0 6.0 1.0	-	-	-
NOV.	15.24*	ns	2.0 4.0 5.0 3.0 1.0 6.0	-	-	-
DEC.	4.52*	ns	2.0 3.0 1.0 5.0 6.0 4.0	-	-	-
1985 MARCH	0.86ns	ns	1.0 2.5 5.5 6.5 4.5 3.5	0.50ns	ns	2.5 5.5 6.5 4.5 3.5
APRIL(1)	1.00ns	1.00*	1.0 2.0 3.5 4.5 5.5 6.5	-	-	-
MAY(1)	16.00*	1.00*	1.0 2.0 4.5 5.5 6.5 3.0	-	-	-
JUNE	8.58*	0.96*	0.5 1.5 2.5 3.5 6.0 4.5	8.07*	0.96*	1.5 2.5 3.5 6.0 4.5
AUG.	13.34*	ns	0.5 1.5 4.5 3.5 5.5 2.5	6.68*	ns	1.5 4.5 3.5 5.5 2.5
SEPT.	1.73ns	0.72*	0.5 5.5 4.5 2.5 3.5 1.5	1.15ns	0.72*	5.5 4.5 2.5 3.5 1.5
OCT.	1.75ns	0.93*	2.0 1.0 4.0 6.0 5.0 3.0	1.62ns	0.93*	2.0 4.0 6.0 5.0 3.0
1986 JAN.	0.62ns	ns	4.5 3.5 5.5 6.5	-	-	-
FEB.	4.16ns	0.97*(2)	5.5 4.5 6.5	-	-	-
MARCH(1)	1.00ns	ns	6.5 5.5	-	-	-

TABLE 3.15 - Analysis of the number of serpulid mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	4.90ns	ns	2.0 1.0	-	-	-
JULY	2.88ns	ns	3.0 2.0 1.0	-	-	-
AUG.	9.53*	ns(2)	1.0 3.0 2.0 4.0	-	-	-
SEPT.	10.68*	ns(2)	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.	1.47ns	0.98*	1.0 2.0 4.0 3.0 5.0 6.0	-	-	-
NOV.	14.95*	0.74*(2)	1.0 4.0 3.0 5.0 6.0 2.0	-	-	-
DEC.	10.80*	ns	1.0 2.0 3.0 5.0 4.0 6.0	-	-	-
1985 MARCH	3.51*	ns	1.0 2.5 3.5 4.5 6.5 5.5	2.31ns	ns	2.5 3.5 4.5 6.5 5.5
APRIL	3.84*	0.87*	1.0 2.0 3.5 5.5 4.5 6.5	-	-	-
MAY(1)	1.33ns	ns	1.0 2.0 4.5 5.5 6.5 3.0	-	-	-
JUNE	5.15*	0.97*	0.5 3.5 2.5 1.5 6.0 4.5	4.83*	0.97*	3.5 2.5 1.5 6.0 4.5
AUG.	6.82*	0.63*	0.5 1.5 2.5 4.5 5.5 3.5	3.67*	ns	1.5 2.5 4.5 5.5 3.5
SEPT.	7.68*	ns	0.5 2.5 1.5 4.5 3.5 5.5	2.60ns	ns	2.5 1.5 4.5 3.5 5.5
OCT.	3.26*	0.83*	2.0 1.0 4.0 6.0 5.0 3.0	2.63ns	0.83*	2.0 4.0 6.0 5.0 3.0
1986 JAN.	2.01ns	0.96*	4.5 3.5 6.5 5.5	-	-	-
FEB.	2.33ns	0.99*	5.5 4.5 6.5	-	-	-
MARCH	1.14ns	ns	6.5 5.5	-	-	-

4.36, $P<0.05$; 'S-N-K', $P>0.05$). At the lower site, significant differences were evident during periods of high sponge mortality, for example, August 1985 (F = 27.78 or 25.90, $P<0.05$), and also in September 1984 (F = 3.75, $P<0.05$), although no differences were detected in the 'S-N-K' test over the latter period. Differences also occurred in October 1985 (F = 6.97 or 6.08, $P<0.05$) and January 1986 (F = 8.00, $P<0.05$ ('C & B', $P<0.05$)). Where significant differences among the panel sets were recorded, they were generally between one or both of the 2 highest-ranked panel sets and one or more of the lower-ranked sets, among which there were no significant differences.

(c) Serpulid Recruitment and Mortality:- (Tables 3.12. - 3.15.)

Spirorbids recruited most abundantly at the lower site, and were recorded throughout almost the whole study period, although recruitment declined to low numbers in the winter and spring months. Peak recruitment was recorded on panels between August and December. At the upper site, spirorbids were generally less abundant, and were not recorded on panels in the late winter; greatest numbers of spirorbid recruits were observed on the panels in September and October. The second serpulid species observed was *Pomatoceros triqueter* (L.), which also recruited in greatest abundance to panels immersed at the lower site. At both

sites *P.triqueter* recruits were observed on panels principally between June and December, with a peak in abundance in July - August. (See Tables 3.1. and 3.2.)

Although there was no consistent pattern among the sampling periods at both sites, in general, panels with the lowest numbers of serpulid recruits were those that had been most recently immersed, and in many instances the greatest numbers of recruits were recorded on panels immersed for intermediate periods (i.e. 2 to 4 months), otherwise most recruits were on the longest-immersed panels. At the upper site this pattern varied seasonally, the greatest numbers of recruits were observed on the longest-immersed panels in the winter/spring months when recruitment was at a low level and frequently no recruits were observed on the most recently-immersed panels. The pattern was more variable among the months at the lower site.

At the upper site, a number of significant differences were evident among the numbers of serpulid recruits recorded on the panels of different immersion periods. In July 1984 (F = 15.12, P<0.05) and August 1985 (F = 23.13 or 4.77, P<0.05) significantly fewer recruits were recorded on the lowest-ranked sets of panels, which in both cases included the most recently-immersed set. Conversely, in November 1984 (F = 4.37, P<0.05 ('C & B', P<0.05)), May 1985 (F = 24.92 or 24.15, P<0.05 ('C & B', P<0.05)), June 1985 (F = 7.15 or 5.91, P<0.05 ('C & B', P<0.05)), and October 1985 (F = 5.78, P<0.05 ('C & B',

$P<0.05$)) the highest-ranked set of panels, which was of a different immersion period in the different months, but was never the most recently-immersed set, had significantly more recruits than all the other panels. Similarly, in June 1984 ($F = 9.60$, $P<0.05$), January 1985 ($F = 4.25$, $P<0.05$), and November 1985 ($F = 4.07$, $P<0.05$), the highest-ranked set of panels had significantly more serpulid recruits than were observed on one or more of the lowest-ranked sets. In the other sampling periods there was no evidence of significant differences among the panels of varying 'ages' (but note for the complete April 1985 data set, $F = 4.00$, $P<0.05$ ('C & B', $P<0.05$); 'S-N-K', $P>0.05$). Therefore there were no patterns evident in the distribution of significant differences among the different months, i.e. significant differences among panels were recorded in months of low and high serpulid recruitment.

At the lower site, fewer significant differences were recorded among the panels of different 'ages', and there was no apparent relationship between the incidence of significant differences and the month, or extent, of serpulid recruitment. In all except one of the cases where significant differences arose, there were significantly more recruits on the highest-ranked panel set (which was often immersed for 5 or 6 months) than on any of the lower-ranked panels. This was the situation in November 1984 ($F = 15.24$, $P<0.05$), May 1985 ($F = 16.00$, $P<0.05$ ('C & B', $P<0.05$)), June 1985 ($F = 8.58$ or 8.07, $P<0.05$ ('C & B', $P<0.05$)), and August 1985 ($F =$

13.34, $P<0.05$). In the latter data set there were also significantly fewer recruits recorded on the most recently-immersed panels; if these were excluded from the analysis, the highest-ranked panel set had significantly more recruits than were observed on the 2 sets of lowest-ranked panels ($F = 6.68$, $P<0.05$). A similar situation arose in December 1984 ($F = 4.52$, $P<0.05$) which was the only other data set where significant differences among the panels were evident.

Serpulid mortalities were recorded throughout the year at the lower site, the lowest numbers occurred in the winter and early spring months. This was also the case at the upper site, except that no mortalities were observed in May 1984 or April 1985. Generally, the greatest number of mortalities occurred on the longest-immersed panels, and were less frequent on more recently-immersed panels. This pattern was particularly evident in the first year of the study at the upper site, but was less evident during the second year, and at the lower site. In these cases there was a tendency for a particular set of panels to dominate the high-ranking positions, for example, the July 1985 and August 1985 panels at the upper site, and the May 1984 and August 1985-initiated panels at the lower site. There were numerous significant differences evident among the differently 'aged' panels at both sites.

At the upper site, in September 1984 ($F = 40.40$, $P<0.05$), October 1984 ($F = 5.59$, $P<0.05$ ('C & B',

$P<0.05$)), March 1985 (F = 6.75, $P<0.05$ ('C & B', $P<0.05$)), May 1985 (F = 339.40 or 336.40, $P<0.05$), and January 1986 (F = 7.84, $P<0.05$), the highest-ranked panel set, which in each case was also the longest-immersed, had significantly more serpulid mortalities than were recorded on any of the other panels. Also, in September 1984, there was a significant difference between the second highest-ranked panel set and the 2 most recently initiated sets. In December 1984 (F = 4.49, $P<0.05$), January 1985 (F = 4.13, $P<0.05$), June 1985 (F = 5.05 or 4.33, $P<0.05$ ('C & B', $P<0.05$)), and August 1985 (F = 12.22, $P<0.05$) the highest-ranked panels, which in the first 2 sampling periods were also those which were immersed longest, had significantly more mortalities than were recorded on one or more of the lower-ranked panel sets. Also, in the August 1985 data set the August 1985 -initiated panels had significantly fewer mortalities than were recorded on the other panels. However, if the December 1984 and August 1985-initiated panels were excluded from their respective data sets, no significant differences were evident among the panels. In August 1984 (F = 19.11, $P<0.05$ ('C & B', $P<0.05$)) the 2 most recently-immersed panel sets had significantly fewer mortalities than the higher-ranked panels. In none of the other sampling periods was there evidence of significant differences between the panels of varying 'ages' (but note that for November 1985, F = 4.36, $P<0.05$ ('C & B', $P<0.05$); 'S-N-K', $P>0.05$). Thus there appeared to be no relationship between the incidence of

significant differences among the panels and the periods of high or low serpulid mortalities.

At the lower site, there were also a number of significant differences between the panels in terms of serpulid mortalities, but they were not generally as well-defined as those observed at the upper site. There were significantly fewer mortalities recorded on the most recently-immersed panels than on those immersed for longer periods in August 1984 (F = 9.53, P<0.05), September 1984 (F = 10.68, P<0.05), December 1984 (F = 10.80, P<0.05), and the complete data set in September 1985 (F = 7.68, P<0.05). However, in the latter case, no significant differences were evident if the September 1985 panels were excluded from the analysis. Conversely, in April 1985 (F = 3.84, P<0.05 ('C & B', P<0.05)), June 1985 (F = 5.15 or 4.83, P<0.05 ('C & B', P<0.05)), and August 1985 (F = 6.82 or 3.67, P<0.05 ('C & B', P<0.05, for the complete data set)) the high-ranking sets of panels, immersed for 4 to 6 months, had significantly more serpulid mortalities than were recorded on one or more of the lower-ranked, more recently-immersed panel sets. In the November 1984 (F = 14.95, P<0.05) data set, the recently-immersed October 1984 panels had significantly more mortalities than were observed on the other panels, among which there was a further significant difference between the longest-immersed and most recently initiated sets of panels. The October 1984 panels also had the greatest number of

TABLE 3.16 - Analysis of the number of barnacle recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	189.35*	ns	1.0 1.5	-	-	-
JUNE	101.70*	ns	1.0 2.0 2.5	-	-	-
JULY(1)	4.00ns	1.00*	1.0 2.0 3.0 3.5	-	-	-
AUG.	3.78*	ns	1.0 2.0 3.0 4.0 4.5	-	-	-
SEPT.(1)	1.00ns	1.00*	1.0 3.0 4.0 5.0 2.0	-	-	-
OCT.(1)	0.80ns	0.80*	3.0 4.0 5.0 1.0 2.0	-	-	-
NOV.(1)	1.00ns	1.00*	0.5 1.5 2.5 4.5 3.5	-	-	-
DEC.	-	-	-	-	-	-
1985 JAN.(1)	1.00ns	1.00*	1.0 2.0 4.0 5.0 3.0	-	-	-
FEB.	-	-	-	-	-	-
MARCH(1)	4.00*	1.00*	0.5 1.5 3.0 4.0 5.0	4.00ns	1.00*	1.5 3.0 4.0 5.0
APRIL	10.58*	0.99*	0.5 1.5 2.5 4.0 5.0	10.35*	0.99*	1.5 2.5 4.0 5.0
MAY	4.45*	ns (2)	1.5 2.5 3.5 0.5 5.0	12.60*	0.81* (2)	1.5 2.5 3.5 5.0
JUNE	1.80ns	ns	0.5 4.5 2.5 3.5 1.5	0.19ns	ns	4.5 2.5 3.5 1.5
AUG.	2.30ns	ns	0.5 1.5 2.5 4.5 3.5	1.64ns	ns	1.5 2.5 4.5 3.5
SEPT.(1) (middle)	4.83*	ns	0.5 1.5 3.5 2.5 4.5	3.28ns	ns	1.5 3.5 2.5 4.5
SEPT.(1) (end)	1.70ns	ns (2)	3.0 4.0 2.0 1.0 5.0	-	-	-
OCT.(1)	2.00ns	ns (2)	1.0 2.0 5.0 4.0 3.0	-	-	-
NOV.	-	-	-	-	-	-
1986 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.17 - Analysis of the number of barnacle mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	2.40ns	ns	1.0 2.0 2.5	-	-	-
JULY	15.07*	0.99*	1.0 2.0 3.0 3.5	-	-	-
AUG.	161.23*	0.83*	1.0 2.0 3.0 4.0 4.5	-	-	-
SEPT.	64.21*	0.99*	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.(1)	8.50*	1.00*	1.0 2.0 3.0 4.0 5.0	-	-	-
NOV.(1)	1.00ns	1.00*	0.5 2.5 3.5 4.5 1.5	-	-	-
DEC.(1)	1.00ns	1.00*	0.5 1.5 2.5 4.5 3.5	1.00ns	1.00*	1.5 2.5 4.5 3.5
1985 JAN.	-	-	-	-	-	-
FEB.(1)	1.00ns	1.00*	0.5 2.0 3.0 5.0 4.0	1.00ns	1.00*	2.0 3.0 5.0 4.0
MARCH	-	-	-	-	-	-
APRIL	75.34*	ns	0.5 1.5 2.5 4.0 5.0	73.76*	ns	1.5 2.5 4.0 5.0
MAY	37.42*	0.78*	0.5 1.5 2.5 3.5 5.0	36.39*	0.78*(2)	1.5 2.5 3.5 5.0
JUNE	1.71ns	ns	0.5 1.5 3.5 4.5 2.5	0.24ns	ns	1.5 3.5 4.5 2.5
AUG.	1.92ns	0.74*(2)	0.5 2.5 1.5 4.5 3.5	1.64ns	ns	2.5 1.5 4.5 3.5
SEPT. (middle)	1.46ns	1.00*	0.5 1.5 2.5 3.5 4.5	1.45ns	1.00*	1.5 2.5 3.5 4.5
SEPT. (end)	1.50ns	1.00*	1.0 3.0 4.0 2.0 5.0	-	-	-
OCT.(1)	1.00ns	1.00*	1.0 3.0 4.0 5.0 2.0	-	-	-
NOV.(1)	0.44ns	ns	2.0 3.0 5.0 4.0	-	-	-
1986 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.18 - Analysis of the number of barnacle recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	4.50ns	ns	2.0 1.0	-	-	-
JULY[1]	1.00ns	1.00*	1.0 2.0 3.0	-	-	-
AUG.[1]	1.00ns	1.00*	2.0 3.0 4.0 1.0	-	-	-
SEPT.	-	-	-	-	-	-
OCT.	-	-	-	-	-	-
NOV.	-	-	-	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL[1]	7.00*	0.75*	3.5 4.5 5.5 6.5 1.0 2.0	-	-	-
MAY	4.53*	ns	6.5 4.5 1.0 5.5 2.0 3.0	-	-	-
JUNE	3.24*	ns	0.5 6.0 2.5 1.5 3.5 4.5	0.35ns	ns	6.0 2.5 1.5 3.5 4.5
AUG.[1]	0.81ns	0.64*	0.5 2.5 1.5 3.5 4.5 5.5	0.61ns	ns	2.5 1.5 3.5 4.5 5.5
SEPT.[1]	0.81ns	0.64*	0.5 5.5 4.5 3.5 1.5 2.5	0.61ns	ns	5.5 4.5 3.5 1.5 2.5
OCT.[1]	3.20*	ns[2]	1.0 2.0 4.0 6.0 3.0 5.0	3.00ns	ns[2]	2.0 4.0 6.0 3.0 5.0
1986 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

TABLE 3.19 - Analysis of the number of barnacle mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	(a) COCHRAN'S TEST	(a) S-N-K	(b) ANOVA	(b) COCHRAN'S TEST	(b) S-N-K
1984 JUNE[1]	0 ns	ns	1.0 2.0	-	-	-
JULY[1]	4.00ns	1.00*	1.0 3.0 2.0	-	-	-
AUG.[1]	0.80ns	0.90*	2.0 3.0 1.0 4.0	-	-	-
SEPT.[1]	4.00*	1.00*	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.[1]	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 6.0	-	-	-
NOV.[1]	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 6.0	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL[1]	2.10ns	ns[2]	3.5 4.5 5.5 6.5 1.0 2.0	-	-	-
MAY[1]	2.97ns	ns	4.5 6.5 1.0 2.0 5.5 3.0	-	-	-
JUNE	9.09*	ns	0.5 1.5 2.5 3.5 6.0 4.5	7.41*	ns	1.5 2.5 3.5 6.0 4.5
AUG.	4.53*	0.72*[2]	0.5 1.5 2.5 4.5 3.5 5.5	4.02*	0.72*[2]	1.5 2.5 4.5 3.5 5.5
SEPT.[1]	0.84ns	0.80*	0.5 1.5 3.5 4.5 2.5 5.5	0.80ns	0.80*	1.5 3.5 4.5 2.5 5.5
OCT.[1]	1.33ns	ns	1.0 2.0 4.0 3.0 5.0 6.0	1.17ns	ns	2.0 4.0 3.0 5.0 6.0
1986 JAN.[1]	1.00ns	1.00*	3.5 4.5 6.5 5.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

serpulid recruits in the previous sampling period. These results are thus illustrative of the high post-settlement mortality characteristic of this study. There were no other significant differences recorded (but note that for the complete data sets in March 1985, $F = 3.51$, $P<0.05$, 'S-N-K', $P>0.05$; and October 1985, $F = 3.26$, $P<0.05$ ('C & B', $P<0.05$), 'S-N-K', $P>0.05$). Thus the presence of significant differences between the panels of varying 'ages' apparently varied among the sampling periods irrespective of the season, and consequently, irrespective of the numbers of serpulid mortalities recorded.

(d) Barnacle Recruitment and Mortality:- (Tables 3.16. - 3.19.)

The barnacles *Semibalanus* spp. (= *S.balanoides* (L.) and *S.crenatus* (Bruguière)), *Elminius modestus* Darwin and *Verruca stroemia* (O.F. Müller) were recorded primarily between April/May and October/November during the study period, and in greatest abundance at the upper site. *Semibalanus* spp. recruited most abundantly during the months of May and June; and low numbers of the other 2 species were recorded irregularly during the whole period. (See Tables 3.1. and 3.2.)

Although in many of the sampling periods, at both sites, fewer barnacle recruits were recorded on the more recently-immersed panels than on those immersed for longer periods, the pattern was not consistent

throughout. Exceptions of particular interest were the panels initiated at the upper site in April 1984 and May 1985 during the period of greatest barnacle recruitment. These panels were consistently highest-ranked for the duration of their respective immersion periods, i.e. the April 1984 panels had the greatest number of barnacle recruits from May 1984 through to the end of August 1984, and similarly, for the May 1985 panels between mid-June 1985 and the end of September 1985. These results suggested that initially barnacle cyprids recruited preferentially onto recently-immersed substrata, after which gregarious settlement behaviour may have been important. A similar pattern was evident for the panels initiated in February 1985 at the lower site, which had the greatest numbers of recruits from April 1985 through to June 1985.

At both sites, the majority of the significant differences between the numbers of barnacle recruits recorded on the panels of varying 'ages', occurred during the periods of greatest recruitment. At the upper site, in the spring/summer of 1984, the April 1984-initiated panel set had significantly more barnacle recruits than the other panels in May 1984 (F = 189.35, $P<0.05$) and June 1984 (F = 101.70, $P<0.05$). In August 1984 (F = 3.78, $P<0.05$) significantly more recruits were recorded on the April 1984 panels than on the newly-immersed August 1984 panels. In the spring/summer of 1985 the only significant difference concerning the May 1985-initiated panels occurred in mid-September 1985 (F =

4.83, $P<0.05$), where significantly more recruits were recorded on these panels than on the 2 most recently-immersed sets. Nonetheless, when the September 1985- initiated panels were excluded from the analysis, no significant differences were evident among the panels. The other significant differences occurred in April 1985 (F = 10.58 or 10.35, $P<0.05$ ('C & B', $P<0.05$)), and May 1985 (F = 4.45 or 12.60, $P<0.05$), where the longest-immersed set of panels, in both cases, had significantly more recruits than the other sets. However, if the newly-immersed May 1985 panels were included in the May 1985 analysis, there were no significant differences between these and the longest-immersed panel set. At none of the other sampling dates were significant differences evident (but note that for the complete data set in March 1985, F = 4.00, $P<0.05$ ('C & B', $P<0.05$); 'S-N-K', $P>0.05$).

At the lower site, significant differences among the numbers of barnacle recruits recorded were observed only during the periods of greatest settlement in the spring of 1985, i.e. April 1985 (F = 7.00, $P<0.05$ ('C & B', $P<0.05$)), May 1985 (F = 4.53, $P<0.05$) and June 1985 (F = 3.24, $P<0.05$), although if the newly initiated June 1985 panels were excluded from the analysis in the last period there were no significant differences between the panels. For each of these sampling periods significantly more recruits were recorded on the February 1985-initiated panels than on one or more of the lower-ranked panel

sets. There were no further significant differences evident in any of the other sampling periods (but note that for the complete data set in October 1985, $F = 3.20$, $P<0.05$; 'S-N-K', $P>0.05$).

Barnacle mortalities were recorded during most months of the study except during the winter/early spring period. At the lower site, most mortalities were recorded between June and August, and at the upper site, between April/May and September, i.e. closely related to the periods of greatest barnacle recruitment. At both sites an overall pattern was for most mortalities to be recorded on the longest-immersed panels and the most recently-immersed panels were lowest-ranked; frequently no mortalities were observed on the lowest-ranked panels. As with the recruitment data, however, the highest-ranked position was often dominated by those panels on which recruitment was most abundant, i.e. the April 1984 and May 1985 panel sets at the upper site, and those immersed in February 1985 at the lower site. There were relatively few statistically significant differences evident between panels of varying 'ages', at either site. At the upper site, significant differences occurred principally during the periods of greatest barnacle mortality; *viz.* July 1984 ($F = 15.07$, $P<0.05$ ('C & B', $P<0.05$)), August 1984 ($F = 161.23$, $P<0.05$ ('C & B', $P<0.05$)), September 1984 ($F = 64.21$, $P<0.05$ ('C & B', $P<0.05$)), October 1984 ($F = 8.50$, $P<0.05$ ('C & B', $P<0.05$)), April 1985 ($F = 75.34$ or 73.76, $P<0.05$), and May 1985 ($F = 37.42$ or 36.39, $P<0.05$ ('C & B', $P<0.05$,

TABLE 3.20 - Analysis of the number of anomiid recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	(a) COCHRAN'S TEST	(a) S-N-K	(b) ANOVA	(b) COCHRAN'S TEST	(b) S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
JULY	-	-	-	-	-	-
AUG.	-	-	-	-	-	-
SEPT.	-	-	-	-	-	-
OCT.(1)	1.00ns	1.00*	2.0 3.0 4.0 5.0 1.0	-	-	-
NOV.	-	-	-	-	-	-
DEC.(1)	0.88ns	0.94* (2)	0.5 1.5 4.5 2.5 3.5	0.84ns	0.94* (2)	1.5 4.5 2.5 3.5
1985 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
AUG.(1)	0.50ns	ns	0.5 1.5 2.5 3.5 4.5	0.33ns	ns	1.5 2.5 3.5 4.5
SEPT. (middle)	3.91*	ns	0.5 3.5 2.5 4.5 1.5	2.98ns	ns	3.5 2.5 4.5 1.5
SEPT. (end)	0.90ns	0.81*	4.0 5.0 1.0 2.0 3.0	-	-	-
OCT.	32.93*	0.73*	1.0 5.0 2.0 4.0 3.0	-	-	-
NOV.(1)	3.17ns	ns	2.0 3.0 4.0 5.0	-	-	-
1986 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.21 - Analysis of the number of anomiid mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
JULY	-	-	-	-	-	-
AUG.	-	-	-	-	-	-
SEPT.	-	-	-	-	-	-
OCT.	-	-	-	-	-	-
NOV.	-	-	-	-	-	-
DEC.	-	-	-	-	-	-
1985 JAN.(1)	0.85ns	0.90*	1.0 2.0 3.0 4.0 5.0	-	-	-
FEB.(1)	1.00ns	1.00*	0.5 2.0 3.0 4.0 5.0	1.00ns	1.00*	2.0 3.0 4.0 5.0
MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
AUG.	-	-	-	-	-	-
SEPT.(1) (middle)	2.07ns	0.91* (2)	0.5 2.5 3.5 4.5 1.5	1.95ns	0.91* (2)	2.5 3.5 4.5 1.5
SEPT.(1) (end)	0.85ns	0.90*	1.0 4.0 5.0 3.0 2.0	-	-	-
OCT.	1.14ns	0.85*	1.0 5.0 3.0 2.0 4.0	-	-	-
NOV.	25.91*	ns (2)	2.0 3.0 5.0 4.0	-	-	-
1986 JAN.	3.67ns	ns	3.5 4.5 5.5	-	-	-
FEB.(1)	1.00ns	ns	4.5 5.5	-	-	-

TABLE 3.22 - Analysis of the number of anomiid recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	(a) COCHRAN'S TEST	(a) S-N-K	(b) ANOVA	(b) COCHRAN'S TEST	(b) S-N-K
1984 JUNE	-	-	-	-	-	-
JULY	-	-	-	-	-	-
AUG.	-	-	-	-	-	-
SEPT.	-	-	-	-	-	-
OCT.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 6.0 5.0	-	-	-
NOV.	-	-	-	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
AUG.(1)	0.80ns	ns(2)	0.5 1.5 3.5 4.5 2.5 5.5	0.75ns	ns(2)	1.5 3.5 4.5 2.5 5.5
SEPT.	2.43ns	ns(2)	5.5 0.5 1.5 4.5 2.5 3.5	2.28ns	ns(2)	5.5 1.5 4.5 2.5 3.5
OCT.	6.48*	0.87*	2.0 6.0 1.0 3.0 4.0 5.0	6.54*	0.89*	2.0 6.0 3.0 4.0 5.0
1986 JAN.(1)	1.00ns	1.00*	3.5 4.5 5.5 6.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

TABLE 3.23 - Analysis of the number of anomiid mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	-	-	-	-	-	-
JULY	-	-	-	-	-	-
AUG.	-	-	-	-	-	-
SEPT.	-	-	-	-	-	-
OCT.	-	-	-	-	-	-
NOV.	-	-	-	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
AUG.	-	-	-	-	-	-
SEPT.(1)	1.33ns	ns	0.5 4.5 5.5 2.5 3.5 1.5	1.17ns	ns	4.5 5.5 2.5 3.5 1.5
OCT.	2.18ns	0.94*	1.0 2.0 3.0 6.0 4.0 5.0	1.92ns	0.94*	2.0 3.0 6.0 4.0 5.0
1986 JAN.(1)	0.89ns	ns	4.5 3.5 5.5 6.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH(1)	1.00ns	ns	6.5 5.5	-	-	-

for the complete data set)). In each case the longest-immersed, highest-ranked panel set had significantly more mortalities than the other panels. In these data sets the heterogeneous variances (i.e. significant Cochran and Bartlett's tests) arose because on the panels with greatest barnacle recruitment there were a large and variable number of mortalities recorded which were being compared, in the analysis, with panels on which only low numbers of mortalities were observed. At the lower site, significant *F*-values were obtained in September 1984 (F = 4.00, $P<0.05$ ('C & B', $P<0.05$)), June 1985 (F = 9.09 or 7.41, $P<0.05$) and August 1985 (F = 4.53 or 4.02, $P<0.05$), i.e. the periods of greatest barnacle mortality, but only in June 1985 were significant differences between the panels detected in the 'S-N-K' test. In June 1985 significantly more mortalities were recorded on the highest-ranked, February 1985-initiated panels, than on the 2 or 3 most recently-immersed sets, depending on whether the June 1985 panels were included in the analysis or not.

(e) Anomiid Recruitment and Mortality:- (Tables 3.20. - 3.23.)

Relatively few anomiids were recorded during the study period, and the greatest numbers occurred in the second year. They were recorded on the panels principally between August and November, in both years and at both sites. Peak abundance occurred in October 1985. During the periods of low anomiid recruitment,

recruits were observed sporadically, on only 1 or 2 of the panels immersed at that time. Anomiids were most frequently observed on panels at the upper site. (See Tables 3.1. and 3.2.)

At the lower site, anomiid recruits were recorded more frequently on the longer-immersed panels, than on those immersed for shorter intervals. In all the sampling periods where anomiids were recorded, no recruits were observed on one or more of the lowest-ranked, and often most recently-immersed, panel sets. Conversely, at the upper site, there was no consistent pattern; panel sets of all immersion periods were variably ranked in the different sampling intervals. For example, in October 1984 recruits were only recorded on the October 1984-initiated panels, and in August 1985 the greatest numbers of recruits occurred on the longest-immersed April 1985-initiated panels. The only significant differences among the numbers of anomiid recruits recorded on the different panel sets occurred, at both sites, during the period of greatest recruitment in October 1985 (but note that for the complete data set in mid-September 1985, at the upper site, $F = 3.91$, $P<0.05$; 'S-N-K', $P>0.05$). At both the upper and lower sites in October 1985 ($F = 32.93$, $P<0.05$; $F = 6.48$ or 6.54, $P<0.05$, respectively ('C & B', $P<0.05$ in all cases)), the highest-ranked panel set (that initiated in August 1985 at the upper site and June 1985 at the lower) had significantly more anomiid recruits than were recorded on any of the other panels.

TABLE 3.24 - Analysis of the number of hydroid recruits recorded on the panels of different immersion periods (i.e. 'age) at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	2.12ns	ns	1.5 1.0	-	-	-
JUNE	3.26ns	ns	1.0 2.0 2.5	-	-	-
JULY	4.44*	0.87* (2)	2.0 1.0 3.5 3.0	-	-	-
AUG.(1)	0.27ns	ns	1.0 3.0 2.0 4.5 4.0	-	-	-
SEPT.(1)	1.67ns	ns	2.0 5.0 1.0 3.0 4.0	-	-	-
OCT.(1)	0.58ns	ns (2)	3.0 5.0 1.0 2.0 4.0	-	-	-
NOV.(1)	2.00ns	ns (2)	1.5 2.5 4.5 3.5 0.5	-	-	-
DEC.(1)	1.00ns	1.00*	0.5 2.5 3.5 4.5 1.5	1.00ns	1.00*	2.5 3.5 4.5 1.5
1985 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-
APRIL(1)	25.00*	1.00*	0.5 1.5 2.5 4.0 5.0	25.00*	1.00*	1.5 2.5 4.0 5.0
MAY	4.46*	0.69* (2)	0.5 1.5 3.5 2.5 5.0	4.10*	ns	1.5 3.5 2.5 5.0
JUNE	2.30ns	0.97*	0.5 4.5 2.5 3.5 1.5	2.12ns	0.97*	4.5 2.5 3.5 1.5
AUG.	6.67*	ns (2)	0.5 4.5 1.5 2.5 3.5	5.44*	ns	4.5 1.5 2.5 3.5
SEPT.(1) (middle)	0.80ns	0.93* (2)	0.5 2.5 1.5 3.5 4.5	0.73ns	0.93* (2)	2.5 1.5 3.5 4.5
SEPT.(1) (end)	0.85ns	0.90*	1.0 2.0 4.0 3.0 5.0	-	-	-
OCT.(1)	0.50ns	ns	5.0 2.0 4.0 1.0 3.0	-	-	-
NOV.(1)	1.00ns	1.00*	3.0 4.0 5.0 2.0	-	-	-
1986 JAN.(1)	1.00ns	1.00*	4.5 5.5 3.5	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.25 - Analysis of the number of hydroid mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	16.79*	ns	1.0 2.5 2.0	-	-	-
JULY	5.98*	ns	1.0 2.0 3.0 3.5	-	-	-
AUG.	7.40*	0.88* (2)	1.0 3.0 2.0 4.0 4.5	-	-	-
SEPT.(1)	1.68ns	0.93*	1.0 2.0 4.0 3.0 5.0	-	-	-
OCT.(1)	1.08ns	ns	3.0 1.0 2.0 4.0 5.0	-	-	-
NOV.(1)	0.75ns	ns (2)	1.5 2.5 3.5 0.5 4.5	-	-	-
DEC.(1)	0.58ns	ns (2)	0.5 2.5 3.5 4.5 1.5	0.44ns	ns	2.5 3.5 4.5 1.5
1985 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY(1)	1.50ns	ns (2)	0.5 5.0 2.5 3.5 1.5	1.27ns	ns	5.0 2.5 3.5 1.5
JUNE	1.38ns	0.95*	0.5 2.5 4.5 3.5 1.5	1.24ns	0.95*	2.5 4.5 3.5 1.5
AUG.	3.08ns	0.94*	0.5 1.5 2.5 4.5 3.5	2.74ns	0.94*	1.5 2.5 4.5 3.5
SEPT.(1) (middle)	6.75*	1.00*	0.5 1.5 2.5 3.5 4.5	6.75*	1.00*	1.5 2.5 3.5 4.5
SEPT.(1) (end)	4.70*	0.80*	1.0 3.0 4.0 2.0 5.0	-	-	-
OCT.(1)	1.67ns	ns	2.0 3.0 4.0 1.0 5.0	-	-	-
NOV.(1)	2.00ns	ns	3.0 2.0 5.0 4.0	-	-	-
1986 JAN.(1)	0.60ns	ns	5.5 3.5 4.5	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.26 - Analysis of the number of hydroid recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	0.44ns	ns	2.0 1.0	-	-	-
JULY	4.20ns	ns	2.0 1.0 3.0	-	-	-
AUG.(1)	0.61ns	ns	3.0 4.0 2.0 1.0	-	-	-
SEPT.(1)	3.00ns	ns(2)	1.0 2.0 5.0 3.0 4.0	-	-	-
OCT.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 6.0	-	-	-
NOV.(1)	1.00ns	1.00*	2.0 3.0 4.0 5.0 6.0 1.0	-	-	-
DEC.	-	-	-	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL(1)	(3)	(3)	1.0 3.5 4.5 5.5 6.5 2.0	-	-	-
MAY	3.66*	ns	2.0 5.5 1.0 6.5 3.0 4.5	-	-	-
JUNE	3.86*	ns	0.5 6.0 1.5 3.5 2.5 4.5	2.31ns	ns	6.0 1.5 3.5 2.5 4.5
AUG.(1)	2.97ns	ns	0.5 4.5 1.5 5.5 2.5 3.5	2.50ns	ns	4.5 1.5 5.5 2.5 3.5
SEPT.(1)	1.00ns	1.00*	0.5 1.5 2.5 4.5 5.5 3.5	1.00ns	1.00*	1.5 2.5 4.5 5.5 3.5
OCT.(1)	7.50*	0.67*	3.0 4.0 5.0 2.0 6.0 1.0	0.75ns	ns(2)	3.0 4.0 5.0 2.0 6.0
1986 JAN.	-	-	-	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

TABLE 3.27 - Analysis of the number of hydroid mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	0.34ns	ns	1.0 2.0	-	-	-
JULY	24.42*	0.90*(2)	1.0 2.0 3.0	-	-	-
AUG.	2.84ns	0.91*(2)	1.0 2.0 3.0 4.0	-	-	-
SEPT.(1)	1.00ns	ns	1.0 3.0 4.0 5.0 2.0	-	-	-
OCT.(1)	1.64ns	ns(2)	1.0 2.0 3.0 5.0 6.0 4.0	-	-	-
NOV.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0 6.0	-	-	-
DEC.(1)	1.00ns	1.00*	1.0 3.0 4.0 5.0 6.0 2.0	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL(1)	1.00ns	1.00*	1.0 3.5 4.5 5.5 6.5 2.0	-	-	-
MAY(1)	0.84ns	0.80*	2.0 4.5 5.5 6.5 3.0 1.0	-	-	-
JUNE	7.17*	ns	0.5 3.5 1.5 2.5 6.0 4.5	4.66*	ns	3.5 1.5 2.5 6.0 4.5
AUG.	3.61*	ns	0.5 1.5 2.5 3.5 4.5 5.5	2.81ns	ns	1.5 2.5 3.5 4.5 5.5
SEPT.(1)	3.25*	ns	0.5 1.5 2.5 3.5 5.5 4.5	2.88ns	ns	1.5 2.5 3.5 5.5 4.5
OCT.(1)	5.03*	ns(2)	2.0 3.0 4.0 6.0 5.0 1.0	1.00ns	1.00*	2.0 3.0 4.0 6.0 5.0
1986 JAN.(1)	0.67ns	ns	5.5 6.5 3.5 4.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

During the first year no mortalities were recorded at the lower site, and only low numbers in January and February 1985 at the upper site. Most anomiid mortalities occurred, at both sites, between September and February in the second year. There was no consistent pattern in the ranking of the mean numbers of anomiid mortalities recorded on the panels of differing 'ages' at either site. In many instances, no mortalities were recorded on the lower-ranked panels irrespective of the duration of immersion. Furthermore, no statistically significant differences between the panels were recorded for any of the sampling dates at the lower site, and for only one at the upper site. In November 1985 ($F = 25.91$, $P<0.05$) significantly more mortalities were observed on the August 1985-initiated panels than for any of the other panel sets; the August 1985 panels had significantly more anomiid recruits than the other panels in the previous sampling period.

(f) Hydroid Recruitment and Mortality:- (Tables 3.24. - 3.27.)

Hydroids (predominantly *Dynamena* and *Campanularia* species) were present on panels immersed at both sites, primarily between May and November/December, although they also occurred, in relatively low numbers, during the winter and spring at the lower site. They were recorded in greatest abundance on panels during May and

June, and were also relatively abundant in July at the lower site. (See Tables 3.1. and 3.2.)

There were no consistent patterns evident in the ranking of the differently 'aged' panels, on the basis of the numbers of hydroid recruits recorded. Panels of all immersion durations were ranked in various positions in the different sampling periods. During periods of low hydroid recruitment any potential pattern was disrupted because many of the panels had so few recruits. A characteristic pattern evident in the data for the upper site was for hydroids to recruit in greatest abundance onto a particular set of panels, which were subsequently highest-ranked for most of the duration of the immersion period, for example, the panels initiated in May 1984 and 1985. These panel sets were characterized by relatively high densities of barnacle recruits, onto which many of the hydroids recruited.

Both sites were characterized by data sets for hydroid recruitment among which relatively few significant differences were evident. At the upper site, in April 1985 (F = 25.00, $P<0.05$ ('C & B', $P<0.05$)) and May 1985 (F = 4.46 or 4.10, $P<0.05$ (but note that for the incomplete data set, 'S-N-K', $P>0.05$)), the highest-ranked, longest-immersed panel sets had significantly more hydroid recruits than were observed on the other panels. In August 1985 (F = 6.67 or 5.44, $P<0.05$) the highest-ranked panel set had significantly more recruits than were recorded on 1 or 3 of the lower-ranked panel

sets, depending on whether or not the newly-immersed panels were excluded from the analysis. The only other significant *F*-value was obtained in July 1984 ($F = 4.44$, $P<0.05$), but no significant differences among the panels were detected in the 'S-N-K' test. Similarly, there were few significant differences evident at the lower site. In April 1985 (see Table 3.26.) and the complete October 1985 ($F = 7.50$, $P<0.05$ ('C & B', $P<0.05$)) data set, significantly more hydroid recruits were recorded on the recently initiated February 1985 and October 1985 panels respectively; in April 1985, the February 1985 panels were the only ones on which recruits were observed. If the October 1985 panels were, however, excluded from the October 1985 analysis no significant differences were evident between the panels. In May 1985 ($F = 3.66$, $P<0.05$) and June 1985 ($F = 3.86$, $P<0.05$) the highest-ranked panel sets had significantly more hydroid recruits than 1 or 2 of the lowest-ranked sets. However, if the newly-immersed June 1985 panels were excluded from the June 1985 analysis, there were no significant differences between the panels. There were no other significant differences. Thus, at both sites, significant differences between the panels of various 'ages' appeared to be independent of the month of sampling, and consequently of the numbers of hydroids recruiting to the panels.

Hydroid mortalities were generally recorded between May/June and December/January at both sites, and in

greatest frequency between June and August, i.e. immediately following the peak recruitment period. At the upper site, in both years, the panels initiated in April and May, which had the greatest numbers of hydroid recruits for the duration of their immersion, were also highest-ranked over several sampling periods, in terms of the numbers of hydroid mortalities recorded. During the periods of high hydroid mortality, at both sites, in general the longer-immersed panels had more hydroid mortalities than those which were immersed for shorter periods; this pattern was not, however, absolutely consistent. During periods of lower hydroid mortality, the low numbers and complete absence of mortalities from a number of panels disrupted the overall pattern, although in general, greater numbers of mortalities were recorded on the longer-immersed panels. As with hydroid recruitment, there were relatively few significant differences evident in the data sets, and they were not restricted to a particular sampling period or intensity of hydroid mortality. In June 1984 (F = 16.79, $P<0.05$), August 1984 (F = 7.40, $P<0.05$), mid-September 1985 (F = 6.75, $P<0.05$ ('C & B', $P<0.05$)), and late-September 1985 (F = 4.70, $P<0.05$ ('C & B', $P<0.05$)) at the upper site, the highest-ranked panel sets, which in all except the first sampling period were also the longest-immersed panels, had significantly more mortalities than were observed on the other panels. The only other significant difference occurred in July 1984 (F = 5.98, $P<0.05$), where the 2 highest-ranked, longest-immersed sets of

TABLE 3.28 - Analysis of the number of ctenostome recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	0 ns	ns	1.0 1.5	-	-	-
JUNE	0.10ns	ns	1.0 2.0 2.5	-	-	-
JULY(1)	1.83ns	ns	1.0 2.0 3.5 3.0	-	-	-
AUG.(1)	1.00ns	1.00*	1.0 3.0 4.0 4.5 2.0	-	-	-
SEPT.	-	-	-	-	-	-
OCT.	-	-	-	-	-	-
NOV.	-	-	-	-	-	-
DEC.	10.19*	ns	0.5 1.5 4.5 2.5 3.5	7.70*	ns	1.5 4.5 2.5 3.5
1985 JAN.	3.42ns	ns	1.0 2.0 3.0 5.0 4.0	-	-	-
FEB.	10.42*	ns	0.5 2.0 5.0 4.0 3.0	7.64*	ns	2.0 5.0 4.0 3.0
MARCH(1)	0.58ns	ns (2)	0.5 1.5 4.0 5.0 3.0	0.44ns	ns	1.5 4.0 5.0 3.0
APRIL	13.10*	0.77* (2)	1.5 0.5 2.5 5.0 4.0	11.38*	0.77* (2)	1.5 2.5 5.0 4.0
MAY(1)	0.92ns	0.97* (2)	0.5 1.5 2.5 3.5 5.0	0.86ns	0.97* (2)	1.5 2.5 3.5 5.0
JUNE	0.77ns	0.82* (2)	0.5 2.5 3.5 4.5 1.5	0.61ns	0.82* (2)	2.5 3.5 4.5 1.5
AUG.	1.02ns	0.93* (2)	1.5 4.5 0.5 3.5 2.5	1.06ns	0.96* (2)	1.5 4.5 3.5 2.5
SEPT.(1) (middle)	0.75ns	ns (2)	0.5 2.5 3.5 1.5 4.5	0.67ns	ns	2.5 3.5 1.5 4.5
SEPT. (end)	-	-	-	-	-	-
OCT.(1)	2.82ns	0.82*	2.0 5.0 1.0 3.0 4.0	-	-	-
NOV.	2.57ns	ns	3.0 4.0 2.0 5.0	-	-	-
1986 JAN.	35.64*	ns	4.5 3.5 5.5	-	-	-
FEB.	0.85ns	ns	5.5 4.5	-	-	-

TABLE 3.29 - Analysis of the number of ctenostome mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	5.62*	ns	2.5 2.0 1.0	-	-	-
JULY	2.30ns	ns	1.0 2.0 3.0 3.5	-	-	-
AUG.(1)	1.00ns	0.90*	1.0 2.0 3.0 4.0 4.5	-	-	-
SEPT.(1)	1.00ns	1.00*	1.0 2.0 4.0 5.0 3.0	-	-	-
OCT.	-	-	-	-	-	-
NOV.	-	-	-	-	-	-
DEC.	-	-	-	-	-	-
1985 JAN.	3.85*	ns	1.0 3.0 2.0 4.0 5.0	-	-	-
FEB.	8.32*	0.93*	0.5 2.0 3.0 4.0 5.0	8.19*	0.93* (2)	2.0 3.0 4.0 5.0
MARCH(1)	4.67*	ns	0.5 1.5 3.0 4.0 5.0	3.89ns	ns	1.5 3.0 4.0 5.0
APRIL(1)	5.00*	ns (2)	0.5 1.5 2.5 4.0 5.0	3.97ns	ns	1.5 2.5 4.0 5.0
MAY	14.42*	0.88* (2)	0.5 2.5 1.5 3.5 5.0	13.11*	0.88* (2)	2.5 1.5 3.5 5.0
JUNE(1)	1.17ns	ns	0.5 2.5 1.5 3.5 4.5	0.89ns	ns	2.5 1.5 3.5 4.5
AUG.(1)	0.80ns	0.80*	0.5 1.5 4.5 3.5 2.5	0.73ns	0.80*	1.5 4.5 3.5 2.5
SEPT.(1) (middle)	0.50ns	ns	0.5 2.5 1.5 3.5 4.5	0.33ns	ns	2.5 1.5 3.5 4.5
SEPT.(1) (end)	0.75ns	ns (2)	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.(1)	1.00ns	1.00*	1.0 2.0 3.0 4.0 5.0	-	-	-
NOV.(1)	0.44ns	ns	3.0 2.0 4.0 5.0	-	-	-
1986 JAN.	3.57ns	0.92*	5.5 4.5 3.5	-	-	-
FEB.	0.02ns	ns	5.5 4.5	-	-	-

TABLE 3.30 - Analysis of the number of ctenostome recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	315.06*	ns	1.0 2.0	-	-	-
JULY	2.75ns	ns	1.0 2.0 3.0	-	-	-
AUG.	-	-	-	-	-	-
SEPT.	-	-	-	-	-	-
OCT.(1)	2.20ns	0.75*	1.0 3.0 4.0 6.0 5.0 2.0	-	-	-
NOV.	3.47*	ns	2.0 6.0 1.0 4.0 3.0 5.0	-	-	-
DEC.	0.98ns	ns	5.0 1.0 4.0 6.0 2.0 3.0	-	-	-
1985 MARCH	2.98ns	0.64*(2)	1.0 5.5 3.5 2.5 6.5 4.5	2.10ns	ns	5.5 3.5 2.5 6.5 4.5
APRIL(1)	13.80*	ns	1.0 6.5 3.5 4.5 5.5 2.0	-	-	-
MAY	3.25*	0.62*	2.0 6.5 1.0 3.0 4.5 5.5	-	-	-
JUNE	2.00ns	ns	0.5 1.5 2.5 3.5 6.0 4.5	1.62ns	ns	1.5 2.5 3.5 6.0 4.5
AUG.	1.46ns	0.72*(2)	0.5 1.5 4.5 5.5 3.5 2.5	1.09ns	0.72*(2)	1.5 4.5 5.5 3.5 2.5
SEPT.(1)	1.00ns	1.00*	0.5 2.5 3.5 4.5 5.5 1.5	1.00ns	1.00*	2.5 3.5 4.5 5.5 1.5
OCT.	6.15*	0.97*	1.0 2.0 3.0 6.0 4.0 5.0	6.16*	0.98*	2.0 3.0 6.0 4.0 5.0
1986 JAN.	1.37ns	ns	3.5 4.5 6.5 5.5	-	-	-
FEB.	1.66ns	0.93*(2)	4.5 5.5 6.5	-	-	-
MARCH	0.68ns	ns	6.5 5.5	-	-	-

TABLE 3.31 - Analysis of the number of ctenostome mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	98.94*	ns	1.0 2.0	-	-	-
JULY	51.04*	ns	1.0 2.0 3.0	-	-	-
AUG.	3.85ns	0.84*	1.0 2.0 3.0 4.0	-	-	-
SEPT.(1)	2.12ns	0.75*	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.	-	-	-	-	-	-
NOV.(1)	2.10ns	ns(2)	1.0 2.0 4.0 6.0 5.0 3.0	-	-	-
DEC.(1)	1.00ns	1.00*	1.0 3.0 4.0 5.0 6.0 2.0	-	-	-
1985 MARCH	3.27*	ns	1.0 2.5 3.5 4.5 5.5 6.5	2.72ns	ns	2.5 3.5 4.5 5.5 6.5
APRIL	3.52*	0.91*	1.0 2.0 6.5 4.5 3.5 5.5	-	-	-
MAY	1.00ns	0.92*	2.0 1.0 5.5 6.5 3.0 4.5	-	-	-
JUNE	6.50*	0.72*(2)	0.5 1.5 2.5 3.5 4.5 6.0	5.94*	0.72*(2)	1.5 2.5 3.5 4.5 6.0
AUG.	2.43ns	ns	0.5 1.5 2.5 3.5 4.5 5.5	1.86ns	ns	1.5 2.5 3.5 4.5 5.5
SEPT.(1)	1.51ns	ns(2)	0.5 1.5 2.5 3.5 4.5 5.5	1.43ns	ns(2)	1.5 2.5 3.5 4.5 5.5
OCT.(1)	1.33ns	ns	1.0 2.0 4.0 3.0 6.0 5.0	1.17ns	ns	2.0 4.0 3.0 6.0 5.0
1986 JAN.(1)	1.63ns	ns	4.5 6.5 5.5 3.5	-	-	-
FEB.	4.07ns	ns	6.5 4.5 5.5	-	-	-
MARCH	0.02ns	ns	6.5 5.5	-	-	-

panels had significantly more mortalities than one or both of the lowest-ranked, panel sets. Similarly, at the lower site there were relatively few significant differences between the panels of different 'ages'. In July 1984 (F = 24.42, $P<0.05$) significantly fewer mortalities were recorded on the most recently initiated panel set. Conversely, in October 1985 (F = 5.03, $P<0.05$) there were significantly more mortalities on the highest-ranked, most recently initiated panel set, than on the lower-ranked panels, on most of which no hydroid mortalities were observed. In June 1985 (F = 7.17 or 4.66, $P<0.05$) and September 1985 (F = 3.25, $P<0.05$) a number of significant differences were evident between the highest-ranked, longer-immersed sets of panels and the lower-ranked, more recently-immersed sets. In the August 1985 (F = 3.61, $P<0.05$; 'S-N-K', $P>0.05$), September 1985 and October 1985 data sets, if the most recently-immersed panels were excluded from the analyses, no significant differences were evident between the panels. Otherwise there were no further significant differences within the sampling periods.

(g) Ctenostome Bryozoan Recruitment and Mortality:- (Tables 3.28. - 3.31.)

All 3 species or 'groupings' included in the ctenostome taxonomic group (= *Alcyonidium* spp., *Flustrellidra hispida* (Fabricius), and ctenostome ancestrulae (principally *Alcyonidium* spp.)) were recorded in greatest abundance on the panels immersed at the lower

site. *F.hispida* was recorded, at both sites, on panels between May and September, and in greatest abundance in June and July. Ctenostome ancestrulae were not observed on panels at either site until December 1984, and were then recorded on panels throughout most of the remainder of the study period, albeit in low numbers during the summer months. The greatest numbers were recorded on panels examined in December 1985. Similarly, for *Alcyonidium* spp., which were first observed on the panels in November 1984, the numbers recorded increased during the winter and then generally declined to low numbers during the spring/summer months. In November 1985 the numbers of recruits began to increase again, and the greatest numbers of *Alcyonidium* spp. colonies were recorded on panels in January and February 1986. These broad recruitment periods for the ctenostome ancestrulae and *Alcyonidium* spp. were probably at least partially attributable to the presence of a number of different species within the 'species groups'. The numbers of ctenostome and *Alcyonidium* spp. recruits recorded on the panels exhibited a marked increase over the 2 years of the study; conversely, there was a decline in the numbers of *F.hispida* observed.

There was no consistent pattern in the ranking of the panels of varying 'ages' from one sampling period to the next. However, in general, the lowest numbers of ctenostome recruits were recorded on the most recently initiated sets of panels, and frequently ctenostomes

recruited predominantly to intermediate 'aged' panels, rather than those immersed for the longest periods. Furthermore, there were very few significant differences evident among the sets of panels of differing 'ages', and most significant differences occurred during the periods of greatest ctenostome and *Alcyonidium* spp. recruitment. At the upper site, in December 1984 (F = 10.19 or 7.70, $P<0.05$), January 1985 (F = 3.42, $P>0.05$; 'S-N-K', $P<0.05$), February 1985 (F = 10.42 or 7.64, $P<0.05$), and April 1985 (F = 13.10 or 11.38, $P<0.05$) numerous significant differences were evident between the highest-ranked sets of panels, which were generally immersed for 3 or 4 months, and the lower-ranked, more recently-immersed panels. The only other significant difference was recorded in January 1986 (F = 35.64, $P<0.05$), where the highest-ranked, longest-immersed panel set had significantly more ctenostome recruits than the other panels. At the lower site there were only 3 sampling periods where there was evidence of significant differences between the panels. In June 1984 (F = 315.06, $P<0.05$), April 1985 (F = 13.80, $P<0.05$), and October 1985 (F = 6.15 or 6.16, $P<0.05$ ('C & B', $P<0.05$)) the highest-ranked panel set, which was of variable 'age' in the differenet sampling periods, had significantly more ctenostome recruits than the lower-ranked sets of panels. In November 1984 (F = 3.47, $P<0.05$) and May 1985 (F = 3.25, $P<0.05$ ('C & B', $P<0.05$)) no significant differences among the panel sets were detected with the 'S-N-K' test.

More ctenostome mortalities were recorded at the lower site than the upper, which was in accordance with the distribution of recruits among the sites. The greatest numbers of mortalities occurred in the spring and summer and declined to low numbers in the autumn and winter, numbers increased again in January and February.

There was a distinct pattern in the ranking of the panels of varying 'ages', which was evident in most of the sampling periods: generally most mortalities were recorded on the longest-immersed panels and frequently there were no mortalities on the most recently initiated set of panels. This pattern was evident, at both sites, in periods of low and high ctenostome mortality. There were a number of significant differences between the panels of different 'ages', and in all cases, significantly more mortalities were observed on the higher-ranked, longer-immersed panels than on one or more of the lower-ranked, more recently initiated panel sets. Significant differences in data sets were generally restricted to periods of high ctenostome mortality. At the upper site, in January 1985 (F = 3.85, $P<0.05$), February 1985 (F = 8.32 or 8.19, $P<0.05$ ('C & B', $P<0.05$, for the complete data set)), and May 1985 (F = 14.42 or 13.11, $P<0.05$) the longest-immersed, highest-ranked set of panels had significantly more mortalities than were recorded on any of the other panel sets. In March 1985 (F = 4.67, $P<0.05$; but note that for the incomplete data set, F = 3.89, $P>0.05$, 'S-N-K', $P<0.05$) and the complete

data set in April 1985 (F = 5.00, P<0.05), the longest-immersed, highest-ranked set of panels had significantly more mortalities than the 2 lowest-ranked, most recently-immersed sets, on which no mortalities were recorded. However, if the April 1985-initiated panels were excluded from the analysis in April 1985, there were no significant differences between the panels. No other significant differences were recorded (but note June 1984, F = 5.62, P<0.05; 'S-N-K', P>0.05). Considering the results for the lower site, in July 1984 (F = 51.04, P<0.05) there were significant differences, in terms of the number of ctenostome mortalities recorded, between all 3 sets of panels immersed during this period. In June 1984 (F = 98.94, P<0.05) significantly more mortalities were recorded on the longest-immersed set of panels; similarly in April 1985 (F = 3.52, P<0.05 ('C & B', P<0.05)), significantly more mortalities were recorded on the highest-ranked panel set than on the other panels. In June 1985 (F = 6.50 or 5.94, P<0.05) the 2 highest-ranked, longest-immersed sets of panels had significantly more mortalities than the other panels, although when the newly initiated June 1985 panels were excluded from the analysis only the highest-ranked set of panels had significantly more mortalities than the 3 lowest-ranked sets. No other significant differences were evident at the lower site (but note that in the complete March 1985 data set, F = 3.27, P<0.05; 'S-N-K', P>0.05).

TABLE 3.32 - Analysis of the number of cheilostome recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE[1]	1.00ns	1.00*	1.0 2.0 2.5	-	-	-
JULY	6.97*	0.92*	1.0 2.0 3.5 3.0	-	-	-
AUG.	4.32*	0.81*	1.0 3.0 2.0 4.5 4.0	-	-	-
SEPT.	1.17ns	ns	4.0 1.0 3.0 2.0 5.0	-	-	-
OCT.	0.85ns	ns	5.0 4.0 1.0 3.0 2.0	-	-	-
NOV.	1.52ns	0.70*[2]	1.5 0.5 3.5 4.5 2.5	-	-	-
DEC.	4.53*	ns	0.5 2.5 4.5 3.5 1.5	3.30ns	ns	2.5 4.5 3.5 1.5
1985 JAN.	2.92ns	ns	2.0 3.0 1.0 4.0 5.0	-	-	-
FEB.	7.30*	ns	0.5 3.0 2.0 5.0 4.0	1.12ns	ns	3.0 2.0 5.0 4.0
MARCH	2.26ns	ns	0.5 1.5 3.0 4.0 5.0	1.12ns	ns	1.5 3.0 4.0 5.0
APRIL	4.53*	ns	0.5 1.5 2.5 5.0 4.0	0.33ns	ns	1.5 2.5 5.0 4.0
MAY	2.33ns	ns[2]	0.5 3.5 2.5 5.0 1.5	1.89ns	ns	3.5 2.5 5.0 1.5
JUNE	1.41ns	ns	0.5 2.5 3.5 1.5 4.5	0.70ns	ns	2.5 3.5 1.5 4.5
AUG.	8.55*	ns	0.5 4.5 2.5 1.5 3.5	2.46ns	ns	4.5 2.5 1.5 3.5
SEPT. (middle)	4.15*	0.69*	0.5 3.5 4.5 2.5 1.5	3.21ns	ns[2]	3.5 4.5 2.5 1.5
SEPT. (end)	3.33ns	0.88*	5.0 1.0 4.0 3.0 2.0	-	-	-
OCT.	12.68*	ns[2]	1.0 2.0 5.0 4.0 3.0	-	-	-
NOV.	2.57ns	ns	3.0 2.0 4.0 5.0	-	-	-
1986 JAN.	35.14*	0.92*[2]	4.5 3.5 5.5	-	-	-
FEB.	0.53ns	ns	4.5 5.5	-	-	-

TABLE 3.33 - Analysis of the number of cheilostome mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
JULY[1]	2.83ns	0.88*	1.0 2.0 3.5 3.0	-	-	-
AUG.	4.34*	0.83* [2]	1.0 2.0 3.0 4.5 4.0	-	-	-
SEPT.	2.36ns	0.97*	2.0 4.0 1.0 3.0 5.0	-	-	-
OCT.[1]	0.40ns	ns	4.0 1.0 2.0 3.0 5.0	-	-	-
NOV.[1]	1.17ns	ns	0.5 4.5 2.5 3.5 1.5	-	-	-
DEC.	3.00ns	0.74* [2]	0.5 2.5 1.5 4.5 3.5	2.21ns	ns	2.5 1.5 4.5 3.5
1985 JAN.[1]	3.20ns	0.80*	1.0 2.0 4.0 3.0 5.0	-	-	-
FEB.	1.55ns	0.73* [2]	0.5 2.0 3.0 4.0 5.0	1.14ns	ns	2.0 3.0 4.0 5.0
MARCH	4.84*	ns	0.5 1.5 3.0 4.0 5.0	3.20ns	ns	1.5 3.0 4.0 5.0
APRIL	12.35*	ns	0.5 2.5 1.5 4.0 5.0	11.96*	ns	2.5 1.5 4.0 5.0
MAY	5.40*	ns	0.5 1.5 2.5 3.5 5.0	2.32ns	ns	1.5 2.5 3.5 5.0
JUNE[1]	0.35ns	ns	0.5 1.5 2.5 3.5 4.5	0.13ns	ns	1.5 2.5 3.5 4.5
AUG.	10.75*	ns	0.5 1.5 4.5 2.5 3.5	1.27ns	ns	1.5 4.5 2.5 3.5
SEPT. (middle)	5.45*	0.71* [2]	0.5 1.5 2.5 3.5 4.5	1.32ns	ns	1.5 2.5 3.5 4.5
SEPT. (end)	1.77ns	0.88*	4.0 1.0 5.0 3.0 2.0	-	-	-
OCT.	6.74*	ns	1.0 2.0 5.0 4.0 3.0	-	-	-
NOV.	3.29ns	0.89*	3.0 2.0 5.0 4.0	-	-	-
1986 JAN.	5.87*	ns	4.5 3.5 5.5	-	-	-
FEB.	14.29*	ns	5.5 4.5	-	-	-

TABLE 3.34 - Analysis of the number of cheilostome recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	0.90ns	ns	1.0 2.0	-	-	-
JULY	3.82ns	ns	1.0 3.0 2.0	-	-	-
AUG.	0.18ns	ns	1.0 3.0 2.0 4.0	-	-	-
SEPT.	3.89*	ns	4.0 2.0 3.0 1.0 5.0	-	-	-
OCT.	1.55ns	ns	3.0 4.0 1.0 2.0 5.0 6.0	-	-	-
NOV.	7.36*	ns	4.0 3.0 1.0 5.0 6.0 2.0	-	-	-
DEC.	0.99ns	ns(2)	5.0 1.0 4.0 6.0 3.0 2.0	-	-	-
1985 MARCH	1.43ns	ns(2)	1.0 2.5 3.5 4.5 5.5 6.5	0.24ns	ns	2.5 3.5 4.5 5.5 6.5
APRIL	1.19ns	0.80*	1.0 2.0 3.5 6.5 5.5 4.5	-	-	-
MAY	0.17ns	ns	1.0 2.0 6.5 4.5 5.5 3.0	-	-	-
JUNE	7.73*	ns	0.5 1.5 6.0 2.5 3.5 4.5	2.45ns	ns	1.5 6.0 2.5 3.5 4.5
AUG.	16.13*	ns	0.5 1.5 4.5 5.5 2.5 3.5	11.15*	ns	1.5 4.5 5.5 2.5 3.5
SEPT.	2.58ns	0.73*	0.5 5.5 4.5 2.5 3.5 1.5	2.17ns	0.73*	5.5 4.5 2.5 3.5 1.5
OCT.	2.45ns	0.82*	1.0 2.0 6.0 4.0 5.0 3.0	2.09ns	0.82*	2.0 6.0 4.0 5.0 3.0
1986 JAN.	5.98*	0.86*(2)	3.5 4.5 6.5 5.5	-	-	-
FEB.	6.32*	0.96*	4.5 5.5 6.5	-	-	-
MARCH	0.01ns	F-ratio = 44.33*	6.5 5.5	-	-	-

TABLE 3.35 - Analysis of the number of cheilostome mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	6.40ns	ns	1.0 2.0	-	-	-
JULY	3.39ns	ns	1.0 3.0 2.0	-	-	-
AUG.	8.45*	ns	1.0 2.0 3.0 4.0	-	-	-
SEPT.	5.57*	ns	1.0 2.0 3.0 5.0 4.0	-	-	-
OCT.	7.36*	ns	1.0 2.0 3.0 5.0 4.0 6.0	-	-	-
NOV.(1)	4.52*	ns(2)	1.0 6.0 3.0 2.0 4.0 5.0	-	-	-
DEC.(1)	0.91ns	ns	1.0 5.0 2.0 4.0 3.0 6.0	-	-	-
1985 MARCH	36.48*	ns	1.0 2.5 3.5 6.5 4.5 5.5	32.60*	ns	2.5 3.5 6.5 4.5 5.5
APRIL	2.11ns	0.96*	1.0 2.0 4.5 6.5 3.5 5.5	-	-	-
MAY	8.39*	ns	1.0 3.0 2.0 4.5 5.5 6.5	-	-	-
JUNE	4.83*	ns	0.5 1.5 2.5 4.5 3.5 6.0	2.45ns	ns	1.5 2.5 4.5 3.5 6.0
AUG.	11.60*	ns(2)	0.5 1.5 2.5 5.5 4.5 3.5	9.68*	ns	1.5 2.5 5.5 4.5 3.5
SEPT.	2.94ns	ns	0.5 1.5 2.5 3.5 5.5 4.5	0.62ns	ns	1.5 2.5 3.5 5.5 4.5
OCT.	7.51*	0.76*	1.0 2.0 4.0 6.0 5.0 3.0	6.34*	0.76*(2)	2.0 4.0 6.0 5.0 3.0
1986 JAN.	3.94ns	0.97*	4.5 3.5 6.5 5.5	-	-	-
FEB.	3.68ns	0.98*	5.5 4.5 6.5	-	-	-
MARCH	1.37ns	ns	6.5 5.5	-	-	-

(h) Cheilostome Bryozoan Recruitment and Mortality:-

(Tables 3.32. - 3.35.)

Cheilostome ancestrulae were recorded on panels in most months throughout the study period; however, at both sites ancestrulae were more abundant on the panels immersed in the second half of the study, which thus complicated the analyses and conclusions. Also, marked seasonality in recruitment would not necessarily be expected for a 'species group' such as cheilostome ancestrulae, which included a number of diverse species. At the lower site, during the first year of the study, there was a peak in the numbers of ancestrulae recorded on the panels between July and August 1984. After a winter decline in recruitment, numbers increased again between February and April 1985; however, the greatest numbers of recruits were recorded in the months after July 1985 through to the end of the study period. Recruits were most abundant on the panels between December 1985 and February 1986. At the upper site, relatively low numbers of recruits were recorded from the beginning of the study until August 1985, with the greatest numbers observed between November 1984 and April 1985. Between August 1985 and March 1986 there was a marked increase in the numbers of ancestrulae recorded on the panels, and a peak in recruitment occurred in January 1986.

Recruitment exhibited a distinct seasonal pattern if particular cheilostome species were considered.

Superimposed on this was a between-year variation because the majority of the species were most abundant in the second year. A number of species recruited in greatest abundance in the autumn and winter; for example, *Callopora* spp. (= *C.lineata* (L.), *C.craticula* (Alder), and *C.aurita* (Hincks)), *Celleporella hyalina* (L.), and *Electra pilosa* (L.). However, recruitment was not necessarily restricted to this period; for example, *E.pilosa* was observed on the panels in most months from summer 1984 through to the end of the study. Other species exhibited a peak in recruitment in the spring and summer; for example, *Phaeostachys spinifera* (Johnston), *Schizoporella unicornis* (Johnston) and *Umbonula littoralis* Hastings. Most species were recorded at both the upper and lower sites; the exceptions were *Schizomavella linearis* (Hassall), *Microporella ciliata* (Pallas), *Haplopoma* spp., and *Escharoides coccinea* (Abildgaard), which were observed sporadically at the lower site, generally being recorded on panels in 1 or 2 months during the summer or autumn. (See Tables 3.1. and 3.2.)

There was no consistent pattern evident, at either site, in the ranking of the panels in terms of the mean numbers of cheilostome recruits recorded. The only exception was that in many of the sampling periods the most recently initiated sets of panels were lowest-ranked. Otherwise panels of all 'ages' occupied different positions in rank. There was also a tendency, which was evident at both sites, for a particular set of panels to

have the highest-rank for much of the duration of their immersion; for example, panels initiated in May 1984, November 1984 and August 1985 at the upper site, and in May 1984 and August 1985 at the lower site.

At the upper site, there were a number of significant differences between panels of differing 'ages'. In February 1985 (F = 7.30, P<0.05), April 1985 (F = 4.53, P<0.05) and August 1985 (F = 8.55, P<0.05) there were significantly fewer recruits recorded on the lowest-ranked, newly-immersed set of panels than on any of the other panels; if, however, the newly-immersed panels were excluded from the analyses, no significant differences were evident among the remaining panels. Conversely, in July 1984 (F = 6.97, P<0.05 ('C & B', P<0.05)), October 1985 (F = 12.68, P<0.05) and January 1986 (F = 35.14, P<0.05), the highest-ranked set of panels, which varied in 'age' between 3 and 5 months in the different sampling periods, had significantly more recruits than the lower-ranked panels. More complex situations occurred in August 1984 (F = 4.32, P<0.05 ('C & B', P<0.05)), December 1984 (F = 4.53, P<0.05) and mid-September 1985 (F = 4.15, P<0.05 ('C & B', P<0.05)), where the highest-ranked set of panels, again of variable 'age' in the different periods, had significantly more recruits than were recorded on one or more of the lower-ranked panel sets. However, in the December 1984 and mid-September 1985 data sets, there were no significant differences between the panels if the most recently-

immersed set of panels in each case was excluded from the analysis. Otherwise, there were no significant differences among the panels of varying 'ages', and it was difficult to determine any consistency in the distribution of significant differences in relation to the period of analysis, and consequently to the seasonality of recruitment. There were also a number of significant differences among the panels at the lower site. In June 1985 (F = 7.73, P<0.05) the most recently initiated panel set had significantly fewer recruits than the other panels; however, if these June 1985 panels were excluded from the analysis no significant differences were evident between the panel sets. Similarly, in August 1985 (F = 16.13 or 11.15, P<0.05) the 2 most recently initiated sets of panels had significantly fewer recruits than the other sets; however, if the August 1985-initiated panels were excluded from the analysis, the lowest-ranked panel set had significantly fewer recruits than were recorded on the 3 highest-ranked panel sets only. Also, in August 1985 significantly more recruits were recorded on the highest-ranked, intermediate 'aged' panel set. In January 1986 (F = 5.98, P<0.05), and February 1986 (F = 6.32, P<0.05 ('C & B', P<0.05)) significantly more recruits were recorded on the highest-ranked, 'older' set of panels, which in both cases was the August 1985-initiated set. In November 1984 (F = 7.36, P<0.05) both the highest-ranked panel sets had significantly more recruits than the other panels; the highest-ranked panel

sets were those initiated in June 1984 and October 1984, and thus of variable 'age'. Finally, in September 1984 ($F = 3.89$, $P<0.05$) there were significantly more recruits on the highest-ranked, longest-immersed panel set, than on the lowest-ranked set only. There were no other significant differences, and, as with the data for the upper site, there was no discernible pattern in the distribution of the significant differences among the sample periods.

At both sites, cheilostome mortalities were recorded throughout most of the study. At the lower site, the lowest numbers were recorded in November and December 1984, but such a decline was not evident in the following autumn and winter when more cheilostome recruits were observed. At the upper site, fewer mortalities were recorded; there were especially low numbers in the autumn/winter 1984 period, but the numbers of mortalities increased markedly after August 1985 which corresponded with the period of increased cheilostome recruitment. Although there were a number of exceptions, in the majority of the sampling periods, at both sites, the lowest-ranked panels were the most recently-immersed, and conversely, more mortalities were generally recorded on the longest-immersed sets. A number of significant differences between the panels were evident. At the upper site, significantly fewer mortalities were recorded on the 'youngest' set of panels compared to the higher-ranked sets in August 1985 ($F = 10.75$, $P<0.05$); but if the August 1985 panels were excluded from the analysis,

no significant differences were evident. In May 1985 (F = 5.40, P<0.05) and mid-September 1985 (F = 5.45, P<0.05) the newly-immersed panel sets had significantly fewer mortalities than were recorded on all but the second most recently-immersed set of panels; but as with the August 1985 data set, if these new panel sets were excluded from the analyses there were no significant differences between the panels. In August 1984 (F = 4.34, P<0.05) the only significant difference was between the recently initiated panel set and the longer-immersed, highest-ranked set. Conversely, in March 1985 (F = 4.84, P<0.05), October 1985 (F = 6.74, P<0.05) and January 1986 (F = 5.87, P<0.05) the highest-ranked, 'older' sets of panels had significantly more cheilostome mortalities than were recorded on one or more of the lower-ranked, more recently initiated panel sets. Note, however, that, if in the March 1985 data set the newly-immersed March 1985 panels were excluded from the analysis, there were no further significant differences between the sets of panels. In April 1985, (F = 12.35 or 11.96, P<0.05) the 2 highest-ranked, longest-immersed panel sets had significantly more mortalities than were recorded on any of the lower-ranked sets. The only other significant difference at the upper site occurred in February 1986 (F = 14.29, P<0.05), where there was a significant difference between the 2 sets of panels immersed at this time. At the lower site, in October 1984 (F = 7.36, P<0.05), March 1985 (F = 36.48 or 32.60, P<0.05), and August 1985 (F = 11.60 or 9.68, P<0.05),

the highest-ranked, 'older' set of panels had significantly more mortalities than all of the lower-ranked sets; in the March 1985 complete data set the second highest-ranked panel set also had significantly more mortalities than the 3 lowest-ranked, most recently initiated panel sets. In October 1985 (F = 7.51 or 6.34, $P<0.05$ ('C & B', $P<0.05$, for the complete data set)) the 2 highest-ranked panel sets had significantly more mortalities than the lower-ranked sets, although the differences were less well marked if the newly initiated October 1985 panels were excluded from the analysis. The highest-ranked panel set had significantly more mortalities than the lowest-ranked sets, on which no mortalities were observed, in November 1984 (F = 4.52, $P<0.05$) and September 1985 (F = 2.94, $P>0.05$; 'S-N-K', $P<0.05$). Nevertheless, in the latter case there were no significant differences between the panels if the September 1985-initiated set was not included in the analysis. There were also significant differences between the higher-ranked, 'older' panels and the lower-ranked, more recently initiated sets in May 1985 (F = 8.39, $P<0.05$). Significantly fewer mortalities were recorded on the most recently initiated set of panels in August 1984 (F = 8.45, $P<0.05$); for September 1984 (F = 5.57, $P<0.05$) and June 1985 (F = 4.83, $P<0.05$) significantly fewer mortalities occurred on the most recently-immersed panels, than those immersed for between 4 and 6 months. If, however, the June 1985-initiated panels were excluded from the June 1985

TABLE 3.36 - Analysis of the number of ascidian recruits recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	0.13ns	ns	1.0 2.5 2.0	-	-	-
JULY	2.09ns	ns	1.0 2.0 3.0 3.5	-	-	-
AUG.	1.13ns	ns	4.5 2.0 1.0 4.0 3.0	-	-	-
SEPT.	1.46ns	ns	3.0 4.0 2.0 5.0 1.0	-	-	-
OCT.	1.53ns	ns	3.0 2.0 4.0 5.0 1.0	-	-	-
NOV.	4.45*	ns	3.5 2.5 1.5 4.5 0.5	-	-	-
DEC.	1.03ns	ns	4.5 0.5 1.5 3.5 2.5	1.31ns	ns	4.5 1.5 3.5 2.5
1985 JAN.(1)	1.00ns	1.00*	1.0 2.0 4.0 5.0 3.0	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE	2.19ns	0.76* (2)	1.5 3.5 2.5 4.5 0.5	0.67ns	ns	1.5 3.5 2.5 4.5
AUG.	6.41*	ns	2.5 0.5 3.5 4.5 1.5	6.53*	ns	2.5 3.5 4.5 1.5
SEPT. (middle)	6.50*	ns	0.5 2.5 3.5 4.5 1.5	4.97*	ns	2.5 3.5 4.5 1.5
SEPT. (end)	1.65ns	ns	4.0 5.0 1.0 3.0 2.0	-	-	-
OCT.	23.56*	ns	1.0 2.0 5.0 4.0 3.0	-	-	-
NOV.	0.74ns	ns	5.0 2.0 4.0 3.0	-	-	-
1986 JAN.(1)	(3)	(3)	3.5 4.5 5.5	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.37 - Analysis of the number of ascidian mortalities recorded on the panels of different immersion periods (i.e. 'age') at the upper site. (see Table 3.4 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 MAY	-	-	-	-	-	-
JUNE	-	-	-	-	-	-
JULY	0.22ns	ns	2.0 3.0 3.5 1.0	-	-	-
AUG.	3.88*	ns	1.0 2.0 3.0 4.0 4.5	-	-	-
SEPT.	2.52ns	ns	1.0 3.0 2.0 4.0 5.0	-	-	-
OCT.	0.31ns	ns	4.0 5.0 1.0 3.0 2.0	-	-	-
NOV.(1)	0.80ns	0.80*	0.5 2.5 3.5 4.5 1.5	-	-	-
DEC.	6.63*	ns	0.5 4.5 1.5 2.5 3.5	2.25ns	ns	4.5 1.5 2.5 3.5
1985 JAN.	2.06ns	ns	1.0 2.0 5.0 4.0 3.0	-	-	-
FEB.(1)	1.00ns	1.00*	0.5 2.0 3.0 4.0 5.0	1.00ns	1.00*	2.0 3.0 4.0 5.0
MARCH(1)	1.00ns	1.00*	0.5 1.5 3.0 4.0 5.0	1.00ns	1.00*	1.5 3.0 4.0 5.0
APRIL	-	-	-	-	-	-
MAY	-	-	-	-	-	-
JUNE(1)	1.00ns	1.00*	0.5 1.5 2.5 3.5 4.5	1.00ns	1.00*	1.5 2.5 3.5 4.5
AUG.	8.69*	0.73* (2)	0.5 1.5 3.5 4.5 2.5	8.14*	ns	1.5 3.5 4.5 2.5
SEPT. (middle)	15.22*	ns	0.5 3.5 4.5 1.5 2.5	12.12*	ns	3.5 4.5 1.5 2.5
SEPT.(1) (end)	0.57ns	ns	1.0 2.0 3.0 4.0 5.0	-	-	-
OCT.	0.40ns	ns	1.0 2.0 5.0 3.0 4.0	-	-	-
NOV.	2.15ns	ns	2.0 3.0 5.0 4.0	-	-	-
1986 JAN.	12.44*	ns	3.5 4.5 5.5	-	-	-
FEB.	-	-	-	-	-	-

TABLE 3.38 - Analysis of the number of ascidian recruits recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

MONTH OF ANALYSIS	(a) ANOVA	COCHRAN'S TEST	S-N-K	(b) ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	1.14ns	ns	1.0 2.0	-	-	-
JULY	0.81ns	ns	2.0 3.0 1.0	-	-	-
AUG.	3.11ns	ns[2]	3.0 2.0 4.0 1.0	-	-	-
SEPT.	9.34*	ns	4.0 3.0 5.0 1.0 2.0	-	-	-
OCT.	0.86ns	ns	2.0 5.0 3.0 4.0 1.0 6.0	-	-	-
NOV.	1.20ns	ns	2.0 3.0 5.0 4.0 6.0 1.0	-	-	-
DEC.[1]	5.25*	ns	2.0 6.0 3.0 4.0 5.0 1.0	-	-	-
1985 MARCH	-	-	-	-	-	-
APRIL	-	-	-	-	-	-
MAY[1]	1.00ns	1.00*	1.0 2.0 3.0 4.5 6.5 5.5	-	-	-
JUNE	1.62ns	0.81*	2.5 0.5 3.5 6.0 4.5 1.5	1.52ns	0.81*[2]	2.5 3.5 6.0 4.5 1.5
AUG.	6.81*	ns	4.5 5.5 0.5 3.5 1.5 2.5	6.71*	ns	4.5 5.5 3.5 1.5 2.5
SEPT.	4.81*	0.65*	0.5 5.5 4.5 2.5 1.5 3.5	4.16*	ns[2]	5.5 4.5 2.5 1.5 3.5
OCT.	5.19*	ns	2.0 1.0 4.0 6.0 3.0 5.0	5.58*	ns	2.0 4.0 6.0 3.0 5.0
1986 JAN.[1]	8.25*	ns[2]	3.5 4.5 5.5 6.5	-	-	-
FEB.	-	-	-	-	-	-
MARCH	-	-	-	-	-	-

TABLE 3.39 – Analysis of the number of ascidian mortalities recorded on the panels of different immersion periods (i.e. 'age') at the lower site. (see Tables 3.4 and 3.6 for details).

	(a)			(b)		
MONTH OF ANALYSIS	ANOVA	COCHRAN'S TEST	S-N-K	ANOVA	COCHRAN'S TEST	S-N-K
1984 JUNE	–	–	–	–	–	–
JULY	1.35ns	ns	2.0 3.0 1.0	–	–	–
AUG.	1.27ns	ns	1.0 3.0 4.0 2.0	–	–	–
SEPT.	5.13*	ns(2)	1.0 3.0 4.0 5.0 2.0	–	–	–
OCT.	0.76ns	ns	5.0 6.0 2.0 1.0 4.0 3.0	–	–	–
NOV.(1)	1.50ns	ns	1.0 2.0 3.0 6.0 4.0 5.0	–	–	–
DEC.(1)	0.94ns	ns	1.0 4.0 5.0 2.0 3.0 6.0	–	–	–
1985 MARCH(1)	0.91ns	ns(2)	1.0 2.5 5.5 6.5 3.5 4.5	0.72ns	ns	2.5 5.5 6.5 3.5 4.5
APRIL(1)	1.28ns	0.80*	1.0 2.0 3.5 6.5 4.5 5.5	–	–	–
MAY	–	–	–	–	–	–
JUNE(1)	3.00ns	1.00*	0.5 1.5 2.5 3.5 4.5 6.0	3.00ns	1.00*	1.5 2.5 3.5 4.5 6.0
AUG.	2.87ns	0.90*	0.5 1.5 4.5 2.5 5.5 3.5	2.50ns	0.90*	1.5 4.5 2.5 5.5 3.5
SEPT.	7.80*	ns	0.5 5.5 4.5 3.5 1.5 2.5	4.19*	ns	5.5 4.5 3.5 1.5 2.5
OCT.	3.19*	0.70*	2.0 1.0 6.0 4.0 3.0 5.0	2.90ns	0.70*	2.0 6.0 4.0 3.0 5.0
1986 JAN.	5.24*	ns	4.5 3.5 6.5 5.5	–	–	–
FEB.(1)	25.00*	1.00*	4.5 5.5 6.5	–	–	–
MARCH	–	–	–	–	–	–

analyses there were no significant differences between the panel sets. There were no further significant differences evident at either site.

(i) <u>Ascidian Recruitment and Mortality</u>:- (Tables 3.36. - 3.39.)

At both sites ascidian recruitment was markedly seasonal in occurrence. Most recruits were observed during the summer and autumn in both years, and the greatest abundance of recruits occurred, in general, between June and August. This pattern applied to *Botryllus schlosseri* (Pallas)/*Botrylloides leachii* (Savigny), *Trididemnum tenerum* Verrill, *Dendrodoa grossularia* (Van Beneden) and the unidentified ascidians. *D.grossularia* recruits were also observed on panels during the winter. There was also a between-year variation evident in ascidian recruitment; for example, *T.tenerum* was recorded predominantly in the first year of the study, and *Molgula manhattensis* (De Kay) was only observed on panels between May and October 1985, and then only in relatively low numbers. The ascidians were generally recorded in greatest abundance on panels immersed at the lower site. (See Tables 3.1. and 3.2.).

A result characteristic of most of the sampling periods, at both sites, was for the recently initiated panels, or those immersed for intermediate periods, to be higher-ranked in terms of the numbers of ascidian

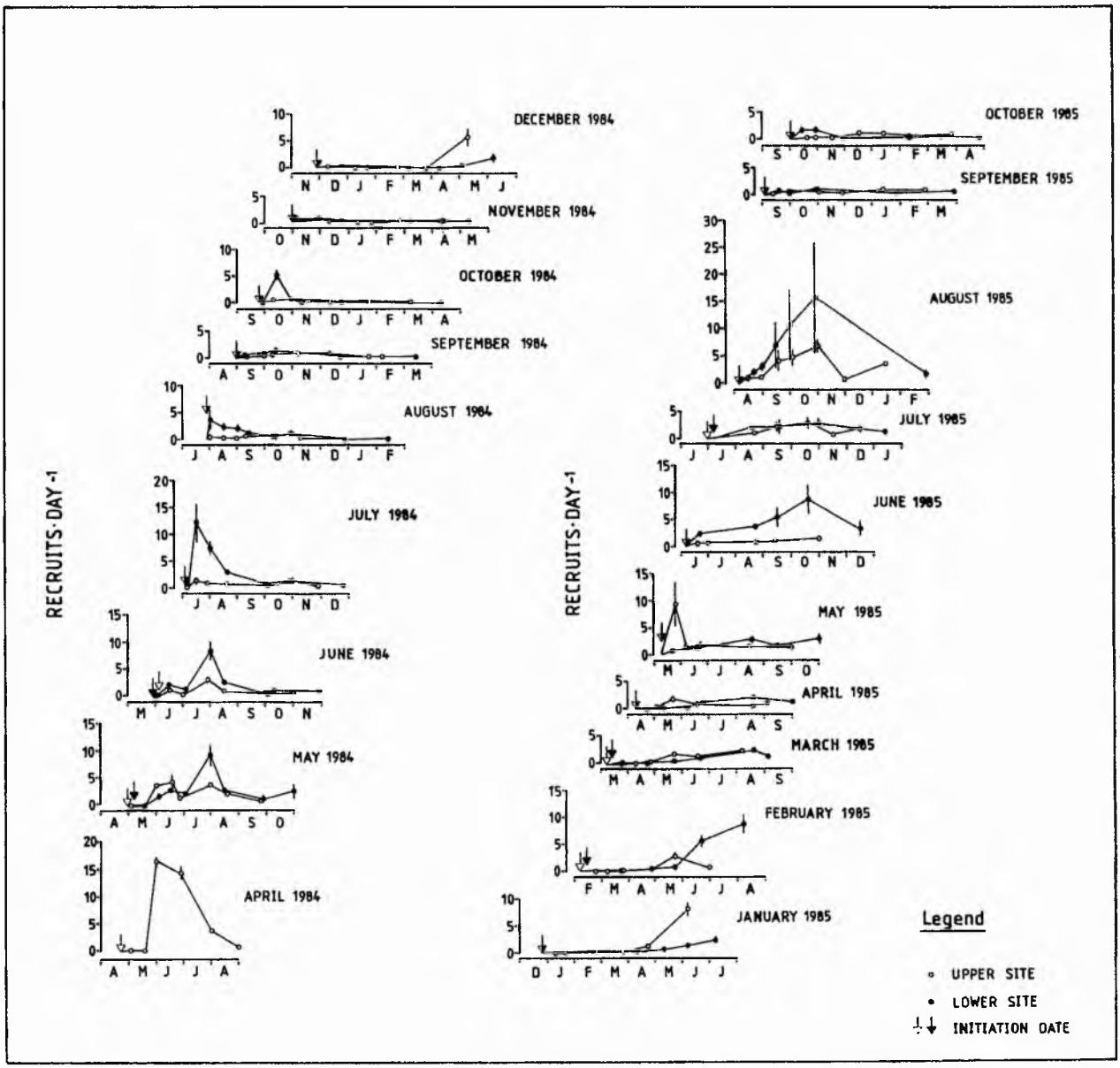
recruits present, than the longer-immersed panels. At the upper intertidal site, all the significant differences were between the highest-ranked set of panels and the lower-ranked sets, which had significantly fewer ascidian recruits. Significant differences were evident in November 1984 (F = 4.45, P<0.05), August 1985 (F = 6.41 or 6.53, P<0.05), mid-September 1985 (F = 6.50 or 4.97, P<0.05), October 1985 (F = 23.56, P<0.05) and January 1986 (see Table 3.36.). In all except the latter period, the highest-ranked set of panels had been immersed for only one-half to 3 months; in the January 1986 data set the highest-ranked set had been immersed for the longest duration. At the lower site, the distribution of significant differences between the variously 'aged' panels was less consistent, but in all cases the highest-ranked panel sets had significantly more recruits than were observed on one or more of the lower-ranked sets. In December 1984 (F = 5.25, P<0.05) and January 1986 (F = 8.25, P<0.05) the highest-ranked panel set (which in December 1984 was the most recently-immersed and in January 1986 the longest-immersed) had significantly more ascidian recruits than any of the other panels. In September 1984 (F = 9.34, P<0.05) both sets of newly-immersed, high-ranked panels had significantly more recruits than the lower-ranked sets. In August 1985 (F = 6.81 or 6.71, P<0.05), September 1985 (F = 4.81 or 4.16, P<0.05 ('C & B', P<0.05, for the complete data set)), and October 1985 (F = 5.19 or 5.58, P<0.05) the highest-ranked set of panels, which in all

cases was that initiated in June 1985, had significantly more recruits than were recorded on one or more of the lowest-ranked panel sets. Even so, similar numbers of recruits occurred on the June 1985-initiated panels and the intermediate-ranked sets. At neither site were there any further significant differences.

At both sites the greatest numbers of mortalities were observed between August and October. The numbers of mortalities declined during the winter months and there were none in the spring and early summer. Thus the pattern of ascidian mortality closely resembled that observed for recruitment, the greatest numbers of mortalities occurred in the months immediately following the period of greatest ascidian recruitment. Although the ranking pattern of the panels of varying 'ages' was highly variable, in general, the lowest-ranked were the newly-immersed panels (often no mortalities were recorded on these), and the highest-ranked were generally the 'older', longer or intermediately-immersed panel sets. Relatively few significant differences were evident at either site. At the upper site, in August 1984 (F = 3.88, $P<0.05$), and December 1984 (F = 6.63, $P<0.05$) the most recently initiated set of panels had significantly fewer mortalities than all the other sets, excluding the second lowest-ranked set of panels. In August 1984 these were also recently initiated, but in December 1984 they were the longest-immersed panels. If the December 1984-initiated panels were excluded from the December 1984 analysis there were no significant differences between

the variously 'aged' panels. Conversely, in August 1985 (F = 8.69 or 8.14, P<0.05), mid-September 1985 (F = 15.22 or 12.12, P<0.05), and January 1986 (F = 12.44, P<0.05) the highest-ranked panel set had significantly more mortalities than were observed on the other panels; in September 1985 there were also significant differences between the second highest-ranked set of panels and those of lower-rank. There were similarly, few significant differences evident at the lower site. For example, in January 1986 (F = 5.24, P<0.05) and February 1986 (F = 25.00, P<0.05 ('C & B', P<0.05)) the highest-ranked panel set , which in both periods was the August 1985-initiated set, had significantly more mortalities than occurred on the other panels. In the complete September 1985 (F = 7.80, P<0.05) data set the highest-ranked set of panels had significantly more mortalities than the 2 lowest-ranked sets, one of which was the newly initiated September 1985 panels, which had significantly fewer mortalities than were recorded on all the panels except the longest-immersed April 1985-initiated set. If the September 1985-initiated panels were excluded from this analysis, the only significant difference occurred between the highest-ranked panel set and the lowest-ranked April 1985-initiated set (F = 4.19, P<0.05). The only other significant difference occurred in September 1984 (F = 5.13, P<0.05), where significantly fewer mortalities were observed on the newly-immersed panel set compared to the other panels. There were no other significant differences evident between the

FIGURE 3.3. The mean (+1 standard error) total number of recruits, standardized for immersion period (i.e. numbers of recruits.day $^{-1}$), recorded at each sampling date.


RECRUITS·DAY⁻¹
DECEMBER 1984
NOVEMBER 1984
OCTOBER 1984
SEPTEMBER 1984
AUGUST 1984
JULY 1984
JUNE 1984
MAY 1984
APRIL 1984
OCTOBER 1985
SEPTEMBER 1985
AUGUST 1985
JULY 1985
JUNE 1985
MAY 1985
APRIL 1985
MARCH 1985
FEBRUARY 1985
JANUARY 1985
Legend
UPPER SITE
LOWER SITE
INITIATION DATE

variously 'aged' panels, in any of the sampling periods (but note that for the complete October 1985 data set, $F = 3.19$, $P<0.05$ ('C & B', $P<0.05$); 'S-N-K', $P>0.05$). At neither site was there a distinct pattern in the distribution of significant results among the sampling periods, with respect to the season or number of mortalities recorded.

(j) Summary of the results:-

There were relatively few significant differences between the number of larval recruits recorded on the panels of differing immersion periods or 'ages'. If the results for all 8 taxonomic groups considered in the study were combined, in 66% of the data sets for the upper site and 70% at the lower site, there were no significant differences between the panels. Furthermore, if those panels not immersed for the whole period under analysis were excluded, these values increased to 72% and 74% respectively. Although these values varied among the different taxonomic groups, the results suggested that the 'age' of the substratum may not itself have been an important determinant of larval recruitment, i.e. larvae recruited in similar numbers to panels of all 'ages'. That this may be the case was also indicated in Figures 3.1. - 3.3.. Figures 3.1. and 3.2. illustrate the mean total numbers of recruits and mortalities recorded on the panels at each sampling date, and Figure 3.3. shows the mean total numbers of recruits standardized for the length of the immersion period between sampling dates.

Despite the low numbers of significant differences between the panels, there were a number of patterns evident in the ranking of the sets of panels in terms of the mean numbers of recruits recorded. Generally, for all the taxonomic groups considered, the lowest numbers of recruits recorded during any sampling period occurred on the most recently initiated set of panels. In 70% of the data sets for the upper site, the most recently-immersed panels had the lowest numbers of recruits, and in 42% of these the numbers recorded were significantly less than one or more of the higher-ranked sets of panels. At the lower site, in 57% of the data sets the most recently-immersed panels were lowest-ranked, and in 26% of these the difference was significant. If the sets of panels not immersed for the whole of the sampling period were not considered, then in 54% of all the data sets at the upper site and 50% at the lower site, the lowest-ranked panel set was also the 'youngest'. Although the pattern was not absolute, i.e. the greatest numbers of recruits were occasionally recorded on the most recently initiated set of panels, the results suggested that the newly-immersed substrata may not initially have been as 'attractive' to recruiting larvae as longer-immersed surfaces.

Considering the highest-ranked panels, the results were considerably more variable and patterns were less clearly delineated. Thus, the highest-ranked set of

panels could be that immersed for the intermediate or longest periods or, more rarely, the most recently initiated set. For example, the longest-immersed panels were highest-ranked in 34% of all the data sets at the upper site and in 28% at the lower site; of these 40% and 18%, respectively, were significantly different from one or more of the lower-ranked panel sets. Patterns were confounded, however, because some of the taxonomic groups exhibited high recruitment to a particular set of panels throughout much of the immersion period of these panels, which thus dominated the highest-ranked position for several months.

Few significant differences were evident among the differently 'aged' panels in terms of the numbers of mortalities recorded. Considering the data sets for all 8 taxonomic groups, in 64% at the upper site and 67% at the lower site there were no significant differences between the panels. These values increased to 71% and 72%, respectively, if the panels not immersed for the whole of the sampling period were not included in the analysis. Patterns in the ranking of the differently 'aged' panels, in terms of the mean numbers of mortalities, were generally more marked than for recruitment, but this was probably at least partially attributable to sampling artefacts. In 87% of the data sets for the upper site and 86% at the lower site, the newly-immersed sets of panels were the lowest-ranked. In 57% and 61% of these cases, respectively, there were no significant differences between the most recently-

immersed panels and one or more of the higher-ranked, longer-immersed sets. Considering the highest-ranked panel set, at the upper site in 55% of the data sets this was the longest-immersed set of panels, and in 47% of these there were significant differences between the panels. At the lower site, the longest-immersed panels were highest-ranked in 39% of the data sets, and in 37% of these significant differences occurred.

3.3. DISCUSSION

Scheer (1945, p. 103) suggested that a basic problem in an examination of the development of a sequence of communities was "...that of distinguishing between seasonal progression and true succession". Seasonal progression results fundamentally from differences in the reproductive seasons of the organisms concerned. Osman (1977) has suggested that seasonality implies a sequential, but annually repeating change in composition. McDougall (1943) concluded that "true" succession did not occur in the pile-dwelling communities at Beaufort, North Carolina, but that because most of the organisms were relatively short-lived, and all showed a wide seasonal variation in abundance, there was probably a similar sequence of events repeated each year, with little progressive change from one year to another. Sutherland and Karlson (1977), similarly concluded that classical succession did not occur in the communities developing on artificial substrata immersed at Beaufort; instead the community composition was always changing unpredictably. They attributed these dramatic changes in community structure to the outcome of the addition of species through larval recruitment and the subtraction of species as a result of adult mortality. Larval recruitment was predominantly seasonal and its intensity varied from year to year; adult residence time was generally less than a year, and mortality and/or disappearance of these adults produced 20-60% free space on an approximately annual basis (Sutherland and Karlson,

1977). Thus seasonal progression appeared to be more important in this community, and Sutherland and Karlson (1977) have suggested that the features of their community (*viz.*, variable recruitment and short-lived adults), are common characteristics of temperate and subtropical fouling communities. Succession, in contrast to seasonal progression, involves definite relations between organisms (Scheer, 1945). At Newport Harbour, California, Scheer (1945) observed that the breeding seasons of most of the fouling organisms involved in the colonization sequences extended throughout the year. Furthermore, he found that panels initiated in December went through the same sequence as those exposed in March or April, and although the time relations varied, the sequence did not. He therefore concluded that there was no evidence of a seasonal progression of the species but that "true" succession was indeed involved. The importance of seasonality, as distinct from "true" succession may not be evident in those studies (e.g. Aleem, 1958; Otsuka and Dauer, 1982; Schoener, 1982; and Hirata, 1987) where assemblage development has been examined on a series of substrata initiated at a single immersion date. If the significance of the roles of succession and seasonality in assemblage development are to be adequately distinguished, then an examination of the assemblages developing on substrata made available to larval recruitment at different submergence times is necessary.

Although Little (1984) disputes whether ecological succession, as defined by Odum (1969), actually occurs in the development of microfouling layers on substrata immersed in the sea, there is little doubt that a distinct sequence of events occurs which eventually results in the formation of a complex fouling layer (see, for example, Zobell and Allen, 1935; Scheer, 1945; Aleem, 1958; Marshall *et al.*, 1971; Marszalek *et al.*, 1979 and Little, 1984). Evidence was seen in the present study that as the microfouling layers developed, or 'aged', there was a corresponding influence on the 'attractiveness' of a surface to settling larvae. A characteristic pattern evident in the results was for the most recently-immersed panels to have fewer recruits than those immersed for longer periods. At the upper site, if the results for the 8 taxonomic groups were combined, in 70% of the data sets the most recently-immersed panels were the lowest-ranked in terms of the numbers of recruits recorded, and in 42% of these, there were significantly fewer recruits than occurred on one or more of the longer-immersed sets of panels. The values were 69% and 39% respectively, if the data sets where significantly fewer recruits were recorded on the newly-immersed set of panels, which were submerged for only half the period of analysis, were not considered. At the lower site, the newly-immersed panels were lowest-ranked in 57% of the data sets, and of these, in 26% of the cases there were significantly fewer recruits than on one or more of the higher-ranked panel sets. If the

incomplete data sets were excluded, as above, the relevant values were 56% and 23% respectively. The ascidians were the principal exception to these generalizations, where in only 5 out of 13 data sets at the upper site and in 3 out of 12 at the lower site were the lowest numbers of recruits recorded on the most recently-immersed panels. That these results may have been the effect of the microfouling components was supported because panels examined over the same time interval, but which had been immersed for longer periods, and presumably therefore had a more developed microfouling complex, received more recruits. This provides evidence that larvae potentially capable of settling were 'available' in the water column (see Figures 3.1.-3.3.). However, this experiment did not distinguish between greater recruitment onto 'older' panels and greater post-settlement mortality on the 'younger' panels. Thus, before the importance of different in the microbial film can be asserted, it would be necessary to elucidate further the selectivity of settling larvae with respect to the different microbial film constituents, and variation in the different potential sources of post-settlement mortality acting on the variously 'aged' substrata. Vagaries in environmental conditions affected all the panels immersed at a particular time and it is unlikely that, in this study, any factor (e.g. desiccation) would have been a more important source of mortality on 'younger' panels. This was because the majority of the assemblages did not

develop sufficiently, over the time periods studied, to for example, increase the water retention capacity of the surface of longer-immersed panels over that of 'younger' panels. It should also be noted that the recently-immersed panels were examined for recruits 2 or 3 times in the first month of immersion, which decreased the likelihood of undetected recruitment occurring through the activity of an unidentified mortality agent.

The importance of the 'age' of the substratum, and thus the extent of development of the microfouling layers, was not absolute. For example, 1 *T.tenerum* recruit was recorded on a panel initiated in August 1984 at the upper site, after the first 24 hours submergence; on the set of panels immersed at the same time at the lower site 1, 3 and 7 ascidian recruits were recorded on the panels after the first 24 hours. Similarly, on a panel immersed at the lower site in June 1984, 1 barnacle cyprid was recorded after 24 hours. Zobell and Allen (1935) observed very few macroscopic organisms attached to glass slides which had been submerged for only 3 days, but numbers of barnacle cyprids and hydroids increased slowly but progressively after 4 to 7 days. After 24 hours immersion they recorded an average of 0.3 macroscopic organisms on 2 square inches of glass slide, with $>2x10^6$ bacteria and 2,500 other microorganisms. These had increased, after 72 hours, to 1.9 macroorganisms, $>24x10^6$ bacteria and 28,000 microorganisms. Scheer (1945) recorded 53 hydroids, 11 bryozoans and 11 ascidian settlers on 3x5 inch glass

plates immersed in seawater for 7 days. The possibility remains, therefore, that 'conditioning' of a substratum may occur rapidly within 1 or 2 days of submersion.

Although larval settlement on immersed substrata may occur in relatively low numbers during the first few weeks of submergence, many studies have recorded most abundant larval settlement on surfaces which have been immersed for longer periods. Nair (1962) examined the fouling and wood-boring organisms on a series of short- and long-term test boards immersed at 5 sites in western Norway, and noted that the short-term blocks (immersed for 30 day intervals throughout the study period) failed to attract a large number of the organisms that readily settled on the long-term blocks. Withers and Thorp (1976) found that for panels immersed in winter months colonization by the hydroids *Sertularia* spp. and *Hydrallmania falcata*, and to a lesser extent the bryozoan *Alcyonidium* spp., was slight on those immersed for less than 4 weeks and heaviest on those immersed for more than 8 weeks. Similarly, on panels immersed in Lynnhaven Bay, Virginia, in April, Otsuka and Dauer (1982) recorded an elapse of approximately 3 weeks before any macroinvertebrate settlement occurred; hydroids, barnacles and *Botryllus schlosseri* were the first species to colonize, and *Molgula manhattensis* and *Polydora ligni* colonized during the following week. Osman (1982) found that over 40% of all the species found on panels during

his study were never found on those that were exposed for less than 2 months. Mawatari and Kobayashi (1954) examined the seasonal settlement of fouling organisms by immersing blackened glass panels at monthly or 10-day intervals, for every month between June 1952 and May 1953. This enabled them to assess the effect of panel 'age' on settlement, by comparing the numbers settling on the monthly panels with those recorded on the panels submerged for the 3 consecutive 10-day periods over the same time interval. Such a comparison indicated that a number of species (e.g. *Hydroides norvegica*, *Bugula avicularia*, *Tubulipora pulchra*, *Mytilus edulis and Botrylloides violaceum)* were consistently more abundant on the 1-month-old panels, others (e.g. *Pteria martensii*) were more abundant on the 10-day-old panels, while a third group of species, including *Spirorbis foraminosus*, *Watersipora cucullata*, *Electra angulata*, *Balanus amphitrite communis*, and *Leptoclinum* sp. showed no consistent patterns. Studies by Marszalek *et al.* (1979) and Little (1984) on microfouling development suggest that larval settlement on immersed substrata may be dependent on the development of a two-tiered microfouling layer. The first tier, or initial layer, is in intimate contact with the substratum and consists primarily of bacteria, fungi, and non-motile diatoms; above is the second tier, consisting of diatoms, ciliates, flagellates, bacteria, fungi and a variety of other organisms in lesser abundance. Marszalek *et al.* (1979) found that after approximately 5 weeks submergence in

subtropical sea-water, the fouling layer on glass and stainless steel substrata developed into a two-tiered structure. It was on samples exposed for more than 5 weeks that they recorded numerous invertebrates in the thick fouling layer. Little (1984) also observed the development of a two-tiered microfouling layer after several weeks submergence; however, she also found a single barnacle attached to aluminium foil after 7 days, before either filamentous bacteria or diatoms were observed. Thus, if there is a prerequisite of a complex microfouling layer for larval settlement it is evidently not an absolute requirement, which supports the conclusions from the present study.

It is evident from the results in this study, and the observations from a number of other fouling assemblages, that estimates of the season of larval settlement based on the number of new settlers on a surface exposed for a relatively brief period may be unreliable. Many studies have estimated larval attachment rates from substrata exposed for short intervals throughout the duration of the principal experiments, for example, McDougall (1943), Osman (1977), Dean and Hurd (1980), Chalmer (1982), Harms and Anger (1983) and Todd and Turner (1986).

A number of studies in the literature have examined the influence of the 'age' of a substratum on settlement by considering larval settlement into epifaunal assemblages of differing 'ages' (e.g. Sutherland and

Karlson, 1977; Breitburg, 1985). However, most of these have considered assemblages which have developed over periods ranging from several months to 2 or 3 years, and have been primarily concerned with the influence of the established resident assemblages on the settling of invertebrate larvae, rather than with examining the initial stages of assemblage development on essentially bare surfaces, where the 'age' of the microbial film itself might be of significance. Zobell and Allen (1935) have, however, stressed that not only do bacteria play an important role as primary film-formers, but they are also found in abundance associated with the assemblages on surfaces during the later stages of fouling. Although the importance of an established assemblage is not disputed, in this study the extent of larval recruitment was so low that larvae were more likely to encounter bare space than another resident, even on panels immersed for 5 to 6 months during peak settlement periods. Thus, if the microbial film was important, it may have had a more significant effect on larval settlement than the resident assemblages in this study. A study more directly comparable to this one is that of Chalmer (1982), who examined the colonization of sets of plates which had been immersed for different periods ranging up to 7 months. He compared the abundance of settlement of *Anomia trigonopsis*, encrusting bryozoans (= *Schizoporella unicornis* and *Watersipora subovoidea*) and *Ostrea* spp. over the same time interval, between sets of plates which had been immersed for different lengths of time. Chalmer

(1982) found evidence that these species settled in reduced numbers, or not at all, on the oldest plates, and that there was a tendency for lower settlement on the newest plates than on those which had been immersed for 1 or 2 months. However, this preference was not consistent and Chalmer (1982) concluded that it probably depended on the identity and abundance of the other organisms, including microorganisms, already on the plates. The results of Chalmer's (1982) study are thus very similar to those observed in this study especially with respect to recruitment onto younger panels. The differences which were noted between the older surfaces in the 2 studies may have arisen because the oldest plates used by Chalmer (1982) bore well-developed fouling assemblages.

Some of the most conclusive evidence regarding the influence of microbial films of different 'ages' on larval settlement has come from studies on the development of epiphytic fauna on marine algae and seagrasses. Stebbing (1972) found that significantly more larvae of *Scrupocellaria reptans*, *Spirorbis (Janua) pagenstecheri* and *S.corallinae* forma *reptans* settled on younger areas of *Laminaria digitata* and fewer settled on older regions. He suggested that the choice of settlement site might be influenced by the presence or absence of a specific epiphytic or epizoic microflora, the spatial distribution of which, on the living substratum, was associated with the age of the substratum; thus the larvae were able to differentiate between young and old pieces of *L.digitata* and settled

preferentially on the younger parts. Nishihira (1968, cited in Chia and Bickell, 1978) examined the distribution of newly settled epiphytic hydroids on marine grasses. The older portions of the plant received the heaviest settlement, which he attributed to the distribution of the microbial and diatom film present on the older parts of the plants. Similarly, Nelson (1979) found that *Janua* (D.) *brasiliensis* preferentially settled on the older portions of the blades of *Zostera marina*. Nelson (1979) attributed this to the fact that young *Z.marina* blades were relatively nonconducive to fouling until a diatom mat had formed covering the epithelium. Kirchman *et al*. (1982) and Mitchell and Kirchman (1984) found that the numbers of bacteria increased significantly from the base to the leaf tip of *Z.marina*, and suggested that the distribution of *J.(D.) brasiliensis* may be determined primarily by the bacterial population rather than by diatoms. Selection for frond age may therefore be of widespread occurrence. It should, however, be noted that other factors, which may or may not be directly related to the 'age' of the alga or seagrass, may also influence the settlement of epiphytic fauna (see, for example, Stebbing, 1972).

The first stage in the development of an invertebrate fouling assemblage on unoccupied substrata, after the formation of a microfouling complex, is the settlement of larvae. However, larval settlement varies markedly both seasonally and annually (see, for example, Osman, 1977;

Sutherland and Karlson, 1977; Harms and Anger, 1983; and Todd and Turner, 1986). As a consequence of these temporal variations in larval abundance, and the continuity of larval settlement, the pattern of assemblage development will vary depending on the time when a bare surface (i.e. new or recently freed substrata) becomes available for colonization. Only those species which are settling when a surface becomes available can colonize it; those species which are not settling at that time will be absent from the assemblage; i.e. the species composition of an assemblage reflects seasonal changes in larval abundance and availability (Osman, 1977).

The marked seasonality of larval availability appears to have been an overriding factor influencing the development of assemblages in this study. Peaks in larval recruitment (e.g. in August and October 1985 at the lower site and May/June 1985 at the upper site) were recorded on all panels immersed at the time, apparently irrespective of panel 'age' - with the exception of the most recently-immersed panels. These patterns are clearly evident in Figures 3.1., 3.2. and 3.3.. Similar results are evident in a number of other studies (Scheer, 1945 (see Tables II, III, IV); Kawahara, 1963 (see Tables 1-4) and 1965 (see Figure 15 and Tables 1 and 2); Harms and Anger, 1983). For example, Scheer (1945) recorded 36, 72 and 44 new erect bryozoan settlers during a 2 week period in June 1944, on glass plates that were 97, 55 and

43-days-old respectively. Kawahara (1963) suggested that although the species recorded on immersed concrete blocks occurred in characteristic developmental stages of the communities, during a period of peak settling activity larvae may be capable of settling in earlier developmental stages than those in which they were usually recorded. Thus, during periods of low larval settling activity a species may be relatively rarely found on an "unfavourable" substratum; conversely, during periods of larval abundance there may be little difference between "favourable" and "unfavourable" substrata with respect to the numbers of attaching larvae of a particular species (Kawahara, 1963).

Scheer (1945) concluded that the character of the sequence of community development did not vary, but the length of time required for the sequence of events did, being dependent on the season of the year - the changes occurred more rapidly during the warmer months. Similarly, Kawahara (1963, 1965) recorded year round changes in the "velocity of community development". Kawahara (1963) found, for example, that the time required to attain the "growth period" (in which the growth of the dominant species became distinct) varied greatly among blocks immersed at different dates, e.g. approximately 84 days on blocks immersed on January 31st compared to 21 days on blocks immersed on April 21st. However, the date of attainment of this stage varied relatively little, occurring between the end of April and mid-May on all the blocks irrespective of block 'age'.

Kawahara (1963) attributed this principally to the settlement of the barnacle *Balanus trigonus* which settled in variable numbers, apparently irrespective of the length of immersion of the blocks; similarly *Bugula neritina* appeared abundantly in late July on all the blocks, but was also lost simultaneously on all blocks in August, irrespective of their 'age'. As well as rapid macroinvertebrate settlement on blocks immersed during the period of peak settlement, Kawahara (1963) also found that the development of the "meso-fouling layer" on newly-immersed blocks, was not a distinct phase but occurred simultaneously with macroinvertebrate settlement. Without further study of the microbial films which developed on the panels in the present study, it was not possible to determine, whether, during the summer, microfouling occurred more rapidly compared to the rate of development during the winter months. This may have rendered panels more 'suitable' for larval settlement at a 'younger age'. Conversely, once panels had developed microbial films during the initial period of submergence, they might have been settled on irrespective of 'age', if there were larvae potentially capable of settling, available in the water column. In other words, was larval selectivity at settlement, or larval availability and abundance, controlling the patterns evident in the results from this study?

The species which characterized the seasonal progression of the pile-dwelling assemblages studied by

McDougall (1943), as well as exhibiting a wide seasonal variation in larval abundance, were also short-lived. Thus the organisms which settled during the winter were for the most part dead or moribund by spring, and were consequently replaced by the species breeding primarily in the spring. Similarly, many of the species recorded in the present study were relatively short-lived. Thus, for example, of the 38 ascidian recruits (15 *D.grossularia* and 23 *T.tenerum*) recorded on the April 1984-initiated panels between 27/6/84 and 28/7/84, at the upper site, all but a single *T.tenerum* were dead by 30/8/84. On the lower site January 1985-initiated panels, 84 spirorbids recruited between 7/5/85 and 4/6/85, of these 52 were dead on 4/6/85 and only 4 were alive on 5/7/85. Similarly, 147 *P.triqueter* recruited between 21/6/85 and 16/8/85 on the lower site March 1985 panels, 102 were dead on 16/8/85 and another 30 had died by 2/9/85. Between 18/6/85 and 17/8/85 46 cheilostome ancestrulae and 45 *S.unicornis* colonies recruited to the May 1985 lower site panels, 40 of each were dead on 17/8/85, and a further 5 and 2 colonies, respectively, were dead on 14/9/85. These patterns were also evident if the average percent mortality recorded during the whole period of panel immersion was considered; for example, 91% of the barnacles (*Semibalanus* spp.) which recruited to the upper site April 1984 panels were dead at the end of the immersion period; at the lower site, for example, 94% of the *P.triqueter* on the May 1984 panels, and on the August 1985 panels 42% of the

cheilostome ancestrulae and 63% of the spirorbids, had died by the end of the respective immersion periods for each set of panels. The assemblages developing in this study were thus characterized by high levels of post-settlement mortality. Very few of the recruits were resident on the panels for the duration of more than one sampling period - this was true apparently irrespective of taxonomic group, site or season. These high post-settlement mortality levels may have been due to physical factors, such as desiccation, or biological factors, including predation and grazing (the influence of herbivorous grazers on the epifaunal assemblages are considered in Chapter 5). High incidences of mortality have been recorded in other studies. Wethey (1985), for example, studying the settlement and survival of *Semibalanus balanoides* at 3 sites along the Yorkshire coast, recorded mortality as high as 90% in 5 days on the high-shore and 60% in the mid-shore. He further concluded that not all initial mortality was associated with the process of metamorphosis. The results were complicated, however, because mortality was consistently high at some sites, low at others and highly variable elsewhere. Furthermore, some cohorts suffered very little mortality while others experienced precipitous declines soon after settlement, and high mortality of one cohort occurred at the same time as very low mortality of other cohorts. Even cohorts that settled as little as 1 day apart showed radically different mortality rates. It was very difficult to identify the causes of such selective

mortality when cohorts differed in age by no more than 1 or 2 days. Wethey (1985) thus concluded that mortality had a strong temporal component, and that risk was age, site and day dependent.

Larval behaviour patterns may also have been influencing recruitment to the panels; some of the larvae may have been exhibiting a gregarious response to the presence of conspecifics. For example during June 1984, at the upper site, 324, 349 and 414 new *Semibalanus* spp. recruits were recorded on the panels initiated in April 1984, on which there were already 207, 225 and 251 barnacles, respectively; on the panels initiated in May 1984, 39, 44 and 51 barnacle recruits were already present at the beginning of June, and 26, 40 and 89 new recruits, respectively, were recorded at the end of the month. On the newly-immersed June 1984 panels, on which there were no established barnacles, only 4, 7 and 16 new recruits were recorded over the same time interval. However, results such as these cannot be taken as irrefutable evidence of gregariousness during settling.

Osman (1977) suggested that there may be a third type of compositional history in epifaunal communities; as well as successional or seasonal, a random pattern may occur which denies the existence of any trends or order within the system. From a study of the establishment and development of epifaunal boulder communities, Osman (1977) found that definite trends did exist, thus the

system was not random (but neither was it totally seasonal or totally successional); he concluded that the system was more likely to be stochastic, with comprehensible probability distributions. Harms and Anger (1983) and Keough (1983), for example, have also regarded larval settlement as a stochastic process. Keough (1983) concluded that even in those instances of predictable larval behaviour (e.g. where a species settles near conspecific adults), the exact patterns of recruitment were likely to be strongly influenced by chance. For species exhibiting gregarious behaviour, for example, although the distribution of subsequent recruits was predictable from a knowledge of the initial distribution of recruits, the latter was likely to be random since there were no settlement cues available to such larvae (Keough, 1983).

The results from this study indicated that the initial stages of development of the epifaunal assemblages examined, may have been dependent on the establishment of an 'attractive' microfouling layer, which may or may not have involved a succession in the microbial assemblages, and superimposed on this was the importance of the seasonality of recruitment. However, there was also evidence of a degree of randomness or stochasticity in larval recruitment. The numbers of recruits often varied considerably between replicate panels; for example, on the May 1985-initiated panels at the upper site, after 2 weeks of immersion, 59, 94 and 257 *Semibalanus* spp. recruits were observed; similarly,

at the lower site, on the February 1985-initiated panels 22, 50 and 232 *B.schlosseri/B.leachii* recruited onto the panels between 20/6/85 and 5/8/85 (no *B.schlosseri/B.leachii* were recorded on the panels prior to this date). The formation of such aggregations on the panels may have been the result of a number of biotic and/or abiotic factors, for example, they may have reflected heterogeneities in the microbial film, or they may have arisen because of patchiness in the distribution of the larvae in the plankton.

That the numbers of larvae settling on a substratum may be dependent not only on larval selectivity for surfaces that are more attractive (or less repellent), but also on the arrival of competent larvae in the immediate vicinity of the substratum, and on the physical characteristics of the water column adjacent to the substratum (which may influence the ability of larvae to attach to the surface) was suggested by Connell (1985). Similarly, Davis (1987) stressed that a highly preferred substratum would not be settled upon if larvae did not encounter it. Processes that alter the concentrations of larvae in the water column, and thus potentially produce large-scale spatial and temporal variability in larval settlement, include the timing of reproductive output by adults, differences in larval mortality rates, nearshore wind and current patterns, tides and other hydrodynamic processes (see Gaines *et al.*, 1985). For example, the spatial and temporal variability in the settling rate of

barnacles in the intertidal has been demonstrated by Shanks (1986) and Shanks and Wright (1987) to be related to the shoreward transport of cyprids by internal wave slicks. From a study of the daily settlement of barnacle cyprids, Shanks (1986) concluded that the cyprids were being transported ashore in the convergence zones, or slicks, over tidally forced internal waves. This was supported by Shanks and Wright (1987) who found that cyprids, other larval invertebrates, and natural flotsam were often significantly more abundant within slicks than in the adjacent water. They also found that the onshore transport of the cyprids influenced the longshore distribution of settling barnacles: barnacle settling rate was approximately 10 times higher in areas into which internal waves transported surface drifters, than in areas where internal waves did not transport drifters.

Connell (1985) assumed that over sites less than approximately 50 cm apart, the rates of arrival of competent planktonic larvae, as well as the physical and biological characteristics of both the water column and the substratum, would be unlikely to differ significantly between adjacent sites. Thus, he attributed any differences between sites to the physical and biological effects of the presence of attached larvae and recently metamorphosed individuals, e.g. pre-emption of space, active larval choice, or post-settlement mortalities. Gaines *et al.* (1985) have, however, emphasized the need to also consider small-scale heterogeneous distributions of larvae in the water column, as potential causes of

variable settlement. In a study of the settlement of *Balanus glandula*, at sites separated by a few metres in Monterey Bay, California, they found that equal densities of cyprids did not reach the sites. That is, the distribution of the cyprids was spatially heterogeneous, and these differences in cyprid concentrations explained more than 85% of the observed variability in barnacle settlement. Although local hydrographic conditions, contact with benthic or pelagic predators etc., could have been responsible for the removal of cyprids from the water column, Gaines *et al.* (1985) proposed that settlement itself was an important cause of the small-scale heterogeneity in larval concentrations. Thus, settlement from a water mass as it passes a seaward site may be a significant drain on larval concentrations reaching subsequent shoreward sites. They estimated that, under the conditions prevailing at the sites under consideration, a $10m^2$ area would "remove" approximately 30% of the available cyprids. Other studies have also suggested the existence of small-scale heterogeneous distributions of larvae. Keough (1983), for example, found evidence of larval "swarms", or small-scale patchiness, in the distribution of the plankton, which he suggested may generate aggregations of recruits on substrata. He concluded, however, that these patches occurred unpredictably in space and time, and that there remained a large amount of variation in recruitment that could not be explained by patchiness in the plankton. Grosberg (1982) examined the

vertical distribution in the plankton of Santa Cruz harbour, of the cyprids of *Balanus glandula* and *B.crenatus*, and found that the species had very different distributions. However, the vertical distribution of the cyprids in the plankton corresponded with the zonation of the newly settled spat and also the subsequent zonation of adult conspecifics. Thus the planktonic larval distribution, rather than larval responses to the substratum characteristics, appeared to determine the vertical limits of distribution of the newly settled individuals of these barnacles. Similar pre-settlement processes may have contributed to the distribution of larvae among the panels in this study.

The effects of substratum 'age' and larval abundance interacted with, and were dependent upon, the intensity of a variety of abiotic and biotic pre- and post-settlement processes, which in combination produced the observed recruitment and mortality patterns. Central to the importance of substratum 'age' on larval settlement is the generation of 'bare' space. However, as well as an essentially 'bare', but suitably 'conditioned' and therefore 'attractive' surface being available for settlement, the timing of space availability is important in the development of epifaunal assemblages, because only those species which are present in the watercolumn, and thus potentially capable of settling when a surface becomes available, can colonize it. The availability of 'bare' space and 'competent' larvae are affected by a

number of physical and biological parameters which exhibit hourly and/or daily random and cyclical variations, super-imposed on which there are seasonal and annual patterns of fluctuation.

Considering larval availability, many species exhibit considerable temporal variability in their reproductive cycles, larval production frequently being limited to a particular season. Gotelli (1987) found, for example, that larval production contributed substantially to temporal variation in recruitment of the compound ascidian *Aplidium stellatum*. Smedes (1984) has suggested that there are many reasons for such variability, most of which are related directly or indirectly to seasonal changes in the physical environment. Water temperature, for example, because it affects the rate of metabolic activities, physiological tolerances and the levels of phytoplankton (Smedes, 1984) is of primary importance in controlling the temporal availability and abundance of larvae through its influence on breeding cycles (see, for example, McDougall, 1943 and Nair, 1962). Smedes (1984) also suggested that seasonal variations in salinity are important factors in some locations, and that seasonal changes in water-circulation patterns could influence the transport of larvae from more distant source areas. Similarly, Gotelli (1987), although finding that water temperature was weakly correlated with the number of eggs recorded in zooids of *A.stellatum*, suggested that other

seasonal variables, such as photoperoid, could be more important than water temperature in controlling egg development.

Substratum clearance and availability may also often exhibit a characteristic seasonal pattern of occurrence. Sutherland and Karlson (1977), for example, found a temporal regularity in space availability, which they attributed to the approximately annual periodicity of adult mortality. Solitary tunicates which settled and grew during the spring and summer were often dislodged in the autumn by tidal currents, along with other organisms growing on or around them, making free-space more available at that time. Similarly, Sousa (1979) found that there was a predictable availability of space on the boulders in his study during the winter months, due to the greater probability of boulder turn-over during winter storms.

Recruitment is, therefore, "...the endpoint of a temporal sequence that includes larval development and release, mortality and losses in the plankton, larval behaviour, settlement, metamorphosis, and early juvenile mortality" (Gotelli, 1987, p. 45). Variation in any one or more of these factors will cause subsequent variation in recruitment (Connell, 1985).

4. BRYOZOAN COMPETITION

4.1. INTRODUCTION

Competition is the active demand by two or more individuals of the same species, or members of two or more different species at the same trophic level, for a common resource or requirement that is actually, or potentially, limiting (Miller, 1967). It leads to a reduction in the survivorship, growth and/or reproduction of the competing individuals concerned (Begon *et al.*, 1986). Competition has long been invoked as a major structuring force in communities; however, there is increasing evidence that other ecological processes may play a dominant or major role (see Connell, 1976; Branch, 1984; and Underwood and Denley, 1984, for example).

The consequences of intra- and interspecific competition are very different, and Underwood (1986) has stressed the importance of simultaneously examining both forms. Competition may be expected to be more intense between conspecifics because they have many fundamental features in common, and they may be expected to have similar resource requirements and to react similarly to the prevailing conditions (Branch, 1984; Begon *et al.*, 1986). The consequences of interspecific competition vary with the species involved, in particular with the amount of resource overlap between the species, the means of competition and the nature of the resource in demand (Branch, 1984). The short- and long-term responses of a species to an interspecific competitor may depend on how intense is its own intraspecific competition (Branch, 1984).

Traditionally the component elements of competition have been distinguished as "interference" and "exploitation" (Brian, 1956). Interference competition refers to any activity which either directly or indirectly limits a competitor's access to a necessary resource or requirement (Miller, 1967). It usually operates in a spatial context and assures the possession of a minimum array of resources required by one individual (Miller, 1967). Branch (1984) concluded that interference is the predominant form of competition in the sea - 80% of the examples he reviewed involved interference. Exploitation is the utilization of a resource once access to it has been achieved, depriving others of the benefits to be gained from these resources (Miller, 1967; Schoener, 1983). Elements of both interference and exploitation are probably inevitably present in competitive interactions (Brian, 1956; Miller, 1967). Schoener (1983) recognized 6 kinds of competition which he considered described the actual mechanisms more exactly than "exploitative" or "interference"; these were consumptive, pre-emptive, overgrowth, chemical, territorial and encounter competition. Pre-emptive competition (which occurs when a unit of space is passively occupied by an individual, thus preventing other organisms from occupying that space before the occupant disappears) includes aspects of both exploitation and interference and is considered to be the most common form of competition among marine organisms (Schoener, 1983).

As well as distinguishing the characteristics of the species involved and the mechanisms of competition, it is necessary to determine the nature of the resource that is competed for. In marine epifaunal assemblages space is generally considered to be the resource primarily in short supply (e.g. Jackson and Buss, 1975; Jackson, 1977a; Buss and Jackson, 1979; Russ, 1982; Paine, 1984; Sebens, 1986). Gordon (1972) considered that the only real competition that concerned bryozoans was that for space, and Vail and Wass (1981) provided unequivocal evidence that space may be a limiting factor in the growth of bryozoans on artificial substrata. A number of bryozoan species exhibited a marked increase in size after all the organisms other than bryozoans were removed from the panels, leaving more space unoccupied: *Rhynchozoon* sp. increased by 475% in the week following manipulation, *Schizoporella unicornis* increased by 257% and colonies of *Valdemunitella valdemunita* exhibited weekly size increases of 108% and 155% (Vail and Wass, 1981).

Space is often an absolute requirement in that all sessile species have a minimum space requirement for attachment, feeding and growth to reproductive maturity. Jebram (1973) found that bryozoan colonies attained maturity only after they had increased to a minimum size or number of zooids, which varied among different species and under different external conditions. Hayward and Ryland (1975) reported minimum sizes of 3.46mm^2 for

fertile colonies of *Alcyonidium hirsutum* growing on *Fucus serratus* and as small as 0.15mm^2 for *Hippothoa sp. on Macrocystis pyrifera*. Similarly, Winston and Jackson (1984) recorded a strong correlation between reproduction and colony size; the abundant species, e.g. *Steginoporella* sp. nov. and *Stylopoma spongites*, reproduced only when colonies reached maximum diameters >20mm. Once this minimum size was attained, fecundity was found to be linearly proportional to the colony area; and since bryozoan colonies have labile and indeterminate growth, and are able to redirect growth when obstructed, the minimum size requirements can be attained by the majority of colonies even where space is limited (Hayward and Ryland, 1975). Primary space is a non-renewable resource in that once it has been occupied by a sessile organism then it only becomes available again with the death of that organism (Branch, 1984; Yodzis, 1986). Also, space, particularly on a hard substratum, is a difficult resource to partition among the species and therefore competition for space frequently leads to competitive exclusion; interference competition is thus important because it enables one species to exclude another without loss of the resource.

It is generally considered that exploitative competition for food is unimportant in epifaunal assemblages - Branch (1984) in a review of competition between marine organisms, found that 4% of sessile filter-feeders competed for food compared to 96%

competing for space. Branch (1984) considered food to be a relative requirement for most marine animals because of their growth plasticity and their ability to exist on limited quantities of food. Furthermore, although food supplies are spatially and temporally unpredictable, food is relatively rapidly renewed and is readily partitionable among species, thus species which do compete for food can potentially coexist for prolonged periods (Branch, 1984). However, filter-feeders are at times able to eliminate food sufficiently rapidly and efficiently that competitors may be left without any food. Buss and Jackson (1981) and Mook (1981a) have examined the removal of suspended particles by fouling communities; Buss and Jackson (1981) found evidence of *in situ* food resource depletion, as a function of the abundance of suspension feeding organisms, in epifaunal communities. The depletion of the food resources may be sufficiently severe to cause competition. For example, high levels of depletion by sponges of the naked cell fraction, which constitutes a major component of bryozoan diets, was found to be potentially limiting to bryozoan populations (Buss and Jackson, 1981). There is increasing evidence that competition for food may play an important role in determining the outcome of spatial encounters between bryozoan species. Dudley (1970) suggested that bryozoans may be specialized to make use of the available food resources. The range of dimensions of the lophophore enabling different species to consume different size ranges of food particles, thus providing a

means by which competition between the species may be ameliorated. However, Ryland (1975) concluded, from an examination of an understone bryozoan community, that the different species had lophophores of dimensions within only restricted limits - although the permissible variation was considerable. Thus, unless the selection of food particles was very finely adjusted, Ryland (1975) suggested that it was probable that the majority of the species were exploiting a common food resource. Buss (1979a) suggested that the outcome of overgrowth interactions between colonies of bryozoans may be mediated by competition for food. Two bryozoan species, *Onychocella alula* and *Antropora tincta* , were found to differ in their lophophore dimensions, and when in contact, the feeding currents produced by the larger lophophores of *O.alula* were found to interfere with those produced by the smaller lophophores of *A.tincta*, causing a local reduction in the clearance rate. *O.alula* therefore effectively reduced the food intake by *A.tincta*; *O.alula* obtained more food, grew faster and thereby overgrew *A.tincta*, the poorer food competitor. Ryland and Warner (1986) suggested that within bryozoans, selective pressures may be operational, favouring a larger lophophore and thus balancing energetic advantage against competitive success. Okamura (1984) found that upstream colonies of *Bugula stolonifera* reduced the relative feeding success of downstream colonies of the same species. However, this was due to an alteration of flow so that the downstream colonies were exposed to a

relatively lower flux of particles, rather than by direct exploitation competition through the feeding activities causing a depletion of food particles. Conversely, the presence of a feeding colony of *Conopeum reticulum* was found to enhance the feeding of zooids of downstream colonies (Okamura, 1985). This was attributed to the active diversion, towards the substratum, of water by the upstream feeding colonies, thus altering the flow pattern over the downstream colonies.

Best and Thorpe (1986a, b) also concluded that there may be significant competition for food between bryozoans. They suggested that the ability to adjust feeding rates in response to fluctuations in food supply, which was observed for a number of bryozoan species (see Best and Thorpe, 1983, 1986a) may be a significant component of competitive ability. They found that the overgrowth ability of a species was related to the clearance rate or feeding current velocity. For example, the competitively dominant species *Flustrellidra hispida* exhibited the highest clearance rates, whereas species such as *Electra pilosa*, showing the smallest increase in feeding rate with particle concentration, were frequently outcompeted. In a comparison of the feeding current velocities of competing bryozoan colonies, Best and Thorpe (1986b) found that for *Alcyonidium hirsutum* or *E.pilosa*, with relatively small lophophores, food supply was severely depleted for polypides close to the edge of a competing colony of *F.hispida*, with larger lophophores. Although at a distance of approximately 3-4mm from the

edge of the "overcapping" colony food supply was enhanced by the availability of a strong current of unfiltered water generated by the *F.hispida* colony, Best and Thorpe (1986b) concluded that overall, "overcapping" was likely to put the colonies with smaller lophophores at a serious competitive disadvantage. Because of the net depletion of food resources available to such colonies, there was a concomitant reduction in the likelihood of overgrowth of species with larger lophophores.

In reality a sessile organism cannot separate spatially and temporally its requirements for space and for food (Buss, 1979a; Best and Thorpe, 1986a,b). Therefore, competition for space and for food are not mutually exclusive and the demonstration of competition for space does not preclude the possibility of competition for food (Jackson and Winston, 1982). Yodzis (1986) suggested that there is a continuum of intermediate strategies between the 2 extremes of consumptive competition and competition for space.

Competition for space in epifaunal assemblages occurs whenever the space available on the hard substratum is reduced sufficiently for the lateral margins of the colonies to come into contact (Buss, 1979a). When 2 such colonies encounter one another, either of 2 results may occur:

(i) the 2 colonies cease growth along the shared margin; any further growth is diverted in

another direction and may thus be termed compensatory.

(ii) 1 or both colonies expand into the space occupied by the other.

Overgrowth or interference competition between colonies is a frequent method of competition for space in epifaunal assemblages, involving especially bryozoans, sponges and ascidians. Overgrowth may result in the death of the overgrown colony, but more frequent is the interruption of growth and a reduction in colony size, acting to limit the area occupied and hence the potential fecundity of the colony (Buss, 1986). Total overgrowth normally results in the death of most species, however epizooism among sponges frequently occurs without harm to either participant (Rützler, 1970). It is unknown how long most invertebrates can withstand overgrowth and the length of time will depend strongly on the overlying species and possibly on the time of year (Sebens, 1986; see also Todd and Turner, 1988). Large solitary organisms may also be able to survive overgrowth as long as their feeding structures remain unhindered (Jackson, 1977a).

Bryozoans exhibit a wide range of morphological strategies (see, for example, Jackson, 1979b) which confer fundamentally different susceptibilities to overgrowth interactions. Buss (1979b), for example, predicted that "sheet-like" forms would be better spatial competitors than more "runner-like" forms. The relative

competitive abilities of "sheet-like" and "runner-like" forms have been documented for a number of environments: Stebbing (1973a), for example, found that *Electra pilosa*, which commonly grows in a "runner-like" form when inhabiting the fronds of *Fucus serratus*, was consistently overgrown (65 - 95% interactions) by the "sheet-like" competitors *Alcyonidium* spp. and *Flustrellidra hispida*. Interactions between the "sheet-like" species invariably resulted in the redirection or cessation of growth, with overgrowth occurring in less than 10% of the interactions. Similarly, Taylor (1979) found that fossil bryozoans with "high overgrowth ability indices" all had "discoidal" morphologies, whereas species with "linear" morphologies tended to have "low overgrowth ability indices". Buss (1979b) also suggested, however, that the highly directional growth exhibited by runner-like forms may represent a morphological response for the location of refuges which are relatively free from interspecific interference competition. For example, the directional growth of *Electra pilosa* on *Fucus serratus* fronds, predominantly towards the youngest and least colonized parts of the substratum, may lead to a decrease in the intensity of competition for space (Ryland and Stebbing, 1971).

Relatively little is known about the mechanisms by which bryozoans overgrow or defend space that is already occupied. Such mechanisms must involve differences in the growth rates of the 2 colonies in the region of overgrowth (Jackson, 1979a), and Buss (1986) suggested

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that a number of bryozoans have evolved structural modifications that allow them to reposition their growing margins in ways that fundamentally alter their competitive abilities. A number of cheilostome bryozoans (e.g. *Schizoporella unicornis floridana* (Banta, 1972); *Stylopoma spongites* and *Parasmittina* sp. (Jackson, 1979a)) are able to add new ("secondary") layers of "adventitious" zooids on the top of the original ("primary") layer of "primogenial" zooids by a process of frontal budding (Banta, 1972). Frontal budding results in the elevation of the colony surface above the substratum, creating relatively massive colonies which may present physical barriers to overgrowth. Alternatively, this may confer a competitive advantage by enabling the overgrowth of neighbouring colonies if the latter do not exhibit a similar capacity to alter the vertical position of their growing margins. Taylor (1979) noted the development of similar multilamellar growth in fossil bryozoans encrusting Jurassic bivalve shells. Gordon (1972) and Osborne (1984) have recorded the development of 2 types of finger-like extensions at, or close to, colony interfaces, representing frontal and terminal stolonal outgrowths. These are localized areas of higher growth rate and increased colony thickness and are thus potentially advantageous as either defensive or aggressive structures in competition for space (Osborne, 1984). The extension of stolonal outgrowths over the zooids of the growing edge of the opposing colony will undoubtedly facilitate overgrowth; furthermore, frontal

stolons may actually form a secondary growing edge which may lead to a reversal in the direction of overgrowth (Osborne, 1984). Conversely, stolonal outgrowths may have a defensive function in preventing overgrowth by neighbouring colonies, or by maintaining gaps beneath the overgrowing colony to prevent the fatal smothering of the overgrown zooids (Osborne, 1984). The formation of specialized barriers to overgrowth is also evident in other species: for example, Stebbing (1973a,b) suggested that the development of elongated frontal spines by *Electra pilosa* zooids is correlated with interspecific competition, preventing or slowing overgrowth at the points where competing colonies come into contact. Other bryozoans exhibit the capacity to redirect growth edges by developing marginal zooids which are unattached to the underlying substratum and which allow erect growth away from the substratum surface (Buss, 1986). The ability to locally lift off the substratum allows a colony considerable capacity for modifying the vertical relief of its growing surface relative to substratum-bound competitors (Buss, 1986). Colonies can thus create barriers to overgrowth and/or may begin to grow up and over neighbouring colonies (Jackson, 1979a). Jackson (1979a) frequently observed raised growing edges among colonies of *Steginoporella* sp. nov., *Stylopoma spongites* and *Parasmittina* sp. where they were in contact with other sessile organisms. Little is known of the cellular and subcellular basis of such differing growth patterns, and genetic data are entirely lacking (Buss, 1986).

Species, and even individual colonies, exhibit marked variability in the degree to which these devices are deployed. Buss (1986) concluded that this variability in the expression of the different morphologies undoubtedly contributes to the unpredictability of outcomes among bryozoans, and to observations that overgrowth results are correlated with the encounter conditions.

Competition may be more subtle than simply direct overgrowth. A number of sponges, cnidarians and ascidians are known to produce allelochemicals important in competition for space (see, for example, Jackson and Buss, 1975). Osborne (1984) has suggested that the possible production of allelochemicals by bryozoan stolonal overgrowths should be investigated; and Dyrynda (1986) reported that the few bryozoan species that have been investigated are rich in sources of secondary metabolites which may act to facilitate or inhibit overgrowth.

Species differ in their abilities to overgrow other competitors, and become locally dominant. The frequency of particular outcomes of overgrowth interactions between pairs of species provides a measure of the competitive ability of the species concerned. Ranking patterns of these competitive abilities may form hierarchies or networks (Gilpin, 1975; Jackson and Buss, 1975; Buss, 1979b; Buss and Jackson, 1979; Petraitis, 1979; see also Karlson and Jackson, 1981; Karlson and Buss, 1984, and Karlson, 1985). A hierarchy, or transitive pattern,

results when all the species of higher-rank outcompete all the species of lower-rank; i.e. species A > species B > species C > species D. Jackson and Buss (1975) suggested that hierarchies will be important in maintaining a high species diversity when coupled with physical or biological disturbance, operating specifically upon the competitive dominant (species A). Networks, or intransitive patterns, occur when the competitive abilities of space occupying organisms do not follow a simple linear sequence or hierarchy; at least one species of lower-rank is able to outcompete one or more species of higher-rank. That is, for example, species A > species B > species C > species D, but species D > species A or B. Buss and Jackson (1979) defined a competitive network as the occurrence of a loop in an otherwise hierarchial sequence of interference competitive abilities. Gilpin (1975) suggested that interference competition permits nontransitive relationships because each interference interaction may be unique. Jackson and Buss (1975) proposed the network model to explain the maintenance of high species diversity in space-limited systems in the absence of high levels of disturbance. They based the model on a study of the epifauna encrusting the undersurfaces of foliaceous reef corals and suggested that allelochemicals may provide the necessary specific mechanism to enable networks to become established. Buss (1980) recognized that competitive rankings may vary from cases of perfect transitivity, through varying degrees of intransitivity

(where species A may or may not displace species B, species B may or may not displace C and species A may or may not displace species C), to occasional cases of perfect intransitivity. He suggested that the term "competitive networks" should be used to describe all situations exclusive of perfect transitivity, and "circular networks" to describe perfect intransitivity.

Where competitive networks occurred, Buss and Jackson (1979) and Buss (1979b) recognized a number of consequences that would arise from basic patterns in settlement, growth and mortality. The exact spatial position occupied by an organism relative to its neighbours, and the rates of overgrowth may determine the resultant species' distribution on the substratum. Furthermore, the time required for a spatial dominant to emerge will be increased by the feedback properties of the network, relative to the time required if a hierarchy existed.

There is increasing evidence, however, that competitive hierarchies and networks are not the only possibilities for competitive dominance relationships. Rather, they represent the extremes of a continuum of relationships that can be produced by contingent interactions, and represent the ideal states which are rarely encountered (see, for example, Connell, 1976; Kay and Keough, 1981; Quinn, 1982; Russ, 1982). Yodzis (1986) suggested that when competitive ability depends on a single attribute, then the ranking of species would be

expected to produce a hierarchy, depending on the degree to which each species possessed that one attribute. For example, if the sole factor determining the outcome of competition between cheilostome bryozoans inhabiting cryptic coral reef communities was maximum growth rate then the species could be ranked in a hierarchy (see Table III, Winston and Jackson, 1984). Thus the fewer the factors determining competitive superiority, the more likely are hierarchies. Conversely, the more species and the more numerous and complex the interactions, then the more likely are networks. The greater the indeterminancy or stochasticity of competition, arising, for example, because of "competitive equivalence" (Kay and Keough, 1981) or "symmetry" (Connell, 1983) of the interacting competitors, then the more likely it is that an intermediate pattern of relationships will arise. Such variation in competitive outcomes, leading to disruption of the theoretical networks or hierarchies, has been attributed to a number of factors. These include differences in the size of the individual competing colonies (Buss, 1980; Russ, 1982; Sebens, 1986; see also Sebens, 1982), the condition of the colony surfaces at the region of contact (Jackson, 1979a; Osman and Haugsness, 1981), spatial heterogeneity (Walters and Wethey, 1986), and the directionality of growth (Jackson, 1979a; Harris and Irons, 1982; Liddell and Brett, 1982; Rubin, 1982).

FIGURE 4.1. The development of competitive interactions between the encrusting bryozoans on 2 panels immersed at Cuan Ferry. The panel on the left was initiated in October 1984 and photographed in May 1985 (a), June 1985 (b) and July 1985 (c); that on the right was initiated in August 1984 and photographed in May 1985 (d), June 1985 (e) and August 1985 (f).

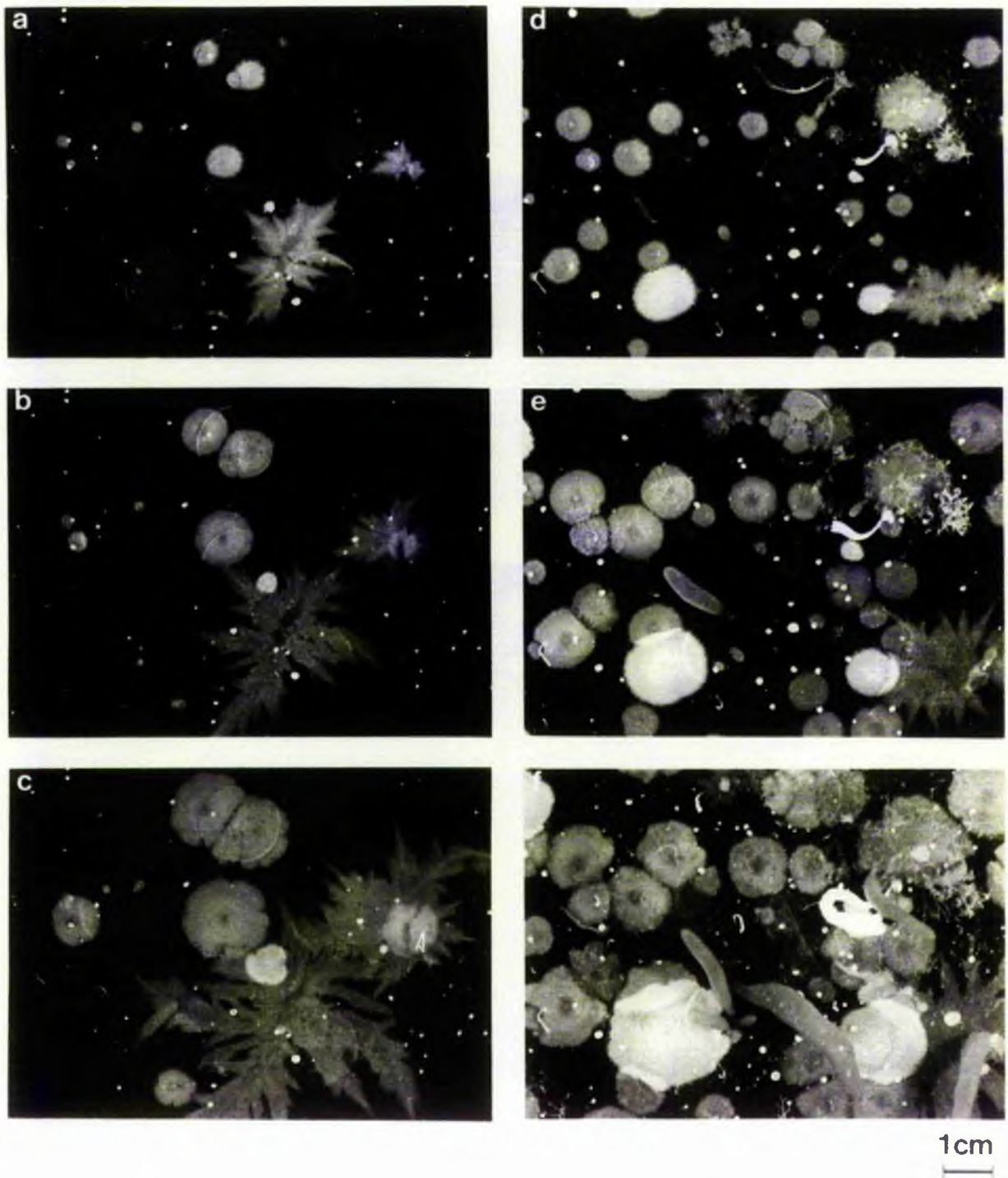

a
b
c
d
e
1cm

TABLE 4.1. - Summary of all the interactions (overgrowths and ties) recorded at 4 sites, in 2 years and among 12 encounter angles (sectors).

	Clachan 1983	Clachan 1984	TOTAL CLACHAN	Cuan 1983	Cuan 1984	TOTAL CUAN	St.Andrews ST 1984	St.Andrews IT 1984	TOTAL 1983	TOTAL 1984	T O T A L
NUMBER OF SPECIES	13	12	14	7	13	14	12	7	14	18	18
NUMBER OF SPECIES PRS	44	50	59	13	30	33	34	13	52	76	82
NUMBER OF INTERACTIONS	362	773	1135	20	184	204	215	207	382	1379	1761
NUMBER OF "OVER - GROWTHS"	262	519	781	11	126	137	152	127	273	924	1197
NUMBER OF "TIES"	100	254	354	9	58	67	63	80	109	455	564

SECTOR	W	T	Total	W	T	Total	W	T	Total	W	T	Total	W	T	Total	W	T	Total	W	T	Total	W	T	Total	W	T	Total	W	T	Total
1	67	30	97	106	78	184	173	108	281	5	2	7	22	15	37	27	17	44	22	8	30	28	22	50	72	32	104	178	123	301	250	155	405
2	33	13	46	77	39	116	110	52	162	1	1	2	15	6	21	16	7	23	17	8	25	18	11	29	34	14	48	127	64	191	161	78	239
3	11	2	13	23	10	33	34	12	46	0	0	0	5	1	6	5	1	6	7	1	8	8	6	14	11	2	13	43	18	61	54	20	74
4	24	9	33	73	27	100	97	36	133	1	1	2	14	9	23	15	10	25	20	11	31	11	7	18	25	10	35	118	54	172	143	64	207
5	5	1	6	6	0	6	11	1	12	0	1	1	2	1	3	2	2	4	6	1	7	2	0	2	5	2	7	16	2	18	21	4	25
6	17	6	23	36	9	45	53	15	68	2	2	4	11	4	15	13	6	19	11	5	16	13	5	18	19	8	27	71	23	94	90	31	121
7	15	2	17	45	7	52	60	9	69	0	0	0	11	7	18	11	7	18	8	1	9	13	7	20	15	2	17	77	22	99	92	24	116
8	16	1	17	28	9	37	44	10	54	0	0	0	6	4	10	6	4	10	12	2	14	3	4	7	16	1	17	49	19	68	65	20	85
9	3	3	6	9	2	11	12	5	17	0	0	0	5	0	5	5	0	5	4	4	8	2	2	4	3	3	6	20	8	28	23	11	34
10	25	9	34	49	27	76	74	36	110	1	2	3	19	6	25	20	8	28	18	6	24	11	2	13	26	11	37	97	41	138	123	52	175
11	13	5	18	17	9	26	30	14	44	0	0	0	7	1	8	7	1	8	9	3	12	6	2	8	13	5	18	39	15	54	52	20	72
12	33	19	52	50	37	87	83	56	139	1	0	1	9	4	13	10	4	14	18	13	31	12	12	24	34	19	53	89	66	155	123	85	208

(W = Wins, T = Ties)

4.2. RESULTS

Figure 4.1. illustrates the development of bryozoan assemblages on the underside of the artificial substrata. Large amounts of free space were available only when the panels were initially immersed. Following larval recruitment, the bryozoan colonies grew in size, resulting in a progressive reduction of space; as the growth margins came into contact with neighbouring colonies, there was increased competition for space. Table 4.1. summarizes all the competitive interactions observed at the 4 sites and in the 2 years of the study. 64% of the interactions were observed at the subtidal site, Clachan, where bryozoans were most prolific. The remaining interactions were approximately equally distributed among the intertidal sites. Eighteen species were observed, the greatest species richness being found at the west coast sites; the east coast sites were comparatively poor in terms of species richness and abundance of bryozoans. Many species were common to all 4 sites, e.g. *Alcyonidium* spp., *Callopora lineata* (L.), *Celleporella hyalina* (L.) and *Cribrilina cryptooecium* Norman. Some were specific to the west coast sites, e.g. *Escharoides coccinea* (Abildgaard), *Microporella ciliata* (Pallas), and *Membraniporella nitida* (Johnston); *Schizomavella linearis* (Hassall) and *Umbonula littoralis* Hastings were only recorded at the east coast sites. *Callopora aurita* (Hincks) was the only species observed solely at the subtidal site.

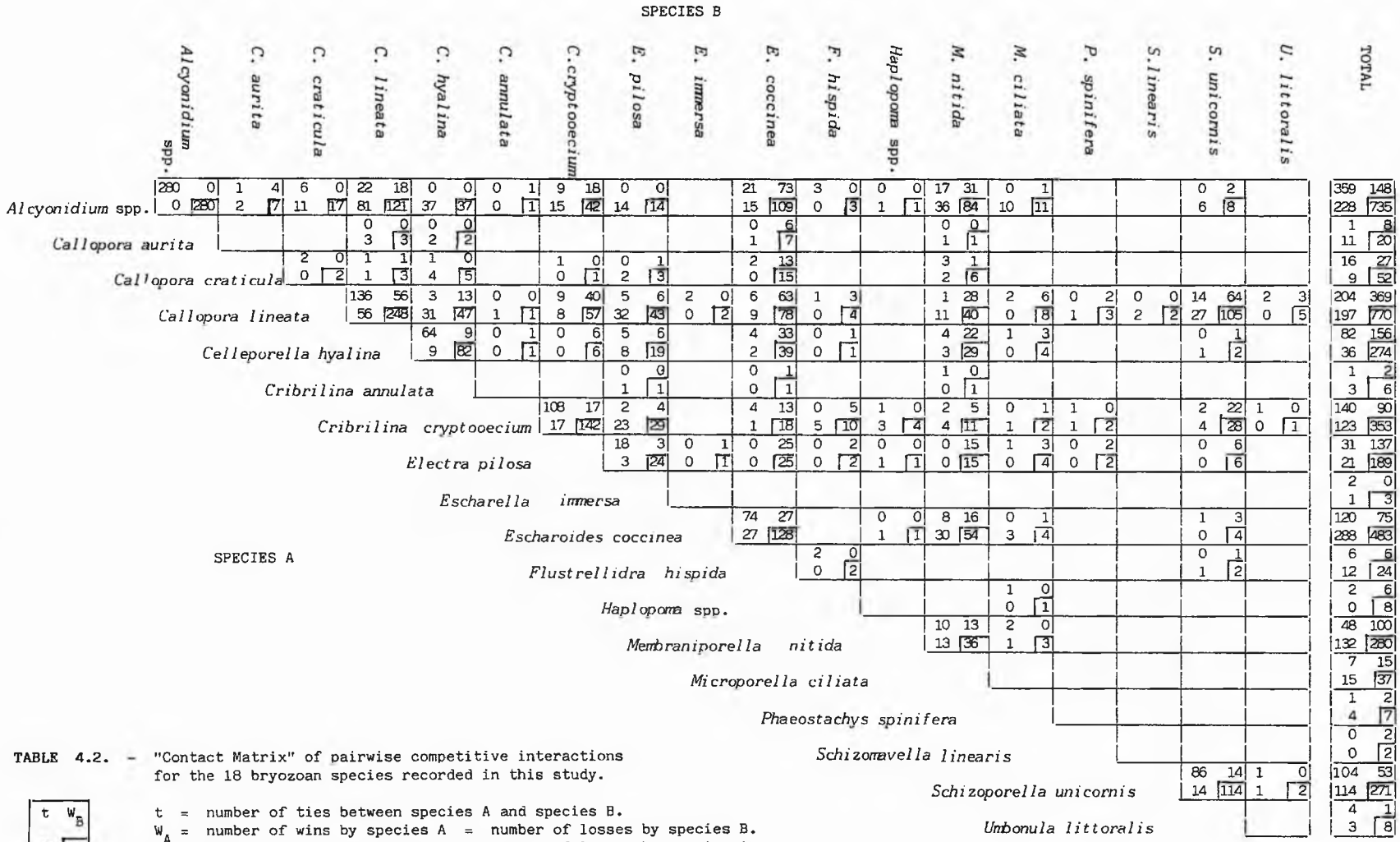


TABLE 4.2. – "Contact Matrix" of pairwise competitive interactions for the 18 bryozoan species recorded in this study.

t	W_B
W_A	T

t = number of ties between species A and species B.
W_A = number of wins by species A = number of losses by species B.
W_B = number of wins by species B = number of losses by species A.
T = total number of interactions between species A and species B.

GRAND TOTALS

- Total Nos. Interactions = 3522
- Total Nos. Wins = 1197
- Total Nos. Losses = 1197
- Total Nos. Ties = 1128

FIGURE 4.2. Examples of overgrowth competition between encrusting bryozoans:

(a) *Cribrilina cryptooecium* (Cc) overgrowing *Alcyonidium* sp. (Al) - note the elongated terminal stolonal outgrowths (sensu Osborne, 1984) of the *C.cryptooecium* colony extending over the *Alcyonidium* sp.. (Scale bar ≏ 0.90mm)

(b) *C.cryptooecium* overgrowing *Electra pilosa* (Ep) - note the elongated terminal stolonal outgrowths of the *C.cryptooecium* colony and the redirected growth of the *E.pilosa*. (Scale bar ≏ 0.90mm)

(c) *Microporella ciliata* (Mc) overgrowing *C.cryptooecium*. (Scale bar ≏ 0.90mm)

(d) *Alcyonidium* sp. overgrowing *E.pilosa*. (Scale bar ≏ 1.40mm)

(e) *Schizoporella unicornis* (Su) overgrowing *Callopora lineata* (Cl). (Scale bar ≏ 0.85mm)

(f) *S.unicornis* overgrowing *C.cryptooecium* - note the unequal distribution of growth along the colony margin of the *C.cryptooecium*. (Scale bar ≏ 1.40mm)

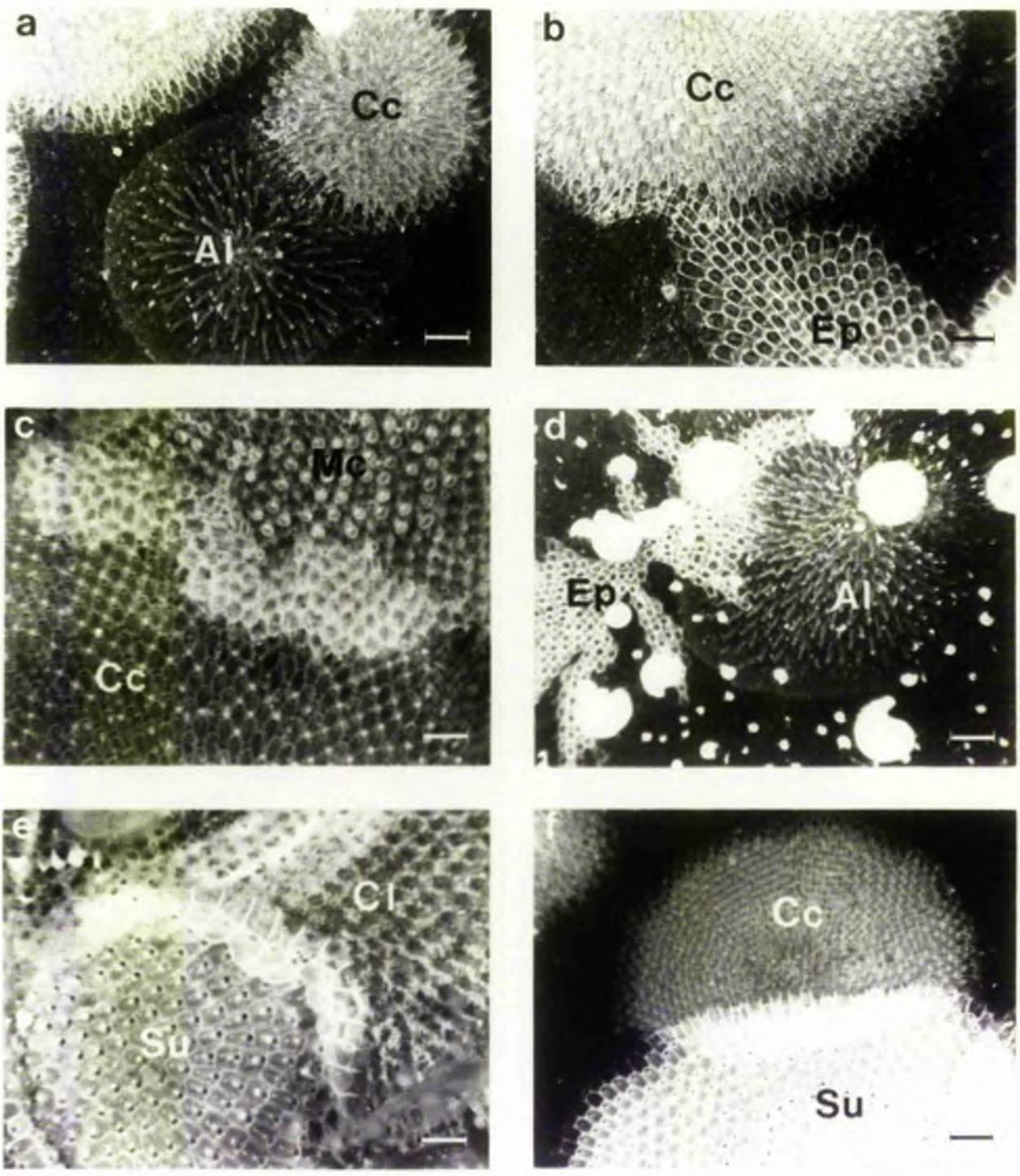

a
Cc
Al
b
Cc
Ep
c
Mc
Cc
d
Ep
Al
e
Cl
Su
f
Cc
Su

FIGURE 4.3. Examples of bryozoan "tie" or "stand-off" interactions:

(a) An intraspecific *Callopora lineata* (Cl) interaction - note that both the colonies are exhibiting vertical growth away from the substratum. (Scale bar ≙ 0.95mm)

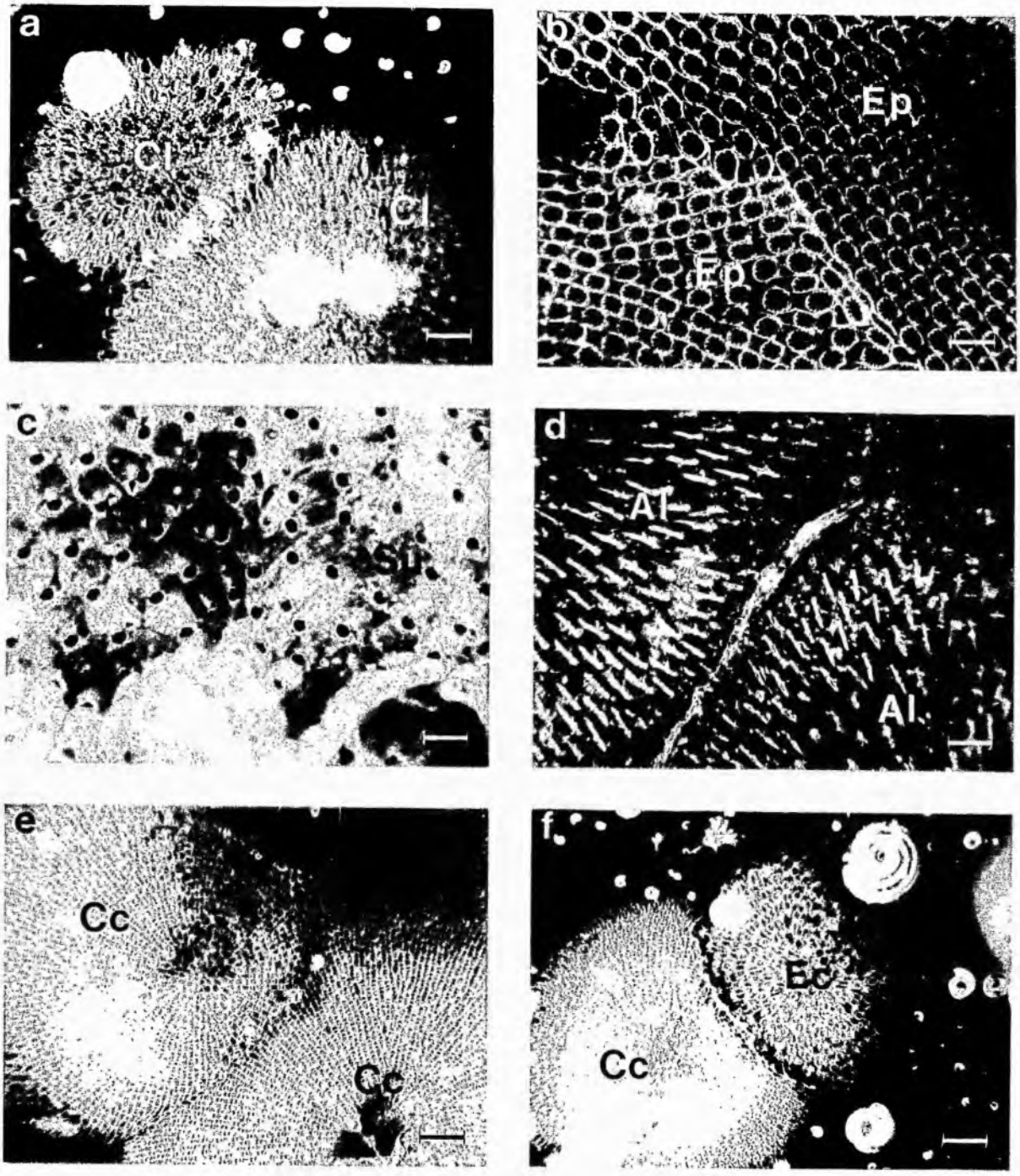
(b) An intraspecific *Electra pilosa* (Ep) interaction - note the marked re-direction of the zooids in the vicinity of the contact margin. (Scale bar ≙ 0.60mm)

(c) An intraspecific *Schizoporella unicornis* (Su) interaction - note the possible occurrence of "homosyndrome" (sensu Knight-Jones and Moyse, 1961) between the zooids of the adjacent colonies. (Scale bar ≙ 0.40mm)

(d) An intraspecific *Alcyonidium* sp. (Al) interaction - note the formation of a distinct 'ridge' at the margin of contact between the 2 colonies. (Scale bar ≙ 0.65mm)

(e) An intraspecific *Cribrilina cryptooecium* (Cc) interaction - note that in the central region of the contact margin there is very little overgrowth of either colony and at the periphery the zooids of each colony are aligned almost parallel to each other. (Scale bar ≙ 1.50mm)

(f) An interspecific interaction between *Escharoides coccinea* (Ec) and *C.cryptooecium* - note that both the colonies are exhibiting vertical growth, away from the substratum, in the zone of colony contact. (Scale bar ≙ 1.55mm)


a
Cl
Cl
b
Ep
Ep
c
Su
d
Al
Al
e
Cc
Cc
f
Bc
Cc

Furthermore, a number of species were recorded only at intertidal sites, e.g. *Escharella immersa* (Fleming), *Flustrellidra hispida* (Fabricius), *S.linearis* and *U.littoralis* (personal observations).

Of the 1761 interactions examined, 68% concerned overgrowths (i.e."wins" or "losses") and 32% were "ties". Irrespective of the numbers of observations, there was little variation in this proportional outcome between sites or between years.

Table 4.1. also summarizes the interaction data in terms of the encounter angle, or sector of contact, between the competing colonies. Irrespective of the site or year, most encounters were observed in the frontal sectors. 23% of all interactions were in sector 1 (see Figure 2.9., Chapter 2) and 48% in sectors 1, 2 and 12. Fewer encounters were recorded for the lateral and terminal sectors; *viz.* 7% in sector 7 and 18% in sectors 6, 7 and 8. There was also an apparent trend in the outcome of the interactions among sectors. More overgrowths occurred in the terminal sectors: 79% of all the interactions recorded in sector 7 were win or loss outcomes, compared to 62% in sector 1. Conversely, there was a greater incidence of ties in the frontal sectors (38% in sector 1) compared to the terminal sectors (21% in sector 7).

Table 4.2. is a "contact matrix" for the competitive interactions of the 18 species observed during the study (see also Figures 4.2. and 4.3.). Of a total of 171

possible intra- and interspecific pair-wise interactions, 82 were observed; of these, 10 were between colonies of the same species. The results illustrated how unpredictable and indeterminate the outcome of competitive encounters between bryozoan species may be. No one species was apparently dominant in all its competitive encounters, although interactions between some pairs of species were entirely deterministic in their outcome. For example, *Alcyonidium* spp. won all their interactions with *C.hyalina* and *Electra pilosa* (L.); similarly, *E.coccinea* overgrew *E.pilosa* in all their encounters. Although encounters involving overgrowth were overwhelmingly the most frequent occurrence, many species were capable of preventing or delaying overgrowth, to result in ties between the competing colonies. For some species, e.g. *Alcyonidium* spp. and *C.cryptooecium*, ties were the most frequently observed outcome of inter-actions. This was also true for a number of particular species-pairs - ties were especially prevalent in intraspecific encounters. All the intraspecific interactions, except encounters concerning *M.nitida*, resulted predominantly in ties. Although most intraspecific contacts also resulted in a number of typical overgrowth outcomes, Alcyonidium spp. interactions were totally deterministic, no outcome other than ties was observed for the 140 interactions.

Rather than there being an absolute "asymmetry" in the outcome of competition, leading to one species of a

FIGURE 4.4. Examples of the variable outcome of bryozoan competition:

(a) *Alcyonidium* sp. (Al) overgrowing *Cribrilina cryptooecium* (Cc). (Scale bar ≙ 1.55mm)

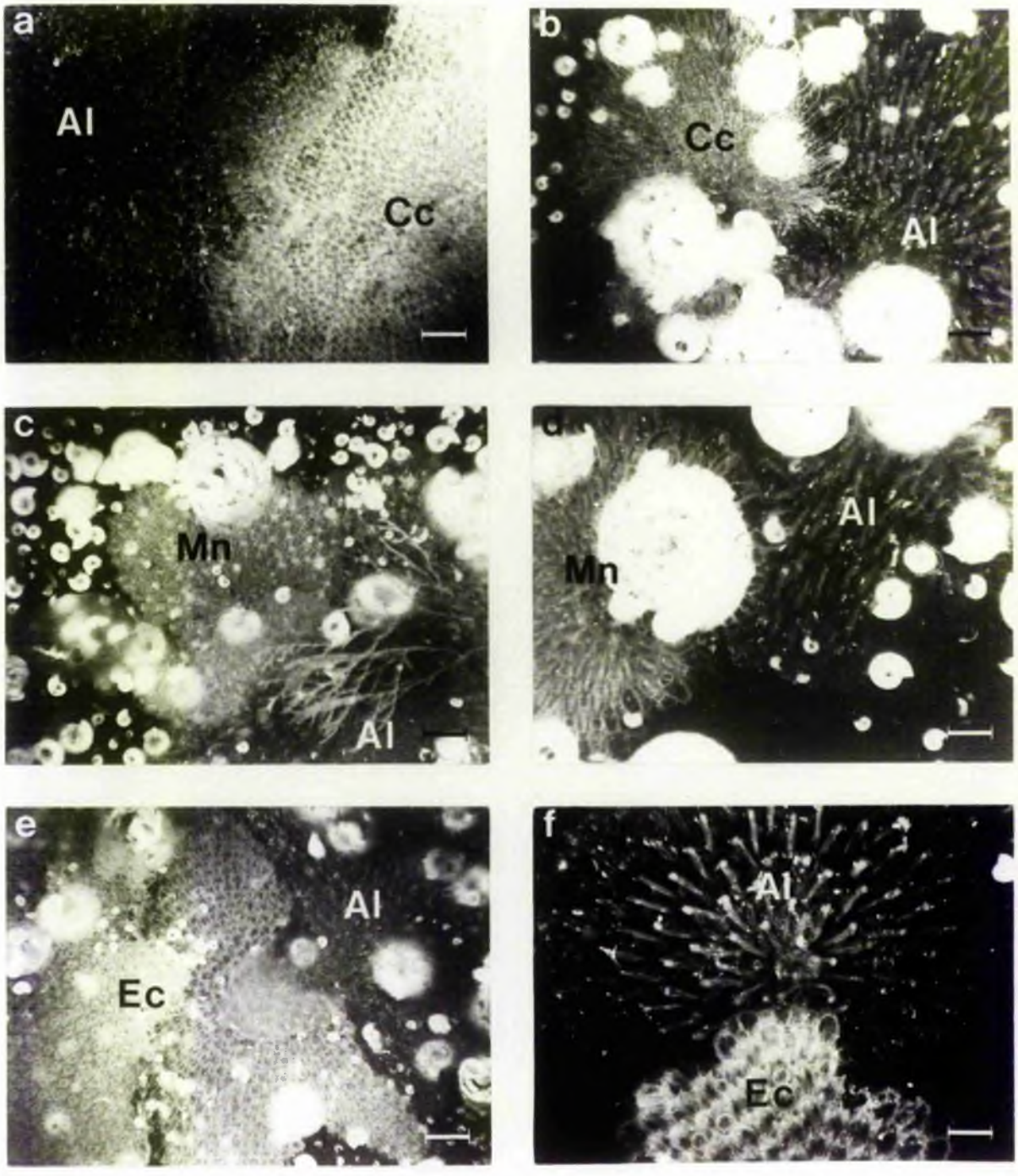
(b) *C.cryptooecium* overgrowing *Alcyonidium* sp. - note the elongated terminal stolonal outgrowths of the former. (Scale bar ≙ 0.90mm)

(c) *Alcyonidium* sp. overgrowing *Membraniporella nitida* (Mn). (Scale bar ≙ 1.15mm)

(d) *M.nitida* overgrowing *Alcyonidium* sp.- note that the *M.nitida* colony may have attained a 'height advantage' through overgrowing the spirorbid. (Scale bar ≙ 0.75mm)

(e) *Alcyonidium* sp. overgrowing *Escharoides coccinea* (Ec) along most of the length of the contact margin. (Scale bar ≙ 1.85mm)

(f) *E.coccinea* overgrowing *Alcyonidium* sp.. (Scale bar ≙ 0.80mm)


a
Al
Cc
b
Cc
Al
c
Mn
Al
d
Al
Mn
e
Al
Ec
f
Al
Ec

particular pair always winning or losing, the majority of species exhibited a degree of "equivalence" in their interactions. Thus, either species was capable, though not necessarily equally capable, of winning an encounter. This led to a high number of reversals in overgrowth interactions (see Figure 4.4.). For example, interactions between *Alcyonidium* spp. and *M.nitida*, or *C.hyalina* and *E.pilosa*, resulted in each species winning and losing approximately equal numbers of interactions. Nevertheless, for many species-pairs, one or other competitor exhibited marked dominance, although this was rarely absolute. Under some circumstances the apparently inferior species was occasionally able to overgrow the normally dominant species. Thus, for example, *E.coccinea* overgrew *C.hyalina* in 33 out of 39 interactions, but *C.hyalina* tied in 4 interactions and reversed the dominance relationship in the remaining 2. Similar patterns were observed between *Schizoporella unicornis* (Johnston) and *C.lineata*, *E.coccinea* and *C.lineata*, and *E.coccinea and M.nitida*.

Information on the numbers of particular outcomes of interactions between pairs of species provides a measure of the relative competitive ability of the species in question. Compilation of such data into a "contact matrix" permits the determination of whether competitive hierarchies or competitive networks exist among the species observed. It was not possible to rank the bryozoan species recorded in this study into a simple linear hierarchy, and there was no single competitively

dominant species. However, the species were separable into 3 broad categories, according to their competitive overgrowth ability.

(i) Overgrowth dominants: these won many of their interactions against the majority of species encountered, e.g. *E.coccinea*.

(ii) Intermediate dominants: these competed poorly against the overgrowth dominants, in contrast to their performance against lower- ranked species. For example, *Alcyonidium* spp. lost the majority of their encounters with *E.coccinea*, but always overgrew *C.hyalina*.

(iii) Inferior overgrowth competitors: these lost the majority of their encounters, but were occasionally able to overgrow or tie with higher-ranked species, e.g. *E.pilosa* and *C.hyalina*.

The lack of distinct or absolute differences in the competitive abilities of the majority of the species (i.e. the frequency of reversals and tie situations between the species) produced a network-like pattern of species' interactions. Thus the interrelationships within the bryozoan assemblages studied here can probably best be considered as an essentially hierarchial ranking of competitive abilities, on which was superimposed a complex network arrangement of species' relationships. A number of factors may have produced such a complex pattern of competitive interactions between the bryozoan species. The influence, primarily, of encounter angle between the interacting colonies, but also the effect of

site and year, on the outcome of competitive interactions were therefore examined in some detail.

Tables 4.3.-4.8. and Figures 4.5.-4.14. represent the results from the development of models using GLIM to examine the importance of these 3 parameters in affecting the outcome of competitive interactions. Of the 18 species recorded, 6 (*Cribrilina annulata* (Fabricius), *E.immersa*, *Haplopoma* spp., *Phaeostachys spinifera* (Johnston) and *S.linearis)* were excluded from the analyses because of the low numbers of interactions observed. Of the remaining 12, only those species-pairs for which there were more than 15 interactions were examined.

Theoretically, the simplest analysis of competition would be to consider the probabilities of a win or a loss, and to exclude ties, producing a binomial model. More information on competitive interactions becomes available, however, by including ties in any analysis, thus producing a trinomial model. This is of particular importance in view of the increasing evidence that ties (or "stand-offs") may exert an important influence in structuring the assemblage (Kay and Keough, 1981; Quinn, 1982; Rubin, 1982). However, before the data were analysed using the trinomial model it was deemed a necessary precaution to undertake a preliminary analysis with a binomial model. If the trinomial model is adequately describing the data then, theoretically,the probabilities of a particular species winning should lie

(a)

Analysis	BINOMIAL		TRINOMIAL
Parameter	Pr WIN	Pr WIN + TIE	Pr WIN
OVERALL	0.310	0.799	0.310
Alcyonidium	0	1	0
C.aurita	0.285	0.428	0.286
C.craticula	0.646	1	0.647
C.lineata	0.668	0.852	0.669
C.hyalina	1	1	1
C.cryptooecium	0.357	0.572	0.357
E.pilosa	1	1	1
E.coccinea	0.137	0.332	0.138
F.hispida	0	1	0
M.nitida	0.428	0.632	0.429
M.ciliata	0.909	0.909	0.909
S.unicornis	0.748	0.750	0.750
SECTOR 1	0.247	0.818	0.247
SECTOR 2	0.305	0.819	0.305
SECTOR 3	0.310	0.724	0.311
SECTOR 4	0.443	0.800	0.443
SECTOR 5	0.444	0.667	0.444
SECTOR 6	0.400	0.943	0.400
SECTOR 7	0.636	0.939	0.636
SECTOR 8	0.410	0.923	0.410
SECTOR 9	0.429	0.857	0.429
SECTOR 10	0.284	0.761	0.284
SECTOR 11	0.310	0.724	0.310
SECTOR 12	0.179	0.687	0.179
Clachan	0.280	0.801	0.280
Cuan	0.600	0.800	0.600
St.Andrews (ST)	0.525	0.775	0.525
St.Andrews (IT)	0.476	0.810	0.476
1983	0.224	0.853	0.224
1984	0.330	0.786	0.330

(b)

BINOMIAL		TRINOMIAL
Pr WIN	Pr WIN + TIE	Pr WIN
0.669	0.851	0.669
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
-	-	-
0.643	0.893	0.643
0.706	0.706	0.706
0.571	1	0.571
0.813	0.937	0.813
1	1	1
1	1	1
0.400	1	0.400
0.875	1	0.875
0.333	0.667	0.333
0.667	0.750	0.667
0.714	0.857	0.715
0.500	0.714	0.500
0.699	0.843	0.699
0.750	0.750	0.750
0.650	0.900	0.650
0.500	0.857	0.500
0.737	0.895	0.737
0.657	0.843	0.657

TABLE 4.3. - Comparison of the probabilities from the binomial and trinomial analysis for (a) the total *Alcyonidium* spp. datum set; and (b) the *Alcyonidium* spp. vs. *Callopora lineata* interaction.

between the probabilities of winning and not losing (i.e. win + tie) calculated from a binomial analysis. Results from the binomial and trinomial models calculated for the total *Alcyonidium* spp. datum set, and for the interactions between *Alcyonidium* spp. and *C.lineata*, suggested that these pre-requisites were indeed met (see Table 4.3.; and Appendix 3 for the complete development of the binomial model). Therefore, the trinomial model would appear to be suitable for the analysis of the competitive outcome data from this study.

The first part of the analysis comprised an examination of all the interactions recorded for each of those 12 species with adequate data sets (Tables 4.4. and 4.5.; Figures 4.5.-4.14.). The results provided only an overall view of the competitive abilities of each species, ignoring one of the most important variables of competition outcome; namely, the identity of the interacting species. Thus, from this, only tentative conclusions can be drawn. The second part of the analysis comprised a more detailed examination of the competitive encounters between a number of deducibly important species-pairs (Tables 4.6. and 4.7.; Figures 4.5.-4.14). It must be stressed that the interpretations, especially of species-specific interactions, must remain tentative due to limitations imposed by small sample sizes. Nevertheless, considerable information on the nature of the competition was available from the data.

SPECIES	*Alcyonidium* spp.		*C.aurita*		*C.craticula*		*C.lineata*		*C.hyalina*		*C.cryptooecium*		*E.pilosa*		*E.coccinea*		*F.hispida*		*M.nitida*		*M.ciliata*		*S.unicornis*	
MODELS	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE
OUTCOME	*	-	ns	-	ns	-	*	-	*	-	*	-	ns	-	*	-	ns	-	*	-	ns	-	*	-
OUTCOME * SPECIES	*	*	ns	ns	ns	*	*	ns	*	*	*	ns	*	*	*	†	*	*	ns	*	*	*		
OUTCOME * SECTOR	*	*	ns	ns	ns	ns	*	*	*	*	ns	ns	*	*	ns	ns	*	*	ns	ns	*	*		
OUTCOME * SITE	*	*	ns	ns	ns	ns	*	*	*	*	ns	*	*	*	ns	ns	*	ns	ns	*	*	*		
OUTCOME * SEASON	*	*	ns	ns	ns	ns	*	ns	*	*	*	ns	*	*	ns	ns	*	*	ns	ns	*	*		

TABLE 4.4. - The significance of the scaled deviance (S.D.) of the models and the change in fit (CHANGE) between the current and minimal models for the 2-factor interaction models developed for the total (pooled) species' data sets.

* - $P < 0.05$; ns = Not significant; † = no convergence in iterative fitting of model (results only approximate)

MODELS / OUTCOME	*ALCY.*	*C.AUR.*	*C.CRAT.*	*C.LIN.*	*C.HYA.*	*C.CRYPT.*	*E.PIL.*	*E.COCC.*	*F.HISP.*	*M.NIT.*	*M.CIL.*	*S.UNI.*
1	*	ns	*	*	*	*	*	*	ns	*	*	*
OUTC(2)	*	ns	*	*	*	*	*	*	ns	*	ns	*
OUTC(3)	*	*	ns	ns	*	ns	ns	*	ns	*	ns	ns
OUTCOME * SECTOR												
1	*	ns	ns	*	ns	ns	*	*	ns	*	ns	ns
OUTC(2)	ns	ns	ns	*	ns	ns	*	*	ns	ns	ns	ns
OUTC(3)	*	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns
SECT(2)	*	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns
SECT(3)	*	–	ns	*	ns	ns	ns	*	ns	ns	–	ns
SECT(4)	ns	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns
SECT(5)	*	–	–	*	ns	ns	ns	*	ns	ns	–	ns
SECT(6)	*	ns	ns	*	ns	*	ns	*	ns	*	ns	ns
SECT(7)	ns	–	ns	*	ns	ns	ns	*	–	ns	ns	ns
SECT(8)	ns	ns	ns	*	ns	*	ns	*	ns	*	ns	ns
SECT(9)	*	ns	–	*	ns	ns	ns	*	ns	ns	ns	ns
SECT(10)	*	ns	ns	*	ns	ns	ns	*	ns	*	ns	ns
SECT(11)	*	ns	ns	*	ns	ns	ns	*	ns	*	ns	ns
SECT(12)	*	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns
OUTC(2). SECT(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2). SECT(3)	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	–	ns
OUTC(2). SECT(4)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
OUTC(2). SECT(5)	ns	–	–	ns	ns	ns	ns	ns	ns	ns	–	ns
OUTC(2). SECT(6)	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
OUTC(2). SECT(7)	*	–	ns	ns	ns	ns	ns	*	–	ns	ns	*
OUTC(2). SECT(8)	*	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
OUTC(2). SECT(9)	ns	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2). SECT(10)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2). SECT(11)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2). SECT(12)	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SECT(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SECT(3)	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	–	ns
OUTC(3). SECT(4)	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SECT(5)	ns	–	–	ns	ns	ns	ns	ns	ns	ns	–	ns
OUTC(3). SECT(6)	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	*
OUTC(3). SECT(7)	*	–	ns	ns	ns	ns	ns	ns	–	ns	ns	ns
OUTC(3). SECT(8)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SECT(9)	ns	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SECT(10)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
OUTC(3). SECT(11)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SECT(12)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

TABLE 4.5. – The significance of the *t* – tests for each parameter of the species' total (pooled) data sets.

* = $P<0.05$; ns = Not significant; – = no observations;
+ = no data for site 1; Δ = no data for season 1.

Species key:- ALCY.= *Alcyonidium* spp.; C.AUR.= *C.aurita;*
C.CRAT.= *C.craticula*; C.LIN.= *C.lineata*;
C.HYA. = *C.hyalina*; C.CRYPT. = *C.cryptooecium*; E.PIL. = *E.pilosa*;
E.COCC. = *E.coccinea*; F.HISP.= *F.hispida*; M.NIT. = *M.nitida*;
M.CIL. = *M.ciliata*; S.UNI. = *S.unicornis*.

TABLE 4.5. (cont.)

MODELS	*ALCY.*	*C.AUR.*	*C.CRAT.*	*C.LIN.*	*C.HYA.*	*C.CRYPT.*	*E.PIL.*	*E.COCC.*	*F.HISP.*	*M.NIT.*	*M.CIL.*	*S.UNI.*
OUTCOME * SPECIES												
1	ns	ns	ns	*	ns	ns	ns	*	ns	*	*	ns
OUTC(2)	ns	ns	ns	*	ns	ns	ns	*	ns	ns	*	ns
OUTC(3)	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
SP2(2)	ns	–	–	ns	ns	–	–	*	–	ns	–	–
SP2(3)	ns	–	ns	ns	ns	ns	ns	*	–	*	–	–
SP2(4)	ns	ns	ns	*	ns	ns	ns	*	ns	ns	ns	*
SP2(5)	ns	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns
SP2(6)	–	–	–	–	–	–	–	–	–	–	–	–
SP2(7)	ns	–	ns	ns	ns	ns	ns	*	ns	*	ns	*
SP2(8)	ns	–	ns	*	ns	ns	ns	*	ns	ns	ns	ns
SP2(9)	–	–	–	–	–	–	–	–	–	–	–	–
SP2(10)	ns	ns	ns	ns	ns	*	ns	*	–	*	ns	ns
SP2(11)	ns	–	–	ns	ns	ns	ns	–	ns	–	–	ns
SP2(12)	–	–	–	–	–	–	–	–	–	–	–	–
SP2(13)	ns	ns	ns	ns	ns	ns	ns	*	–	*	ns	–
SP2(14)	ns	–	–	ns	ns	ns	ns	*	–	ns	–	–
SP2(15)	–	–	–	–	–	–	–	–	–	–	–	–
SP2(16)	–	–	–	–	–	–	–	–	–	–	–	–
SP2(17)	ns	–	–	*	ns	*	ns	ns	ns	–	–	ns
SP2(18)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(2). SP2(2)	ns	–	–	ns	ns	–	–	ns	–	ns	–	–
OUTC(2). SP2(3)	ns	–	ns	ns	ns	ns	ns	ns	–	ns	–	–
OUTC(2). SP2(4)	ns	ns	ns	*	ns	*	ns	ns	ns	*	ns	*
OUTC(2). SP2(5)	ns	ns	ns	*	ns	ns	ns	ns	ns	*	ns	ns
OUTC(2). SP2(6)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(2). SP2(7)	ns	–	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
OUTC(2). SP2(8)	ns	–	ns	*	ns	*	ns	ns	ns	ns	ns	ns
OUTC(2). SP2(9)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(2). SP2(10)	ns	ns	ns	ns	ns	*	ns	*	–	ns	ns	ns
OUTC(2). SP2(11)	ns	–	–	ns	ns	ns	ns	–	ns	–	–	ns
OUTC(2). SP2(12)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(2). SP2(13)	ns	ns	ns	ns	ns	ns	ns	*	–	ns	ns	–
OUTC(2). SP2(14)	ns	–	–	ns	ns	ns	ns	ns	–	ns	–	–
OUTC(2). SP2(15)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(2). SP2(16)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(2). SP2(17)	ns	–	–	ns	ns	*	ns	ns	ns	–	–	ns
OUTC(2). SP2(18)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(3). SP2(2)	ns	–	–	ns	ns	–	–	ns	–	ns	–	–
OUTC(3). SP2(3)	ns	–	ns	ns	ns	ns	ns	ns	–	ns	–	–
OUTC(3). SP2(4)	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns
OUTC(3). SP2(5)	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3). SP2(6)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(3). SP2(7)	ns	–	ns	ns	ns	*	ns	ns	ns	ns	ns	ns
OUTC(3). SP2(8)	ns	–	ns	*	ns	*	ns	ns	ns	ns	ns	ns
OUTC(3). SP2(9)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(3). SP2(10)	ns	ns	ns	ns	ns	ns	ns	*	–	ns	ns	ns
OUTC(3). SP2(11)	ns	–	–	ns	ns	ns	ns	–	ns	–	–	ns
OUTC(3). SP2(12)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(3). SP2(13)	ns	ns	ns	*	ns	ns	ns	ns	–	ns	ns	–
OUTC(3). SP2(14)	ns	–	–	ns	ns	ns	ns	ns	–	ns	–	–
OUTC(3). SP2(15)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(3). SP2(16)	–	–	–	–	–	–	–	–	–	–	–	–
OUTC(3). SP2(17)	ns	–	ns	ns	ns	ns	ns	ns	ns	–	–	ns
OUTC(3). SP2(18)	–	–	–	–	–	–	–	–	–	–	–	–

TABLE 4.5. (cont.)

MODELS	*ALCY.*	*C.AIR.*	*C.CRAT.*	*C.LIN.*	*C.HYA.*	*C.CRYPT.*	*E.PIL.*	*E.COCC.*	*F.HISP.*	*M.NIT.*	*M.CIL.*	*S.UNI.*
OUTCOME * SITE												
1	*	ns	*	ns	*	*	*	*	ns^{+}	*	*	ns
OUTC(2)	*	ns	*	*	*	ns	*	*	ns	*	ns	ns
OUTC(3)	*	*	ns	ns	*	ns	ns	*	ns	*	ns	ns
SITE(2)	*	–	–	*	ns	ns	ns	*	ns	ns	ns	ns
SITE(3)	ns	–	ns	ns	ns	*	ns	–	ns	–	–	ns
SITE(4)	*	–	–	*	ns	ns	–	–	ns	–	–	ns
OUTC(2). SITE(2)	ns	–	–	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2). SITE(3)	ns	–	ns	ns	ns	*	ns	–	ns	–	–	ns
OUTC(2). SITE(4)	ns	–	–	ns	ns	ns	–	–	ns	–	–	ns
OUTC(3). SITE(2)	*	–	–	ns	ns	*	ns	ns	ns	ns	ns	ns
OUTC(3). SITE(3)	*	–	ns	*	ns	ns	ns	–	ns	–	–	ns
OUTC(3). SITE(4)	ns	–	–	*	ns	ns	–	–	ns	–	–	ns
OUTCOME * SEASON												
1	ns	ns	*	ns	*	*	*	*	ns$^{\triangle}$	ns	ns	ns
OUTC(2)	ns	ns	ns	*	*	ns	*	*	ns	*	ns	ns
OUTC(3)	*	ns	ns	ns	ns	*	ns	*	ns	*	ns	ns
SEAS(2)	*	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns
OUTC(2). SEAS(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
OUTC(3). SEAS(2)	*	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns

INTERACTIONS	ALCY. vs. ALCY.		ALCY. vs. C.CRAT.		ALCY. vs. C.LIN.		ALCY. vs. C.HYA.		ALCY. vs. C.CRYPT.		ALCY. vs. E.COCC.		ALCY. vs. M.NIT.		C.CRAT. vs. E.COCC.		C.LIN. vs. C.LIN.		C.LIN. vs. C.HYA.		C.LIN. vs. C.CRYPT.		C.LIN. vs. E.PIL.		C.LIN. vs. E.COCC.		C.LIN. vs. M.NIT.		C.LIN. vs. S.UNI.		C.HYA. vs. C.HYA.		C.HYA. vs. E.PIL.		C.HYA. vs. E.COCC.		C.HYA. vs. M.NIT.		C.CRYPT. vs. C.CRYPT.		C.CRYPT. vs. E.PIL.		C.CRYPT. vs. E.COCC.		C.CRYPT. vs. S.UNI.		E.PIL. vs. E.PIL.		E.PIL. vs. E.COCC.		E.PIL. vs. M.NIT.	
MODELS	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE
(a) OUTCOME	*	-	ns	-	*	-	+ns	-	ns	-	*	-	*	-	ns	-	*	-	ns	-	ns	-	ns	-	ns	-	ns	-	*	-	*	-	ns	-	ns	-	ns	-	*	-	ns	-	+ns	-	+ns	-	+ns	-	+ns	-
OUTCOME *SECTOR	ns	*	+ns	ns	*	*	+ns	ns	ns	ns	*	*	*	*	+ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	*	*	*	*	ns	ns	+ns	ns	+ns	ns	ns	ns	*	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns
OUTCOME *SITE	*	*	ns	ns	*	*	+ns	ns	ns	ns	*	*	*	ns	ns	ns	*	*	ns	ns	ns	ns	ns	*	ns	*	ns	ns	*	*	*	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	+ns	ns	+ns	ns
OUTCOME *SEASON	*	*	ns	ns	*	ns	+ns	ns	ns	ns	*	*	*	*	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	*	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	+ns	ns	+ns	ns
(b) OUTCOME	*	-	ns	-	*	-	+ns	-	ns	-	*	-	*	-	ns	-	*	-	ns	-	ns	-	ns	-	ns	-	ns	-	*	-	*	-	ns	-	ns	-	ns	-	*	-	ns	-	+ns	-	+ns	-	+ns	-	+ns	-
*SECTOR	ns	*	+ns	ns	*	*	+ns	ns	ns	ns	*	*	*	*	+ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	*	*	*	*	ns	ns	+ns	ns	+ns	ns	ns	ns	*	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns
*SITE	*	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	*	*	*	ns	+ns	ns	*	*	+ns	ns	+ns	ns	+ns	ns	ns	ns	ns	*	ns	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	*	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns
*SEASON	Δns	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	*	+ns	*	+ns	ns	+ns	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns
(c) OUTCOME	*	-	ns	-	*	-	+ns	-	ns	-	*	-	*	-	ns	-	*	-	ns	-	ns	-	ns	-	ns	-	ns	-	*	-	*	-	ns	-	ns	-	ns	-	*	-	ns	-	+ns	-	+ns	-	+ns	-	+ns	-
*SEASON	*	*	ns	ns	*	ns	+ns	ns	ns	ns	*	*	*	*	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	*	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	+ns	ns	+ns	ns
*SITE	*	*	+ns	ns	*	*	+ns	ns	ns	ns	*	*	*	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	*	*	*	ns	ns	ns	ns	ns	ns	*	*	ns	ns	ns	ns	ns	ns	+ns	ns	+ns	ns
*SECTOR	Δns	*	+ns	ns	+ns	*	+ns	ns	+ns	ns	+ns	*	+ns	*	+ns	ns	+ns	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	*	+ns	ns	+ns	ns	+ns	ns	+ns	ns	+ns	ns

INTERACTIONS	E.COCC. vs. E.COCC.		E.COCC. vs. M.NIT.		M.NIT. vs. M.NIT.		S.UNI. vs. S.UNI.	
MODELS	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE	S.D.	CHANGE
(a) OUTCOME	*	-	ns	-	ns	-	*	-
OUTCOME *SECTOR	*	*	ns	ns	ns	ns	*	*
OUTCOME *SITE	*	ns	ns	ns	ns	ns	*	*
OUTCOME *SEASON	*	*	ns	*	ns	ns	*	*
(b) OUTCOME	*	-	ns	-	ns	-	*	-
*SECTOR	*	*	ns	ns	ns	ns	*	*
*SITE	*	ns	ns	ns	ns	ns	+ns	*
*SEASON	+ns	*	+ns	ns	+ns	ns	+ns	ns
(c) OUTCOME	*	-	ns	-	ns	-	*	-
*SEASON	*	*	ns	*	ns	ns	*	*
*SITE	*	ns	ns	ns	ns	ns	*	*
*SECTOR	+ns	*	+ns	ns	+ns	ns	+ns	*

TABLE 4.6. – The significance of the scaled deviance (S.D.) of the models and the change in fit (CHANGE) between the current and minimal or pre-current models for (a) the 2-factor interaction models, and (b+c) the multiple interaction models, developed for the species' pairwise competitive interactions. In (a) each parameter is added independently to the minimal model; in (b) and (c) the parameters are sequentially incorporated into the model, the order of parameter addition being reversed in (c).

* = $P < 0.05$; ns = Not significant; Δ = change in degrees of freedom during model fitting (results incorrect); + = no convergence in iterative fitting of model (results only approximate).
See Table 4.5. for species key.

MODELS	ALCY. vs.							C.CRAT. vs.		C.LIN. vs.							C.HYA. vs.						C.CRYPT. vs.						E.PIL. vs.						E.COCC. vs.						M.NIT. vs.						S.UNI. vs.		
	ALCY.	C.CRAT.	C.LIN.	C.HYA.	C.CRYPT.	E.COCC.	M.NIT.	ALCY.	E.COCC.	ALCY.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	M.NIT.	S.UNI.	ALCY.	C.LIN.	C.HYA.	E.PIL.	E.COCC.	M.NIT.	ALCY.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	S.UNI.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	M.NIT.	ALCY.	C.CRAT.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	M.NIT.	ALCY.	C.LIN.	C.HYA.	E.PIL.	E.COCC.	M.NIT.	C.LIN.	C.CRYPT.	S.UNI.
OUTCOME																																																			
1	ns	ns	*	*	ns	ns	*	ns	ns	*	ns	ns	*	ns	*	ns	ns	ns	*	*	ns	*	*	ns	*	*	*	*	*	*	ns	*	*	ns	*	*	*	ns	*	*	*	*	ns	ns	*	*	*	*	ns	ns	*	ns	ns
OUTC(2)	ns	ns	*	ns	ns	*	ns	ns	ns	*	ns	*	*	*	*	*	*	ns	*	ns	ns	*	*	ns	*	ns	*	*	*	*	ns	*	ns	*	ns	ns	*	ns	*	*	*	ns	*	ns	ns	*	*	ns	*	ns	*	*	ns
OUTC(3)	ns	ns	*	ns	ns	ns	*	ns	ns	ns	*	*	ns	*	ns	*	*	ns	*	*	ns	ns	ns	ns	*	*	*	ns	ns	ns	ns	ns	ns	*	ns	ns	*	ns	*	*	*	ns	*	*	ns	*	*	ns	ns	ns	*	*	*
OUTCOME *SITE																																																			
1	ns	ns	*	*	ns	ns	*	ns	ns	ns	ns	*	ns	*	*	ns	+*	ns	ns	ns	ns	*	*	ns	ns	ns	*ns	*	*ns	*	ns	+ns	ns	ns	ns	*	ns	*	*	ns	*	*	*	*	*	*	ns	ns	ns	+*	+ns	+ns	*	ns	ns
OUTC(2)	ns	ns	*	ns	ns	*	ns	ns	ns	*	ns	*	ns	*	*	*	*	ns	*	ns	ns	*	*	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	*	ns	*	*	ns	ns	ns	*	ns	*	*	ns	ns	*	ns	ns
OUTC(3)	ns	ns	*	ns	ns	ns	*	ns	ns	ns	*	*	ns	*	ns	*	*	ns	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	*	ns	ns	ns	*	ns	*	*	ns	ns	*	ns	*
SITE(2)	ns	-	*	ns	ns	ns	-	-	-	ns	ns	-	ns	ns	ns	-	*	ns	-	-	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	-	-	-	ns	-	-	-	*	ns	ns	-	-	-	*	ns	ns
SITE(3)	-	ns	*	ns	ns	-	-	ns	-	ns	*	ns	ns	*	-	-	ns	ns	ns	ns	ns	-	-	ns	ns	ns	ns	-	-	ns	ns	ns	ns	ns	ns	ns	-	-	-	-	-	-	-	-	-	-	-	-	-	*	ns	ns
SITE(4)	-	-	*	-	ns	-	-	-	-	ns	ns	ns	ns	-	-	-	ns	-	ns	-	-	-	ns	ns	ns	-	-	-	ns	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	ns	ns	ns
OUTC(2).SITE(2)	ns	-	ns	ns	ns	ns	-	-	-	ns	ns	-	ns	ns	ns	-	ns	ns	-	-	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	-	ns	ns	-	-	-	-	-	ns	ns	ns	ns	ns
OUTC(2).SITE(3)	-	ns	ns	ns	ns	-	-	ns	-	ns	ns	ns	ns	*	-	-	ns	ns	ns	ns	ns	-	-	ns	ns	ns	ns	-	-	ns	*	ns	ns	ns	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	ns	ns	ns
OUTC(2).SITE(4)	-	-	ns	-	ns	-	-	-	-	ns	ns	ns	ns	-	-	-	ns	-	ns	-	-	-	ns	ns	-	-	-	-	ns	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	ns	ns	ns
OUTC(3).SITE(2)	ns	-	ns	ns	ns	ns	-	-	-	ns	ns	-	ns	ns	ns	-	ns	ns	-	-	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	-	ns	ns	-	-	-	-	-	ns	ns	ns	ns	ns
OUTC(3).SITE(3)	-	ns	ns	ns	ns	-	-	ns	-	ns	ns	ns	ns	ns	-	-	ns	ns	ns	ns	ns	-	-	ns	ns	ns	ns	-	-	ns	ns	ns	ns	ns	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	ns	ns	ns
OUTC(3).SITE(4)	-	-	ns	-	ns	-	-	-	-	ns	ns	ns	ns	-	-	-	ns	-	ns	-	-	-	ns	ns	-	-	-	-	ns	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	ns	ns	ns
OUTCOME *SEASON																																																			
1	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	*	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2)	ns	ns	*	ns	ns	*	ns	ns	ns	*	ns	ns	ns	*	*	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3)	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	*	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	*	ns	ns	ns	ns	*	ns	ns	ns	ns	ns
SEAS(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	*	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SEAS(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SEAS(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

TABLE 4.7. - The significance of the *t*-tests for each parameter of the species' pairwise competitive interactions.

* = $P < 0.05$; ns = Not significant; - = no observations; + = no data for site 1.
See Table 4.5.for species key.

TABLE 4.7. (cont.)

MODELS	ALCY. vs.							C.CRAT. vs.		C.LIN. vs.							C.HYA. vs.							C.CRYPT. vs.							E.PIL. vs.							E.COCC. vs.							M.NIT. vs.							S.UNI. vs.		
	ALCY.	C.CRAT.	C.LIN.	C.HYA.	C.CRYPT.	E.COCC.	M.NIT.	ALCY.	E.COCC.	ALCY.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	M.NIT.	S.UNI.	ALCY.	C.LIN.	C.HYA.	E.PIL.	E.COCC.	M.NIT.	ALCY.	C.LIN.	C.CRYPT.	E.PIL.	E.COCC.	S.UNI.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	M.NIT.	ALCY.	C.CRAT.	C.LIN.	C.HYA.	C.CRYPT.	E.PIL.	E.COCC.	M.NIT.	ALCY.	C.LIN.	C.HYA.	E.PIL.	E.COCC.	M.NIT.	C.LIN	C.CRYPT.	S.UNI.
OUTCOME *SECTOR																																																				
1	ns	ns	*	ns	ns	ns	*	ns	ns	ns	*	*	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	*	ns	*	*	ns	*	*	*	*	*	*	ns	ns	*	ns	ns
OUTC(2)	ns	ns	*	ns	ns	*	ns	ns	ns	*	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3)	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
SECT(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SECT(3)	ns	ns	*	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	-	-	ns	-	ns	ns	ns	ns	ns	ns	-	ns	-	-	-	*	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SECT(4)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SECT(5)	ns	-	ns	-	ns	ns	ns	-	-	ns	ns	-	ns	-	ns	-	ns	ns	ns	ns	-	-	ns	-	-	ns	ns	-	-	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	ns	-	-	ns	-	-	ns	ns	ns	-	ns
SECT(6)	ns	ns	*	ns	ns	ns	-	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SECT(7)	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	-	-	ns	*	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns
SECT(8)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	-	ns	ns	-	ns	*	ns	-	-	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns
SECT(9)	ns	-	*	ns	-	-	ns	-	-	ns	ns	ns	ns	ns	ns	-	ns	-	-	ns	-	-	-	ns	ns	ns	-	-	-	-	-	ns	-	-	-	ns	-	*	*	-	ns	-	ns	-	-	-	-	ns	ns	-	ns
SECT(10)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
SECT(11)	ns	-	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	*	ns	*	-	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SECT(12)	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(3)	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	-	-	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(4)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(5)	ns	-	ns	-	ns	ns	ns	-	-	ns	ns	-	ns	-	ns	-	ns	ns	ns	ns	-	-	ns	-	-	ns	ns	-	-	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	ns	-	-	ns	-	-	ns	ns	ns	-	ns
OUTC(2).SECT(6)	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(7)	ns	-	ns	ns	ns	*	ns	-	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	-	-	ns	*	ns	ns	ns	ns	ns	-	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(8)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(9)	ns	-	ns	ns	-	-	ns	-	-	ns	ns	ns	ns	ns	ns	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	-	-	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	ns	-	-	ns	-	-	ns	ns	ns	-	ns
OUTC(2).SECT(10)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(11)	ns	-	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(2).SECT(12)	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(2)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(3)	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	-	-	ns	-	ns	-	-	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(4)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(5)	ns	-	ns	-	ns	ns	ns	-	-	ns	ns	-	ns	-	ns	-	ns	ns	ns	ns	-	-	ns	-	-	ns	ns	-	-	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	ns	-	-	ns	-	-	ns	ns	ns	-	ns
OUTC(3).SECT(6)	ns	ns	ns	ns	ns	ns	-	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(7)	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns
OUTC(3).SECT(8)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(9)	ns	-	ns	ns	-	-	ns	-	-	ns	ns	ns	ns	ns	ns	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	-	-	-	ns	-	-	ns	-	-	ns	-	-	ns	ns	ns	-	-	ns	-	-	ns	ns	ns	-	ns
OUTC(3).SECT(10)	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(11)	ns	-	ns	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	-	ns	ns	-	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
OUTC(3).SECT(12)	ns	ns	ns	ns	ns	ns	ns	ns	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

4.2.1. The Development of the Interaction Models:- The significances, at the 5% level, of the scaled deviances and the change in scaled deviance between the model fits for the total data sets are presented in Table 4.4.. Only 2-factor interaction models were feasible for the total data sets. These considered independently the interaction between each parameter (i.e. species, sector, site or season), with the minimal model considering outcome alone. A more detailed analysis using multiple interaction models (e.g. OUTCOME*SPECIES*SECTOR, etc.) requires more complete data sets than are currently available. However, both forms of model were developed in the examination of competition between particular species-pairs (Table 4.6.). Two multiple interaction models were examined. In the first, the greatest amount of variation in outcome was considered to be attributable to sector, which was thus incorporated into the model first, followed by site and season. The latter two might reasonably be expected to explain increasingly smaller amounts of variation in outcome. In the second model, the parameters were included in the converse order. Thus the variation attributable to season was removed first and that due to sector removed last. In the interpretation of these interaction models developed with GLIM, a significant scaled deviance indicated that the model in question was totally inadequate in explaining the data. Non-significant values indicated that the data were adequately described by the current model. A significant change in the fit between the models

indicated that a big reduction in the scaled deviance had been obtained by fitting the parameter, and the converse was true for a non-significant change in the fit between models.

Considering the results for the total data sets, it was evident that for a number of species, e.g. *Alcyonidium* spp., *C.cryptooecium*, *E.coccinea* and *S.unicornis*, the 2-Factor interaction models were totally inadequate in explaining the variation in the outcome of the competitive encounters (i.e. there were significant scaled deviances and changes of fit between the models). Similar interpretations can be drawn for *C.lineata* and *M.nitida*, but the non-significant changes in scaled deviances for season and site respectively, indicated that these parameters did not significantly affect the outcome. Their inclusion was, however, still totally inadequate in providing an explanation of the outcome of the encounters (i.e. significant scaled deviances). For the remaining species, e.g. *C.aurita* and *F.hispida*, the results essentially indicated that all the variation in the outcomes may have been explained by the minimal model (i.e. predominantly non-significant scaled deviances or changes in fit between the models). However, these results were probably small sample-size artefacts. Significant values for changes between model fits indicated that the parameter concerned may have made a contribution to the outcome variability. For example, the results suggested that the outcomes observed for

Callopora craticula (Alder) and *F.hispida* were dependent on the species involved in the interactions. Conversely, for *E.pilosa* and *M.ciliata* both species and site may have been important. These latter results have, however, to be interpreted with caution, because many probably arose because of small sample-sizes.

Of the 30 particular species-pairs examined, in only 10 cases were sufficient ($\hat{=}80$) observations available for valid analysis (Table 4.6.). These were interactions between *Alcyonidium* spp. and *C.lineata*, *Alcyonidium* spp. and *E.coccinea*, *Alcyonidium* spp. and *M.nitida*, *C.lineata* and *S.unicornis*, and the intraspecific interactions for *Alcyonidium* spp., *C.lineata*, *C.hyalina*, *C.cryptooecium*, *E.coccinea* and *S.unicornis*. For the remaining species-pairs the high incidence of non-significant scaled deviances and changes of fit were probably small sample-size artefacts.

The 2-factor analyses indicated that addition of any of the parameters into the minimal model produced a significant reduction in the fit of the model, but the highly significant scaled deviances indicated that any of the parameters alone were totally inadequate in explaining the variation within the data. The intraspecific interaction between *Alcyonidium* spp. colonies was the only result for which there was evidence that one of the parameters (sector), independently of the others, produced an interaction model that fully described the data (i.e. a non-significant scaled

deviance was obtained). Other exceptions included interactions between *Alcyonidium* spp. and *M.nitida*, and intraspecific *E.coccinea* encounters, where the addition of the parameter site did not produce a significant change in the fit of the model. For interactions between *Alcyonidium* spp. and *C.lineata*, and intraspecific *C.lineata* contacts, the addition of season, similarly, did not produce a change in the fit of the model.

Of more value in explaining bryozoan competition were multiple factor models (Table 4.6.). The results for the intraspecific *Alcyonidium* spp. encounters suggested that sector alone may have explained all the variation in the outcome of interactions between colonies. However, this result had to be interpreted with caution because development of the multiple interaction models for these encounters produced a change in the degrees of freedom. This arose when a new parameter was added to the model and no further information was available, because it was "aliased" with parameters fitted previously. The results from such fits are, in general, incorrect (The GLIM release 3.77 manual, The Royal Statistical Society, 1986). Otherwise, none of the variation in outcome between species-pairs was explicable solely in terms of sector. But a number of interspecific interactions, for example, those between *Alcyonidium* spp. and *C.lineata*, and *C.lineata* and *S.unicornis*, and also intraspecific *S.unicornis* interactions, were adequately explained by the addition of the variables, sector and site, into the

minimal model. That is, the variation in the outcomes of the aforementioned interactions was explicable by the encounter angle between colonies and differences associated with the sites. The remaining interactions, e.g. those between *Alcyonidium* spp. and *E.coccinea*, and *Alcyonidium* spp. and *M.nitida*, and also intraspecific *E.coccinea* encounters, required the addition of all 3 parameters into the model, before a non-significant scaled deviance was attained.

When the parameters were added into the model in the converse order (i.e. season, site and sector) the variation in the outcome was only adequately explained when all 3 parameters were added into the model. Only with the interaction between *C.hyalina* colonies was the variation in outcome explicable in terms of season and site alone.

In general, these results indicated that sector explained a significant amount (but not all) of the variation in the outcome of competition, the remainder being variously attributable to site and season.

No firm conclusions can be drawn regarding the interactions between species-pairs for which the sample sizes were inadequate. For a number of the interactions, however, significant changes in the fit of the models produced suggested that the parameter concerned may have contributed towards an explanation of the variation in the outcome. For example, site may have been a

significant variable in interactions between *C.lineata* and *E.pilosa*, and *C.lineata* and *E.coccinea*, and season in encounters between *C.hyalina* and *E.coccinea*, and *E.coccinea* and *M.nitida*.

4.2.2. **The *t*-tests**:- Tables 4.5. and 4.7. show the results of the *t*-tests calculated from the estimates and standard errors of the coefficients of the parameters of the model under consideration. Those estimates which have significant *t*-ratios (i.e. approximately twice the standard error) were statistically significant at the 5% level. They provided more detailed information on the significant differences indicated by the overall scaled deviances of the model. For example, consider the *t*-ratios produced for the total *Alcyonidium* spp. datum set, specifically those produced for the interaction model between outcome and sector (Table 4.5.). The results indicated that the difference between wins and ties (OUTC(3)) was highly significant, as was the difference between sector 1 and sector 5 (SECT(5)); similarly, the interaction between losing and sector 6 (OUTC(2).SECT(6)) was significant.

Considering the overall outcomes for the total data sets of each species, the results suggested that many of the species (e.g. *Alcyonidium* spp., *C.hyalina*, and *E.coccinea*) exhibited significant differences between the 3 outcomes. Furthermore, *C.lineata*, *C.cryptooecium*, and *S.unicornis* exhibited significant differences between the numbers of wins and losses, while *C.aurita* differed

significantly between wins and ties. Many of the species (e.g. *C.lineata* and *E.coccinea*) also exhibited significant differences in outcomes with different species. The relative paucity of significant *t*-tests among the different species was probably a small sample-size artefact. However, for species such as *Alcyonidium* (for which there were adequate data), these may be real results. In the particular case of *Alcyonidium* spp. there were no significant differences in the outcomes among the different species encountered by *Alcyonidium* spp..

The results also suggested that outcomes varied according to the angle of encounter (sector) for several species, including *Alcyonidium* spp., *C.lineata*, *E.coccinea* and *M.nitida*. Moreover, the majority of species exhibited significant *t*-ratios for the coefficients of the parameters site (e.g. *Alcyonidium* spp., *C.lineata* and *C.cryptooecium*) and season (e.g. *C.cryptooecium*, *E.coccinea* and *M.nitida*), indicating that significant differences existed.

As with the total data sets for each species, the *t*-tests for particular species-pairs' interactions (Table 4.7.) provided more detailed information on the significant differences that existed between the coefficients of the parameters under consideration. It is important to note, however, that because each interspecific interaction was considered twice in the overall analysis (once in terms of species A, and again

in terms of species B), 2 sets of *t*-tests were produced for each interaction. The results are, although superficially different, directly related and complementary to one another. This illustrates the important point that the order in which the components of the data sets are incorporated into the model will alter markedly the output results. On inspection, however, the differences were entirely predictable. For example, consider the interactions between *Alcyonidium* spp. and *C.lineata*, in which *Alcyonidium* spp. won 81, lost 18 and tied in 22 of the encounters (conversely, *C.lineata* won 18, lost 81 and tied in 22). When the interaction was considered in terms of *Alcyonidium* spp. the *t*-test results indicated significant differences existed between the numbers of wins and losses, and the numbers of wins and ties. When the interaction was analysed in terms of *C.lineata*, however, the only significant difference was that between the numbers of wins and losses. These significant differences would be expected from an examination of the raw data themselves.

Inspection of the results of the *t*-tests for outcome alone, indicated that many pairs of species differed markedly in their competitive abilities. However, the results were further complicated because the nature of the significant differences varied among the different species-pairs. For example, consider 2 of the interspecific encounters exhibited by *C.lineata*. In interactions with *E.pilosa* the results for the *t*-tests

indicated that *C.lineata* won a significantly greater number of times than it lost or tied. Conversely, in encounters with *E.coccinea*, the *t*-tests indicated the reverse result; *viz.* that *C.lineata* lost significantly more often. The results thus confirmed the evidence from the species' total data sets, that a considerable amount of variation in outcome was attributable to the identity of the interacting species. A number of species-pairs produced a lack of significant differences between the 3 outcomes, i.e. the species exhibited a degree of "equivalence" in the outcomes of their encounters. Examples include the encounters between *Alcyonidium* spp. and *C.cryptooecium*, *C.hyalina* and *E.pilosa* and the intraspecific interactions between *M.nitida* colonies.

The results from the *t*-tests thus provided irrefutable statistical evidence in support of the conclusions drawn from an examination of the "contact matrix". Essentially, the bryozoan interactions were complex and variable, with many reversals and ties, or "stand-offs", between species of differing competitive abilities, creating an intricate network relationship among the species.

Similarly, the *t*-tests' results for the model examining the influence of sector, or encounter angle, on the outcome of competition indicated that for many of the interactions, significant differences existed between the sectors; for example, the interactions between *Alcyonidium* spp. and *E.coccinea*, *C.lineata* and

FIGURE 4.5. The probability of the 3 possible outcomes of competitive interactions involving *Alcyonidium* spp., at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *Alcyonidium* spp. competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *Callopora craticula*;
(d) vs. *Callopora lineata*;
(e) vs. *Celleporella hyalina*;
(f) vs. *Cribrilina cryptooecium*;
(g) vs. *Escharoides coccinea*;
(h) vs. *Membraniporella nitida*.

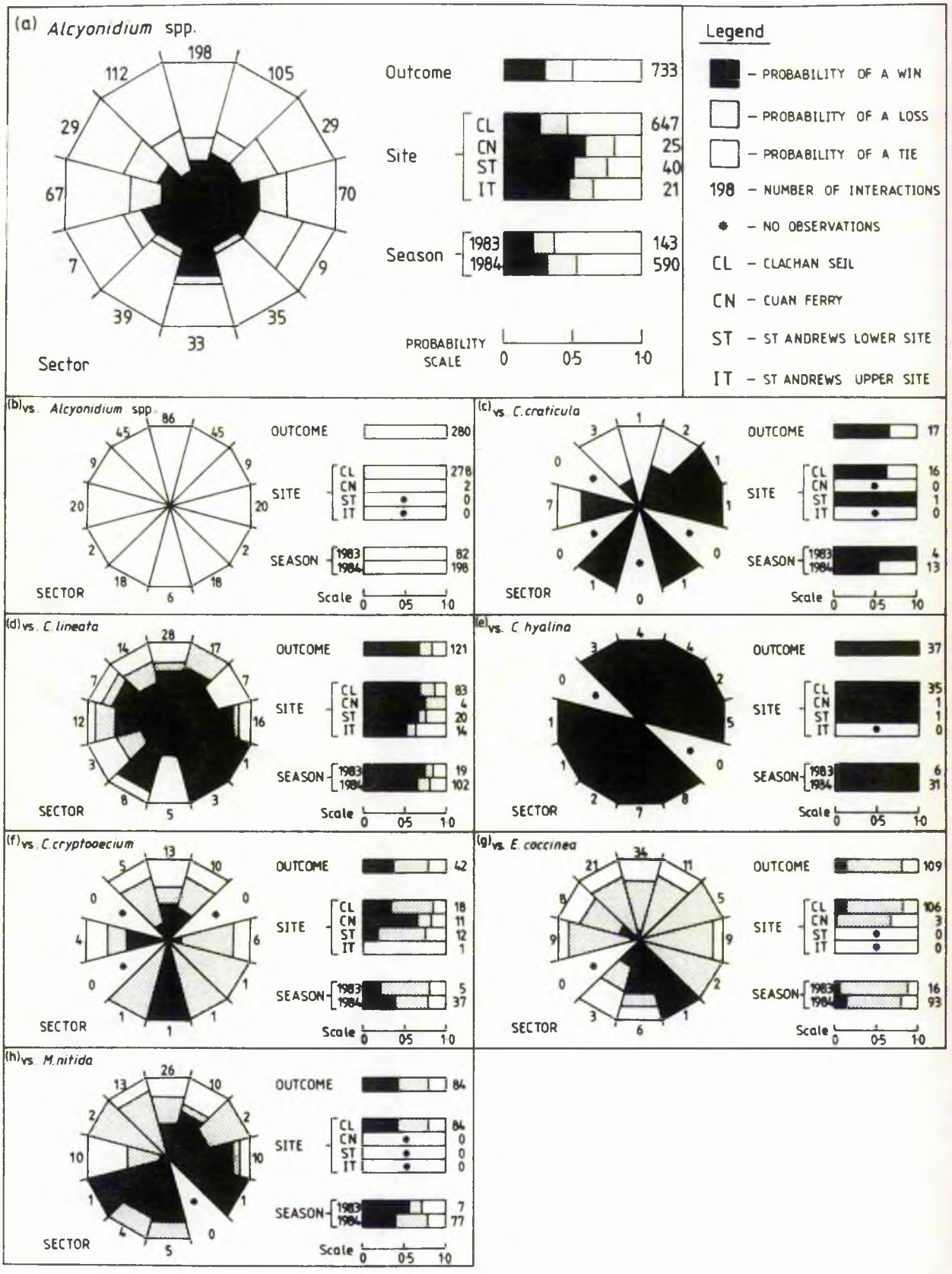

(a) Alcyonidium spp.
198
105
29
70
9
35
33
39
7
67
29
112
Sector
Outcome 733
Site CL 647
CN 25
ST 40
IT 21
Season 1983 143
1984 590
PROBABILITY SCALE 0 0·5 1·0
Legend
– PROBABILITY OF A WIN
– PROBABILITY OF A LOSS
– PROBABILITY OF A TIE
198 – NUMBER OF INTERACTIONS
– NO OBSERVATIONS
CL – CLACHAN SEIL
CN – CUAN FERRY
ST – ST ANDREWS LOWER SITE
IT – ST ANDREWS UPPER SITE
(b) vs. Alcyonidium spp.
86
45
9
20
2
18
6
SECTOR
OUTCOME 280
SITE CL 278
CN 2
ST 0
IT 0
SEASON 1983 82
1984 198
Scale 0 0·5 1·0
(c) vs. C. craticula
3
1
2
0
7
SECTOR
OUTCOME 17
SITE CL 16
CN 0
ST 1
IT 0
SEASON 1983 4
1984 13
Scale 0 0·5 1·0
(d) vs. C. lineata
28
14
17
7
12
16
3
1
8
5
SECTOR
OUTCOME 121
SITE CL 83
CN 4
ST 20
IT 14
SEASON 1983 19
1984 102
Scale 0 0·5 1·0
(e) vs. C. hyalina
4
3
2
0
1
5
SECTOR
OUTCOME 37
SITE CL 35
CN 1
ST 1
IT 0
SEASON 1983 6
1984 31
Scale 0 0·5 1·0
(f) vs. C. cryptooecium
13
5
10
0
4
6
1
SECTOR
OUTCOME 42
SITE CL 18
CN 11
ST 12
IT 1
SEASON 1983 5
1984 37
Scale 0 0·5 1·0
(g) vs. E. coccinea
34
21
11
8
5
9
2
3
6
1
SECTOR
OUTCOME 109
SITE CL 106
CN 3
ST 0
IT 0
SEASON 1983 16
1984 93
Scale 0 0·5 1·0
(h) vs. M. nitida
26
13
10
2
10
1
4
5
SECTOR
OUTCOME 84
SITE CL 84
CN 0
ST 0
IT 0
SEASON 1983 7
1984 77
Scale 0 0·5 1·0

FIGURE 4.6. The probability of the 3 possible outcomes of all the competitive interactions involving (a) *Callopora aurita*, (b) *Flustrellidra hispida* and (c) *Microporella ciliata*, at 12 encounter angles, at 4 sites and in 2 years.

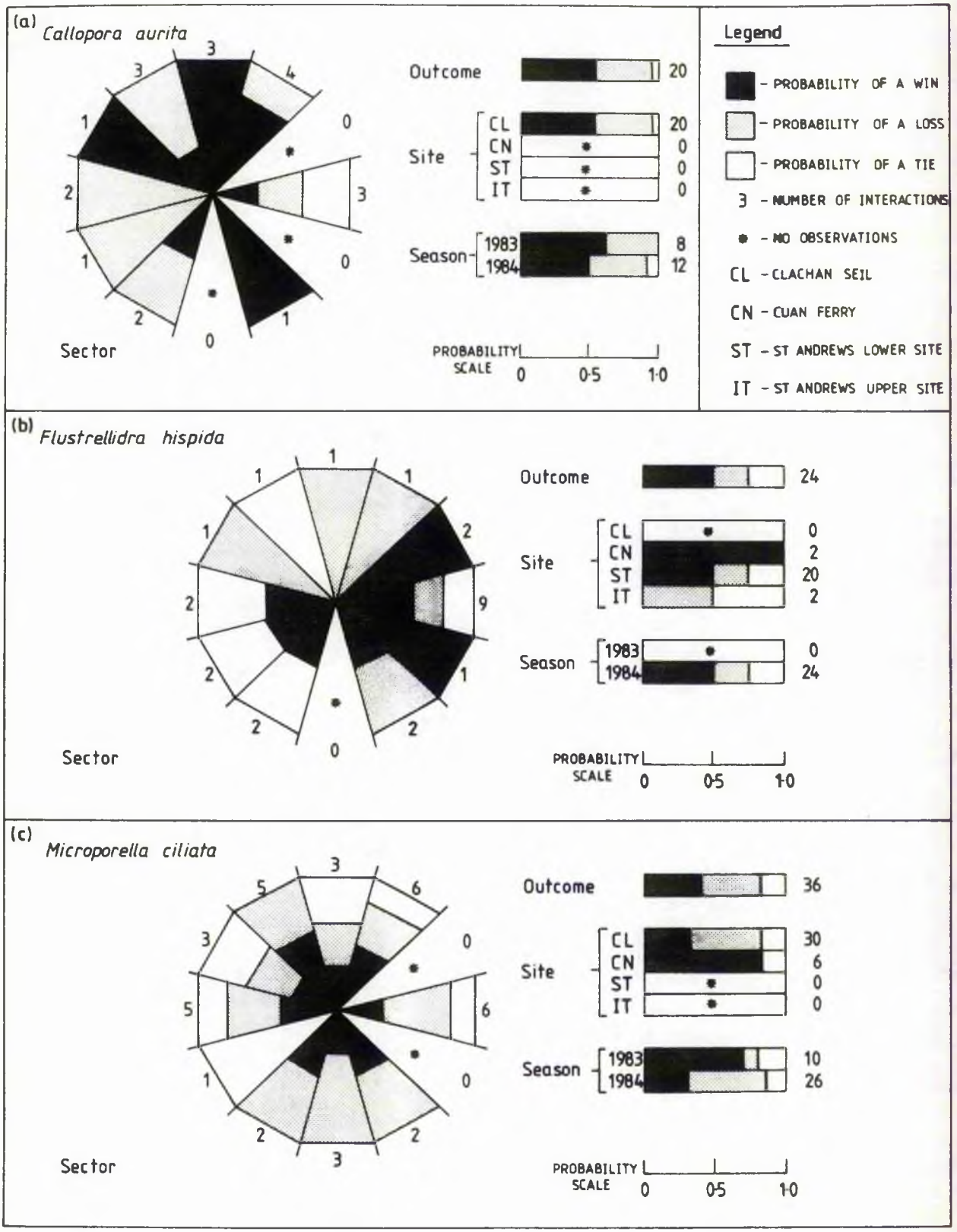

(a) Callopora aurita
Sector
Outcome
20
Site
CL 20
CN 0
ST 0
IT 0
Season
1983 8
1984 12
PROBABILITY SCALE 0 0·5 1·0
Legend
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
3 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b) Flustrellidra hispida
Sector
Outcome
24
Site
CL 0
CN 2
ST 20
IT 2
Season
1983 0
1984 24
PROBABILITY SCALE 0 0·5 1·0
(c) Microporella ciliata
Sector
Outcome
36
Site
CL 30
CN 6
ST 0
IT 0
Season
1983 10
1984 26
PROBABILITY SCALE 0 0·5 1·0

FIGURE 4.7. The probability of the 3 possible outcomes of competitive interactions involving *Callopora craticula*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *C.craticula* competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *Escharoides coccinea*.

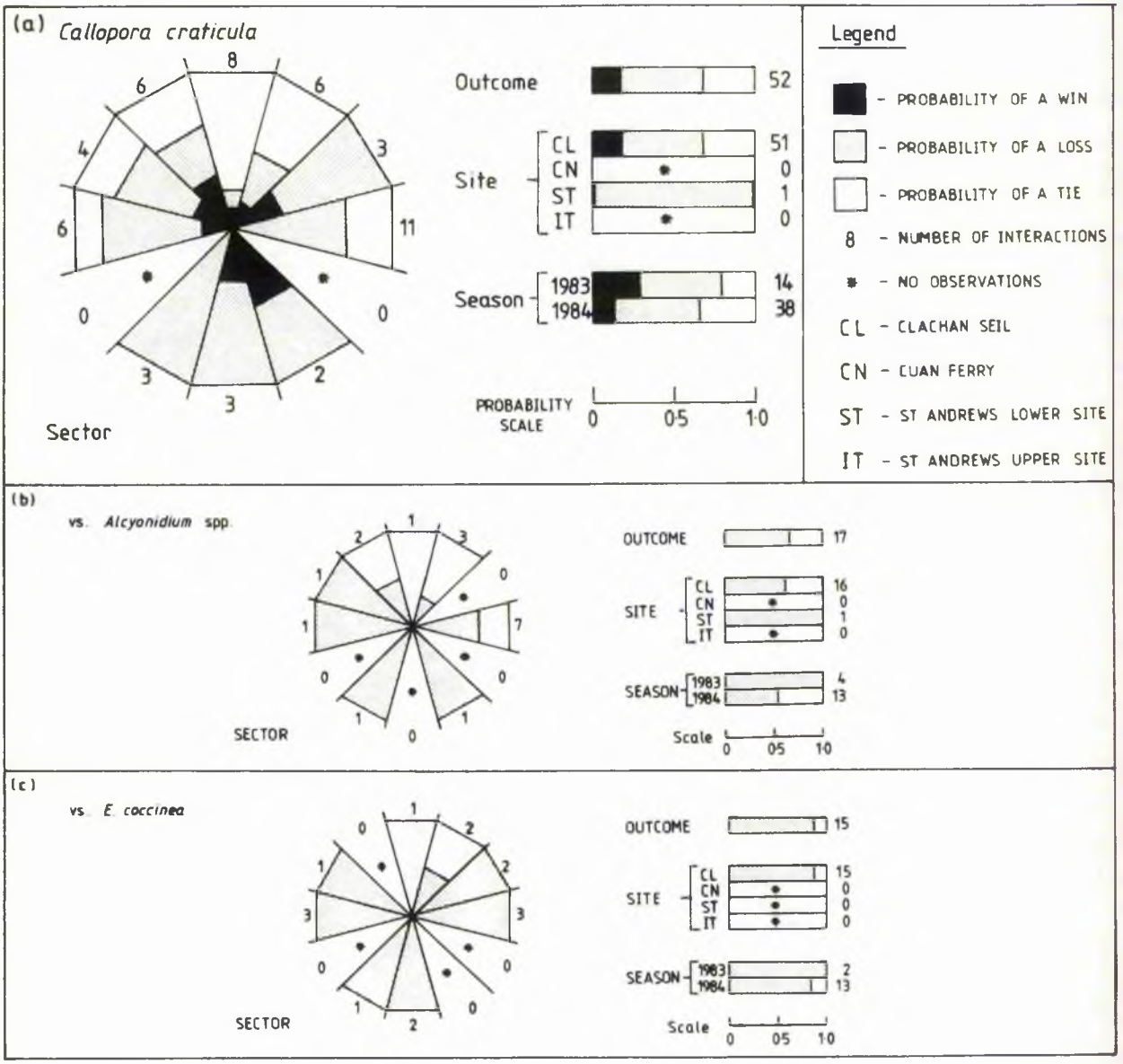

(a) Callopora craticula
8
6
6
4
3
6
11
0
0
3
2
3
Sector
Outcome
52
Site
CL
CN
ST
IT
51
0
1
0
Season
1983
1984
14
38
PROBABILITY SCALE
0
0·5
1·0
Legend
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
8 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b)
vs. Alcyonidium spp.
1
2
3
1
0
1
7
0
0
1
0
1
0
SECTOR
OUTCOME
17
SITE
CL
CN
ST
IT
16
0
1
0
SEASON
1983
1984
4
13
Scale
0
0·5
1·0
(c)
vs. E. coccinea
1
0
2
1
2
3
3
0
0
1
2
0
SECTOR
OUTCOME
15
SITE
CL
CN
ST
IT
15
0
0
0
SEASON
1983
1984
2
13
Scale
0
0·5
1·0

FIGURE 4.8. The probability of the 3 possible outcomes of competitive interactions involving *Callopora lineata*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *C.lineata* competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *C.lineata*;
(d) vs. *Celleporella hyalina*;
(e) vs. *Cribrilina cryptooecium*;
(f) vs. *Electra pilosa*;
(g) vs. *Escharoides coccinea*;
(h) vs. *Membraniporella nitida*;
(i) vs. *Schizoporella unicornis*.

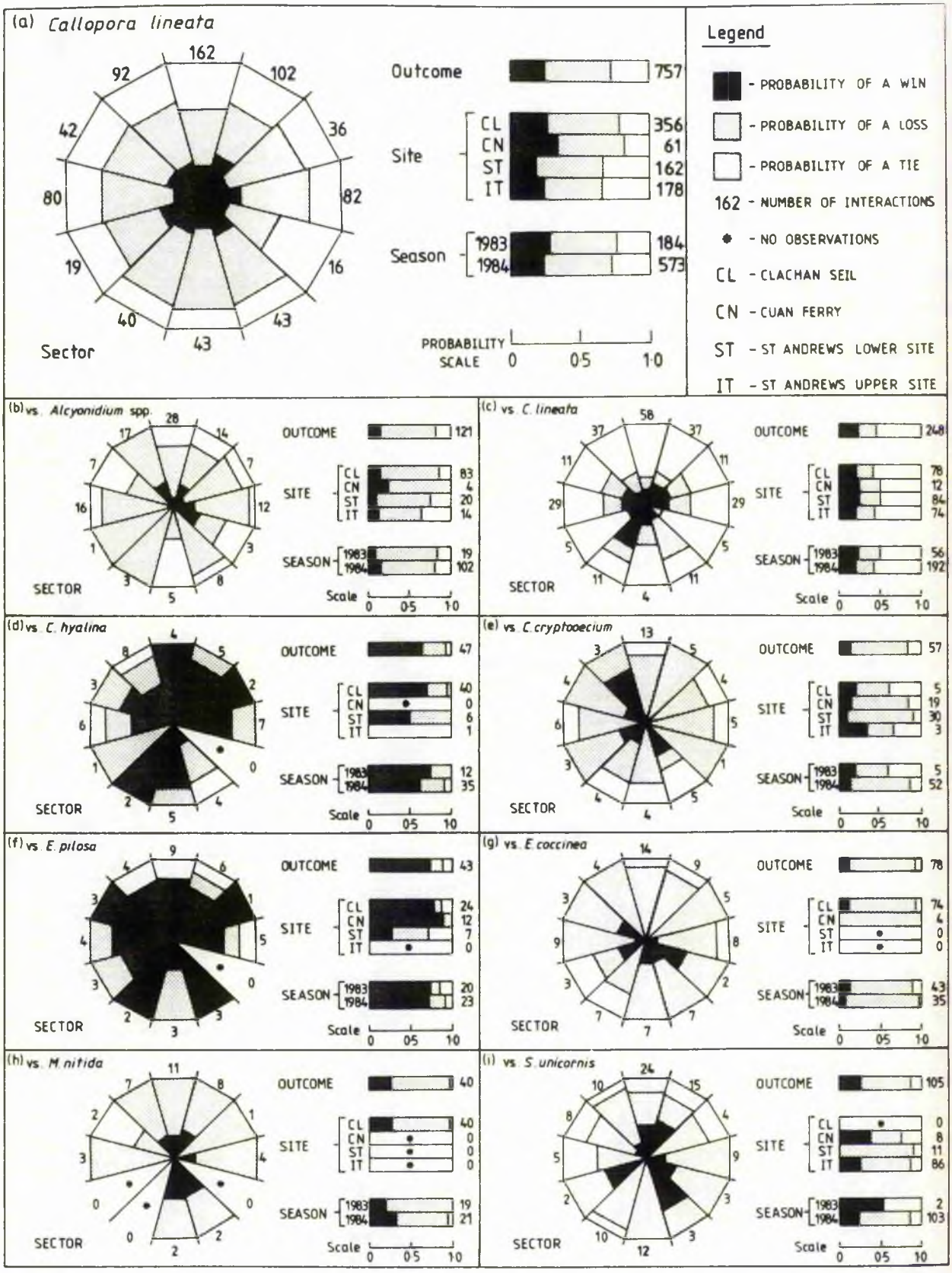

(a) Callopora lineata
162
102
36
82
16
43
43
40
19
80
42
92
Sector
Outcome 757
Site CL 356
CN 61
ST 162
IT 178
Season 1983 184
1984 573
PROBABILITY SCALE 0 0·5 1·0
Legend
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
162 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b) vs. Alcyonidium spp.
(c) vs. C. lineata
(d) vs. C. hyalina
(e) vs. C. cryptooecium
(f) vs. E. pilosa
(g) vs. E. coccinea
(h) vs. M. nitida
(i) vs. S. unicornis
OUTCOME
SITE
SEASON
SECTOR
Scale 0 0·5 1·0

FIGURE 4.9. The probability of the 3 possible outcomes of competitive interactions involving *Celleporella hyalina*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *C.hyalina* competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *Callopora lineata*;
(d) vs. *C.hyalina*;
(e) vs. *Electra pilosa*;
(f) vs. *Escharoides coccinea*;
(g) vs. *Membraniporella nitida*.

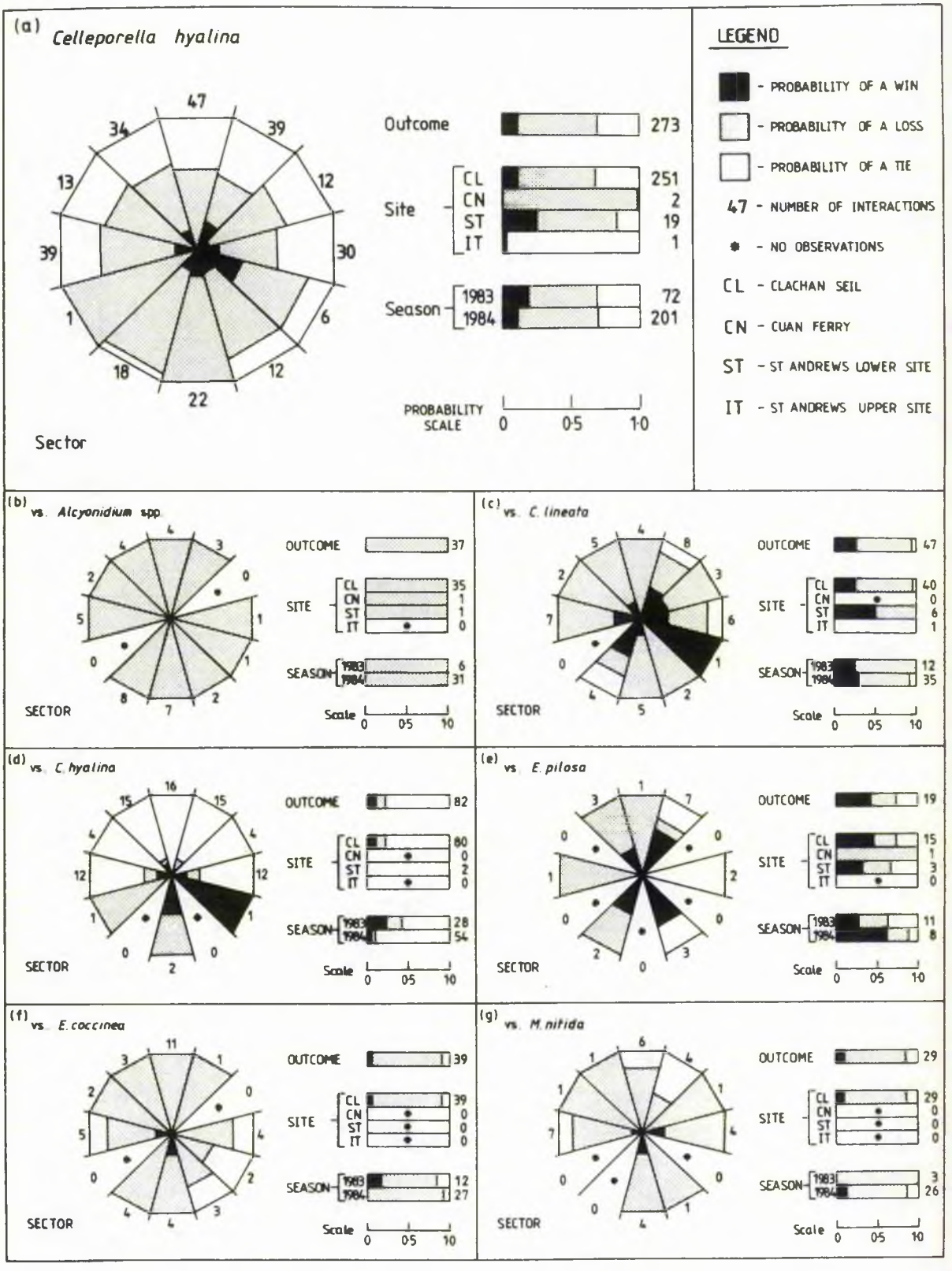

(a) Celleporella hyalina
47
39
12
30
6
12
22
18
1
39
13
34
Sector
Outcome 273
Site CL 251
CN 2
ST 19
IT 1
Season 1983 72
1984 201
PROBABILITY SCALE 0 0·5 1·0
LEGEND
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
47 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b) vs. Alcyonidium spp.
SECTOR
OUTCOME 37
SITE CL 35
CN 1
ST 1
IT 0
SEASON 1983 6
1984 31
Scale 0 0·5 1·0
(c) vs. C. lineata
SECTOR
OUTCOME 47
SITE CL 40
CN 0
ST 6
IT 1
SEASON 1983 12
1984 35
Scale 0 0·5 1·0
(d) vs. C. hyalina
SECTOR
OUTCOME 82
SITE CL 80
CN 0
ST 2
IT 0
SEASON 1983 28
1984 54
Scale 0 0·5 1·0
(e) vs. E. pilosa
SECTOR
OUTCOME 19
SITE CL 15
CN 1
ST 3
IT 0
SEASON 1983 11
1984 8
Scale 0 0·5 1·0
(f) vs. E. coccinea
SECTOR
OUTCOME 39
SITE CL 39
CN 0
ST 0
IT 0
SEASON 1983 12
1984 27
Scale 0 0·5 1·0
(g) vs. M. nitida
SECTOR
OUTCOME 29
SITE CL 29
CN 0
ST 0
IT 0
SEASON 1983 3
1984 26
Scale 0 0·5 1·0

FIGURE 4.10. The probability of the 3 possible outcomes of competitive interactions involving *Cribrilina cryptooecium*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *C.cryptooecium* competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *Callopora lineata*;
(d) vs. *C.cryptooecium*;
(e) vs. *Electra pilosa*;
(f) vs. *Escharoides coccinea*;
(g) vs. *Schizoporella unicornis*.

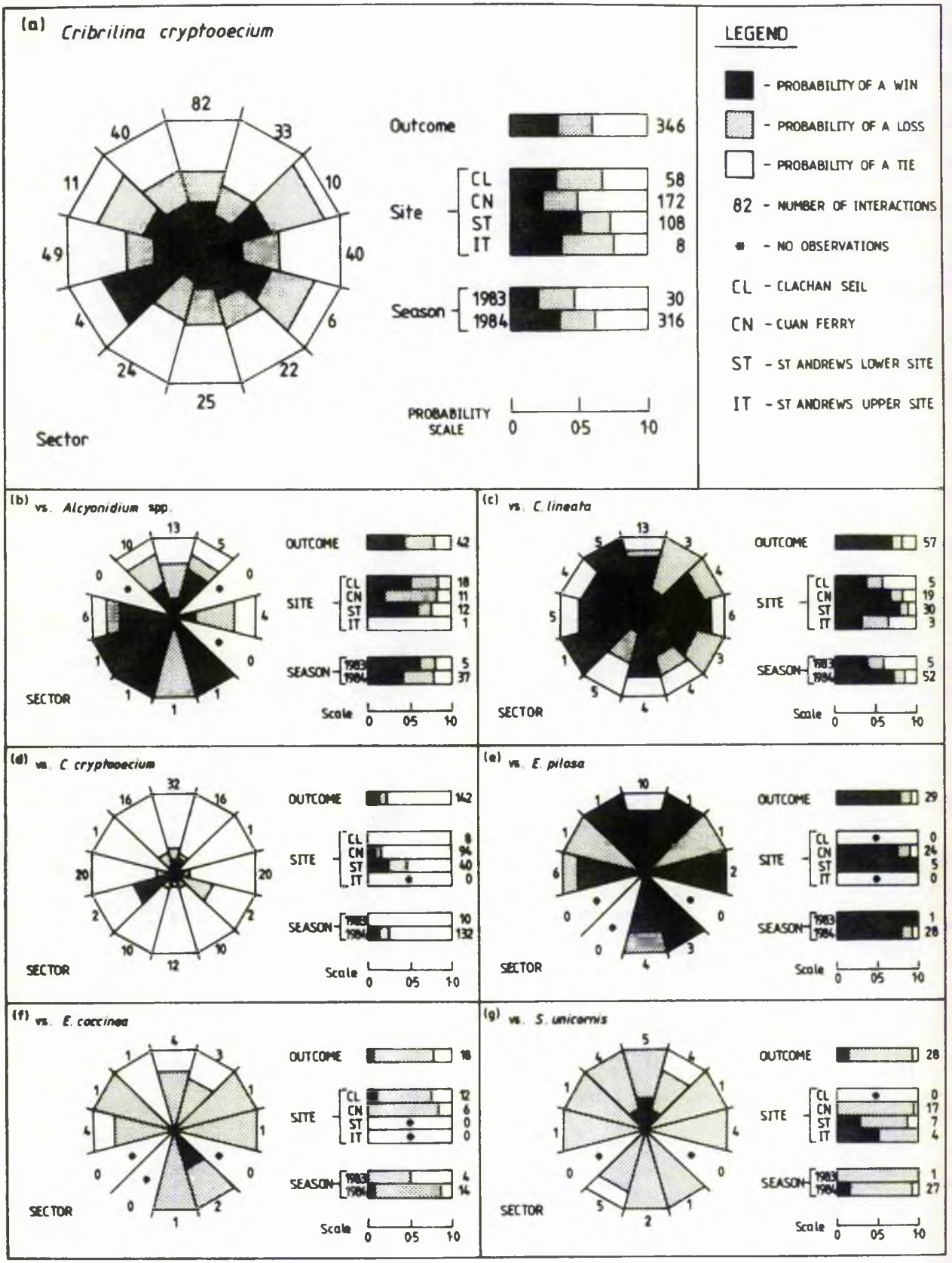

(a) Cribrilina cryptooecium
82
33
10
40
49
11
4
6
24
22
25
Sector
Outcome 346
Site CL 58
CN 172
ST 108
IT 8
Season 1983 30
1984 316
PROBABILITY SCALE 0 05 10
LEGEND
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
82 - NUMBER OF INTERACTIONS
- NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b) vs. Alcyonidium spp.
SECTOR
OUTCOME 42
SITE CL 18
CN 11
ST 12
IT 1
SEASON 1983 5
1984 37
Scale 0 05 10
(c) vs. C. lineata
SECTOR
OUTCOME 57
SITE CL 5
CN 19
ST 30
IT 3
SEASON 1983 5
1984 52
Scale 0 05 10
(d) vs. C. cryptooecium
SECTOR
OUTCOME 142
SITE CL 8
CN 94
ST 40
IT 0
SEASON 1983 10
1984 132
Scale 0 05 10
(e) vs. E. pilosa
SECTOR
OUTCOME 29
SITE CL 0
CN 24
ST 5
IT 0
SEASON 1983 1
1984 28
Scale 0 05 10
(f) vs. E. coccinea
SECTOR
OUTCOME 18
SITE CL 12
CN 6
ST 0
IT 0
SEASON 1983 4
1984 14
Scale 0 05 10
(g) vs. S. unicornis
SECTOR
OUTCOME 28
SITE CL 0
CN 17
ST 7
IT 4
SEASON 1983 1
1984 27
Scale 0 05 10

FIGURE 4.11. The probability of the 3 possible outcomes of competitive interactions involving *Electra pilosa*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *E.pilosa* competitive encounters examined;
(b) vs. *Callopora lineata*;
(c) vs. *Celleporella hyalina*;
(d) vs. *Cribrilina cryptooecium*;
(e) vs. *E.pilosa*;
(f) vs. *Escharoides coccinea*;
(g) vs. *Membraniporella nitida*.

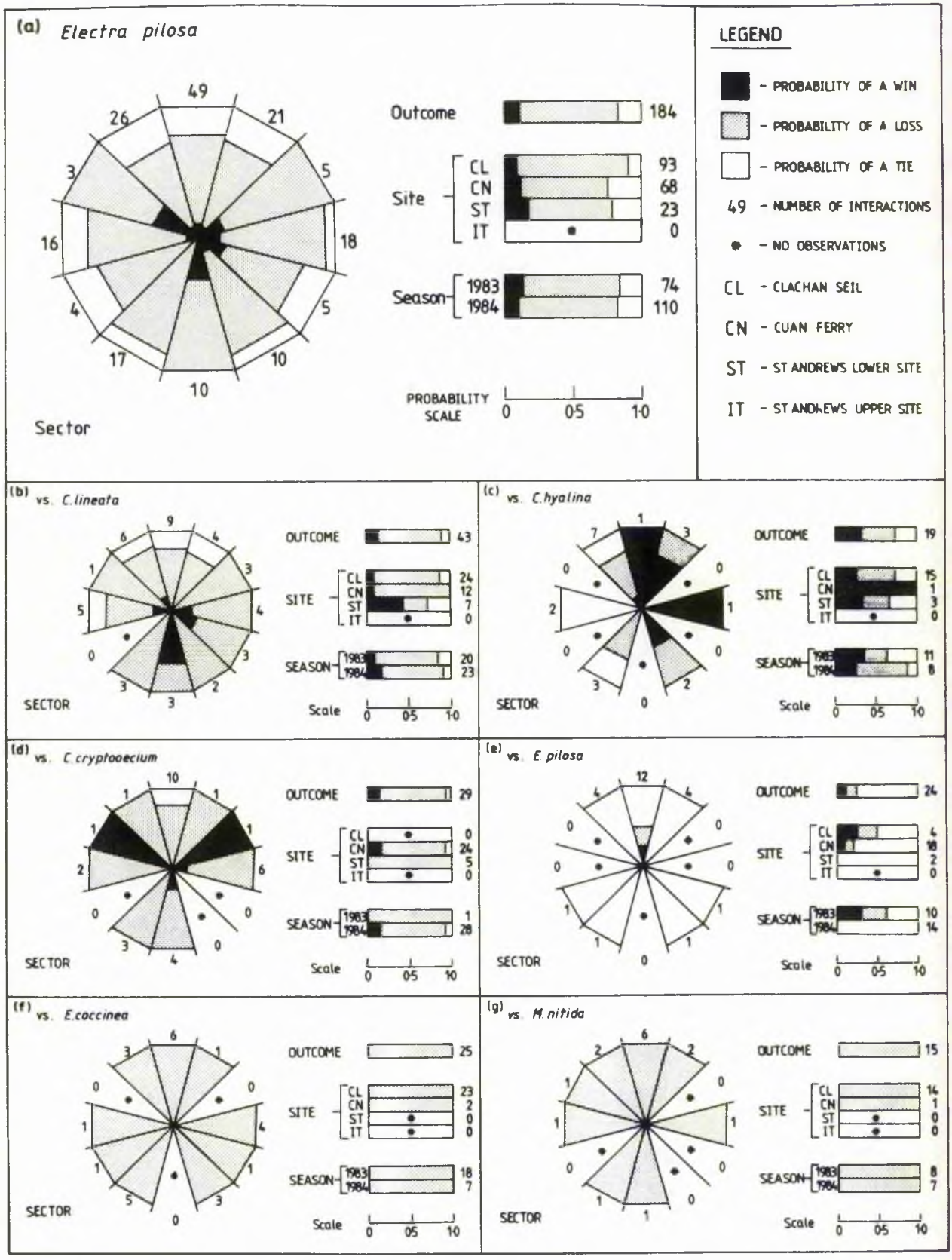

(a) Electra pilosa
49
26
21
3
5
16
18
4
5
17
10
10
Sector
Outcome 184
Site CL 93
CN 68
ST 23
IT 0
Season 1983 74
1984 110
PROBABILITY SCALE 0 0·5 1·0
LEGEND
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
49 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b) vs. C.lineata
SECTOR
OUTCOME 43
SITE CL 24
CN 12
ST 7
IT 0
SEASON 1983 20
1984 23
Scale 0 0·5 1·0
(c) vs. C.hyalina
SECTOR
OUTCOME 19
SITE CL 15
CN 1
ST 3
IT 0
SEASON 1983 11
1984 8
Scale 0 0·5 1·0
(d) vs. C.cryptooecium
SECTOR
OUTCOME 29
SITE CL 0
CN 24
ST 5
IT 0
SEASON 1983 1
1984 28
Scale 0 0·5 1·0
(e) vs. E pilosa
SECTOR
OUTCOME 24
SITE CL 4
CN 18
ST 2
IT 0
SEASON 1983 10
1984 14
Scale 0 0·5 1·0
(f) vs. E.coccinea
SECTOR
OUTCOME 25
SITE CL 23
CN 2
ST 0
IT 0
SEASON 1983 18
1984 7
Scale 0 0·5 1·0
(g) vs. M.nitida
SECTOR
OUTCOME 15
SITE CL 14
CN 1
ST 0
IT 0
SEASON 1983 8
1984 7
Scale 0 0·5 1·0

FIGURE 4.12. The probability of the 3 possible outcomes of competitive interactions involving *Escharoides coccinea*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *E.coccinea* competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *Callopora craticula*;
(d) vs. *Callopora lineata*;
(e) vs. *Celleporella hyalina*;
(f) vs. *Cribrilina cryptooecium*;
(g) vs. *Electra pilosa*;
(h) vs. *E.coccinea*;
(i) vs. *Membraniporella nitida*.

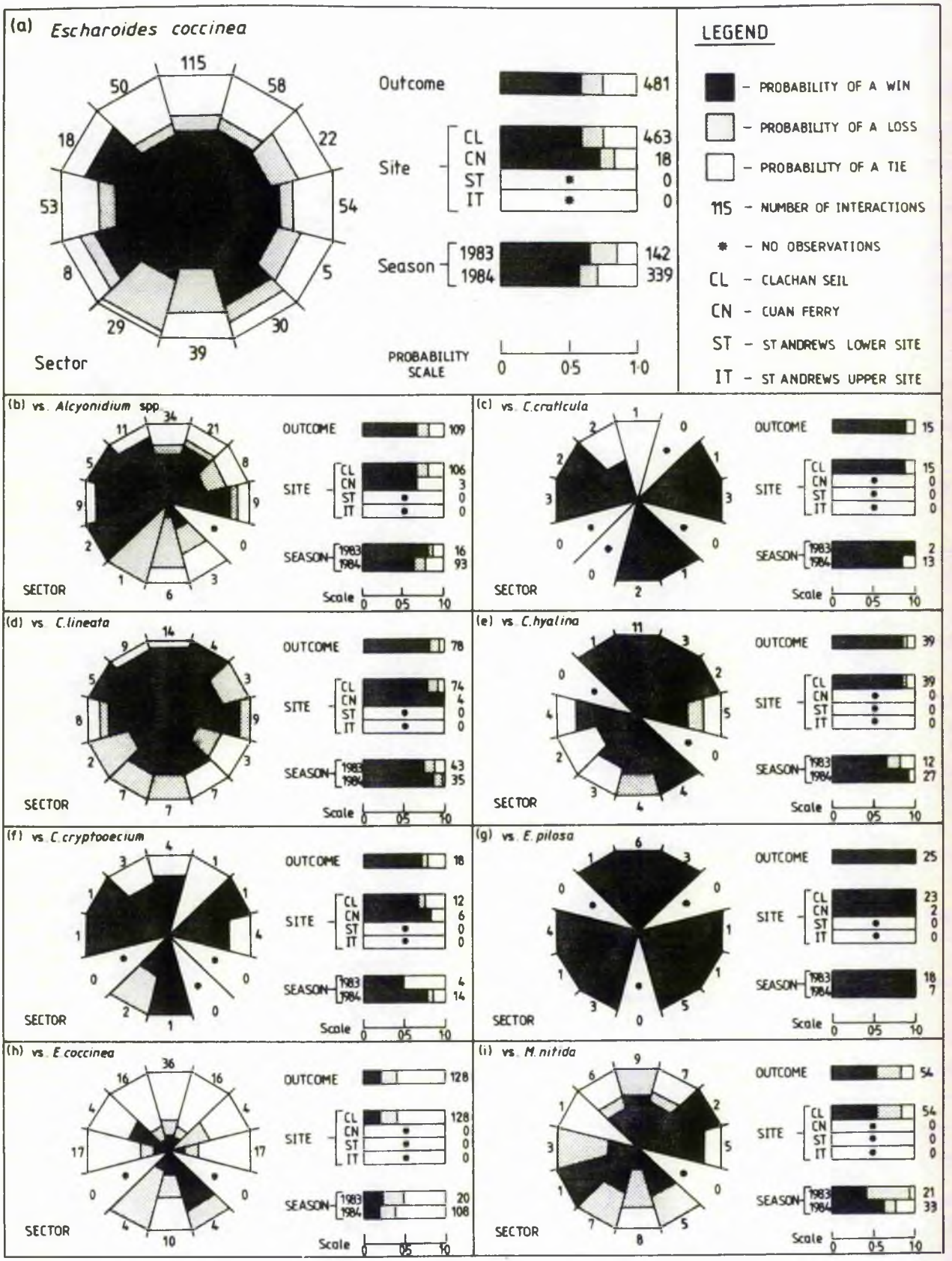

(a) Escharoides coccinea
115
50
58
18
22
53
54
8
5
29
30
39
Sector
Outcome 481
Site CL 463
CN 18
ST 0
IT 0
Season 1983 142
1984 339
PROBABILITY SCALE 0 0·5 1·0
LEGEND
– PROBABILITY OF A WIN
– PROBABILITY OF A LOSS
– PROBABILITY OF A TIE
115 – NUMBER OF INTERACTIONS
* – NO OBSERVATIONS
CL – CLACHAN SEIL
CN – CUAN FERRY
ST – ST ANDREWS LOWER SITE
IT – ST ANDREWS UPPER SITE
(b) vs. Alcyonidium spp.
OUTCOME 109
SITE CL 106
CN 3
ST 0
IT 0
SEASON 1983 16
1984 93
SECTOR
Scale 0 0·5 1·0
(c) vs. C.craticula
OUTCOME 15
SITE CL 15
CN 0
ST 0
IT 0
SEASON 1983 2
1984 13
SECTOR
Scale 0 0·5 1·0
(d) vs. C.lineata
OUTCOME 78
SITE CL 74
CN 4
ST 0
IT 0
SEASON 1983 43
1984 35
SECTOR
Scale 0 0·5 1·0
(e) vs. C.hyalina
OUTCOME 39
SITE CL 39
CN 0
ST 0
IT 0
SEASON 1983 12
1984 27
SECTOR
Scale 0 0·5 1·0
(f) vs. C.cryptooecium
OUTCOME 18
SITE CL 12
CN 6
ST 0
IT 0
SEASON 1983 4
1984 14
SECTOR
Scale 0 0·5 1·0
(g) vs. E.pilosa
OUTCOME 25
SITE CL 23
CN 2
ST 0
IT 0
SEASON 1983 18
1984 7
SECTOR
Scale 0 0·5 1·0
(h) vs. E.coccinea
OUTCOME 128
SITE CL 128
CN 0
ST 0
IT 0
SEASON 1983 20
1984 108
SECTOR
Scale 0 0·5 1·0
(i) vs. M.nitida
OUTCOME 54
SITE CL 54
CN 0
ST 0
IT 0
SEASON 1983 21
1984 33
SECTOR
Scale 0 0·5 1·0

FIGURE 4.13. The probability of the 3 possible outcomes of competitive interactions involving *Membraniporella nitida*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *M.nitida* competitive encounters examined;
(b) vs. *Alcyonidium* spp.;
(c) vs. *Callopora lineata*;
(d) vs. *Celleporella hyalina*;
(e) vs. *Electra pilosa*;
(f) vs. *Escharoides coccinea*;
(g) vs. *M.nitida*.

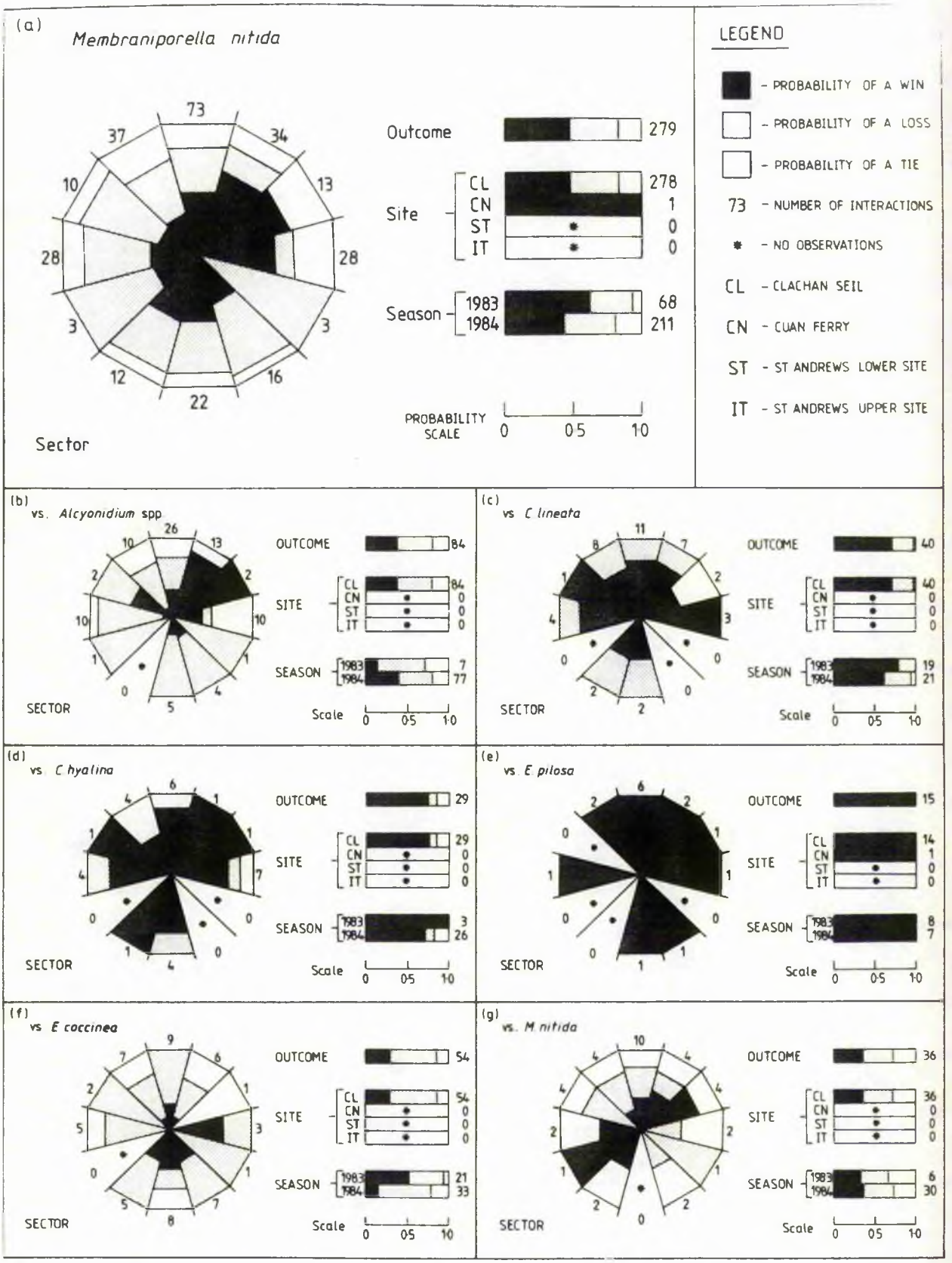
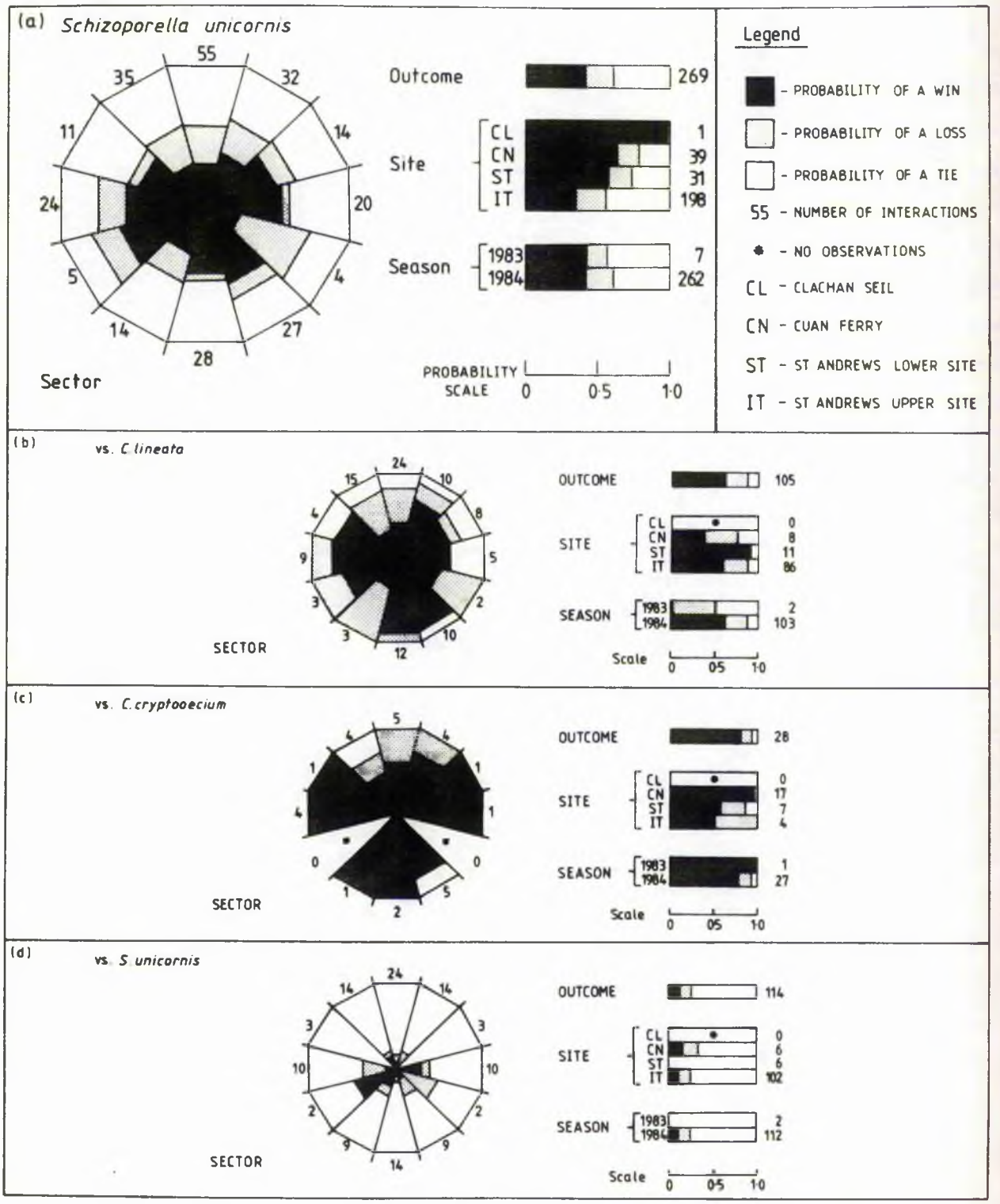

(a)
Membraniporella nitida
73
34
13
28
3
16
22
12
3
28
10
37
Sector
Outcome
279
Site
CL
CN
ST
IT
278
1
0
0
Season
1983
1984
68
211
PROBABILITY SCALE
0
0·5
1·0
LEGEND
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
73 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b)
vs. Alcyonidium spp
SECTOR
OUTCOME
84
SITE
84
0
0
0
SEASON
7
77
Scale
(c)
vs C lineata
OUTCOME
40
SITE
40
0
0
0
SEASON
19
21
(d)
vs C hyalina
OUTCOME
29
SITE
29
0
0
0
SEASON
3
26
(e)
vs E pilosa
OUTCOME
15
SITE
14
1
0
0
SEASON
8
7
(f)
vs E coccinea
OUTCOME
54
SITE
54
0
0
0
SEASON
21
33
(g)
vs. M nitida
OUTCOME
36
SITE
36
0
0
0
SEASON
6
30

FIGURE 4.14. The probability of the 3 possible outcomes of competitive interactions involving *Schizoporella unicornis*, at 12 encounter angles, at 4 sites and in 2 years:
(a) for all the *S.unicornis* competitive encounters examined;
(b) vs. *Callopora lineata*;
(c) vs. *Cribrilina cryptooecium*;
(d) vs. *S.unicornis*.


(a) Schizoporella unicornis
55
35
32
14
11
20
24
5
4
14
27
28
Sector
Outcome
269
Site
CL
CN
ST
IT
1
39
31
198
Season
1983
1984
7
262
PROBABILITY SCALE
0
0·5
1·0
Legend
- PROBABILITY OF A WIN
- PROBABILITY OF A LOSS
- PROBABILITY OF A TIE
55 - NUMBER OF INTERACTIONS
* - NO OBSERVATIONS
CL - CLACHAN SEIL
CN - CUAN FERRY
ST - ST ANDREWS LOWER SITE
IT - ST ANDREWS UPPER SITE
(b)
vs. C. lineata
24
15
10
8
4
9
5
3
2
3
10
12
SECTOR
OUTCOME
105
SITE
CL
CN
ST
IT
0
8
11
86
SEASON
1983
1984
2
103
Scale
0
0·5
1·0
(c)
vs. C. cryptooecium
5
4
4
1
1
4
1
0
0
1
5
2
SECTOR
OUTCOME
28
SITE
CL
CN
ST
IT
0
17
7
4
SEASON
1983
1984
1
27
Scale
0
0·5
1·0
(d)
vs. S. unicornis
24
14
14
3
3
10
10
2
2
9
9
14
SECTOR
OUTCOME
114
SITE
CL
CN
ST
IT
0
6
6
102
SEASON
1983
1984
2
112
Scale
0
0·5
1·0

S.unicornis and the intraspecific contacts between *C.lineata* colonies. Relatively few of the differences were statistically significant, in particular there were few significant interaction terms, but this was almost entirely due to the small data sets for the coefficients concerned.

Differences were also evident in the outcomes observed between the species-pairs at different sites. For example, differences between the sites existed in interactions between *C.lineata* and *S.unicornis*, *C.lineata* and *E.pilosa*, and *C.lineata* intraspecific encounters. Table 4.7. also illustrates the important qualitative differences that existed in the data sets. From this it can be seen that interactions involving particular species were not observed at particular sites. Thus, for example, encounters involving *E.coccinea* and *M.nitida* were never observed at the east coast sites.

The year of observation also appeared to have a marked effect on the outcome of encounters. For example, significant between-year differences were evident in interactions between *E.coccinea* and *M.nitida*, and in intraspecific encounters for *C.hyalina*.

4.2.3. <u>The Outcome Probabilities</u>:- An examination of the probabilities of the 3 outcomes among the different parameters considered illustrated the conclusions that were apparent from the interpretation of the results of the interaction models and the *t*-tests (see Figures 4.5.-4.14.).

The outcome probabilities for the total data sets of each species illustrated that none were entirely deterministic in the outcome of their encounters. That is, each species exhibited a variable probability of winning, losing or tying. The qualitative conclusions suggested by the "contact matrix" for all the interactions (Table 4.2.) were therefore also supported quantitatively by the probabilities of the different outcomes for each species. Thus, *E.coccinea* (Fig. 4.12.a.) and *M.nitida* (Fig. 4.13.a.) may be considered to have been dominant competitors within the west coast assemblages, with the greatest probabilities of winning encounters. *Alcyonidium* spp. (Fig. 4.5.a.) and *C.cryptooecium* (Fig. 4.10.a.) may have been intermediate in competitive ability, both species having exhibited high probabilities of tying in their encounters, and least probability of losing. Conversely, *C.lineata* (Fig. 4.8.a.), *C.hyalina* (Fig. 4.9.a.) and *E.pilosa* (Fig. 4.11.a.) showed the greatest probability of losing, and had a correspondingly low probability of winning. These species were, therefore, the lowest-ranked in terms of their competitive ability.

The complex interrelationships among interacting species were most evident in an examination of the probabilities of the different outcomes observed between different species-pairs. Very few of the interactions between species were entirely deterministic. The

majority of the species-pairs exhibited at least a degree of reversal of outcome, or the development of tie or "stand-off" situations. Exceptions included intraspecific *Alcyonidium* spp. encounters where all the contacts resulted in ties (Fig. 4.5.b.). Other exceptions were interactions between the more highly-ranked *E.coccinea*, *M. nitida* and *Alcyonidium* spp. competing with the low-ranked species *C.hyalina* (Figs. 4.5.e., 4.9.b.) or *E.pilosa* (Figs. 4.11.f., 4.12.g.; 4.11.g., 4.13.e.). Otherwise the outcome probabilities reiterated the trends in competitive abilities inferred from the "contact matrix" (Table 4.2.). The high-ranked species were not absolutely dominant, but they did exhibit a greater probability of winning an encounter rather than losing or tying, irrespective of the opponent species, although this probability varied depending on the species encountered. For example, almost invariably *E.coccinea* overgrew its competitors, but the actual probability varied from 1.0 in encounters with *E.pilosa* (Fig. 4.12.g.), to approximately 0.8 against *C.craticula* (Fig. 4.12.c.), *C.lineata* (Fig. 4.12.d.), and *C.hyalina* (Fig. 4.12.e.), and as low as 0.56 in encounters with *M.nitida* (Fig. 4.12.i.). The low-ranked species *C.hyalina* and *E.pilosa* were both frequently overgrown by other species, the main exception being in encounters between the 2 species, in which they were approximately equivalent in their competitive abilities (Figs. 4.9. and 4.11.). Intermediate species, such as *Alcyonidium* spp., won most frequently in encounters with low-ranked species

e.g. *C.craticula* (Fig. 4.5.c.) and *C.lineata* (Fig. 4.5.d.), lost against high-ranked species, e.g. *E.coccinea* (Fig. 4.5.g.), and were approximately equivalent in competitive ability in encounters with similarly ranked *C.cryptooecium* (Fig. 4.5.f.). *C.cryptooecium* also exhibited a greater probability of losing in encounters with *E.coccinea* (Fig. 4.10.f.) and *S.unicornis* (Fig. 4.10.g.), and of winning in encounters with *C.lineata* (Fig. 4.10.c.) and *E.pilosa* (Fig. 4.10.e.). "Competitive equivalence" was, however, indicated between *C.cryptooecium* and *Alcyonidium* spp. (Fig. 4.10.b.).

For all the intraspecific interactions, except those between *M.nitida* colonies, ties were the most prevalent outcome. Different species exhibited varying degrees of overgrowth success: the probabilities of overgrowth varied between approximately 0.12 for low-ranked species (e.g. *C.hyalina* (Fig. 4.9.d.) and *E.pilosa* (Fig. 4.11.e.)) to 0.20 for highly-ranked species (e.g. *E.coccinea* (Fig. 4.12.h.)). Intraspecific interactions between *M.nitida* colonies most frequently resulted in overgrowth rather than a tie (Fig. 4.13.g.).

It was, therefore, apparent that the competitive abilities of the different species were markedly variable. However, the overall outcome probabilities took no account of the influence of sector, site or year on the outcome, and, as outlined above, these may have caused considerable deviation from the general patterns.

For each species' total data set, a number of important patterns were apparent among the probabilities of the outcomes among different sectors. All the species showed a progressive decrease in the numbers of interactions observed in each sector, from frontal to terminal sectors. For a number of species the probability of a win appeared to be independent of encounter angle, e.g. *C.lineata* (Fig. 4.8.a.), *C.hyalina* (Fig. 4.9.a.) and *M.ciliata* (Fig. 4.6.c.). For *C.cryptooecium* (Fig. 4.10.a.), and possibly *E.coccinea* (Fig. 4.12.a.), there was an apparently greater probability of winning in frontal and lateral sectors compared to terminal sectors, while for *M.nitida* (Fig. 4.13.a.) the greatest probability of a win was in the right frontal-oblique sectors. Conversely, *Alcyonidium* spp. (Fig. 4.5.a.), *C.craticula* (Fig. 4.7.a.) and *S.unicornis* (Fig. 4.14.a.) exhibited greater probabilities of wins in terminal and lateral sectors. The most marked patterns, however, were in the distribution of losses and ties among the sectors. For many species (e.g. *C.craticula* (Fig. 4.7.a.), *C.lineata* (Fig. 4.8.a.), *C.hyalina* (Fig. 4.9.a.), *E.pilosa* (Fig. 4.11.a.), *E.coccinea* (Fig. 4.12.a.), *M.nitida* (Fig. 4.13.a.) and *M.ciliata* (Fig. 4.6.c.)) there was evidence of a greater probability of a tie in the frontal sectors which, in general, decreased in the terminal and lateral sectors. This pattern was accompanied by a concomitant increase in the probability of losing from frontal to terminal sectors. Thus, 2 groups of species appeared to

be present in the bryozoan assemblages. First, those in which the greatest probability of a win was in the frontal sectors (or the probability of a win was relatively unaffected by sector), but in which the number of ties was most frequent in frontal sectors and losses in the terminal sectors. Second, species which showed a greater probability of winning in the terminal sectors and of losing in the frontal sectors. The pattern of probability distributions among outcomes seemed to be independent of the previously inferred species' rankings and was a further indication of the complexity inherent among bryozoan interactions.

The variability of the probability of different outcomes in relation to sector was markedly evident in an examination of the probabilities of the different outcomes among different species-pairs. A number of patterns were evident which may contribute to a further understanding of the complex relationships among competing species.

For those specific interactions which were entirely deterministic in their outcome, the encounter angle apparently had no significant effect on the outcome. For example, *Alcyonidium* spp. overgrew *C.hyalina* irrespective of encounter angle (Figs. 4.5.e., 4.9.b.); similarly, *E.pilosa* was overgrown by *E.coccinea* and *M.nitida* irrespective of the angle of contact between the competing colonies (Figs. 4.11.f., 4.12.g.; 4.11.g., 4.13.e.). It was only the lower-ranked species, such as

E.pilosa and *C.hyalina* , which appeared to be unable to overgrow higher-ranked species irrespective of encounter angle. The majority of the other species were able to overgrow potentially dominant competitors, and the probability of this overgrowth appeared, in a number of instances, to be sector-dependent. *Alcyonidium* spp. was, in general, a poor competitor in encounters with *E.coccinea*, but exhibited a higher probability of overgrowth in terminal sectors, and a relatively high probability of a tie outcome in frontal and lateral sectors (Figs. 4.5.g., 4.12.b.). Similarly, in competition between *E.coccinea* and *C.lineata*, *E.coccinea* was nearly absolutely dominant in frontal sectors, whereas in terminal and lateral sectors there was an increased probability of *C.lineata* winning in encounters (Figs. 4.8.g., 4.12.d.). Low-ranked species were also able to overgrow intermediate-ranked species in terminal sectors, whereas in frontal sectors they were more frequently overgrown. For example, in terminal sectors, there was a greater probability of *C.hyalina* overgrowing *M.nitida* (Figs. 4.9.g., 4.13.d.), and of *E.pilosa* overgrowing *C.lineata* (Figs. 4.8.f., 4.11.b.).

The converse situation was apparent in interactions between *C.cryptooecium* and *S.unicornis* (Figs. 4.10.g., 4.14.c.). The latter species was dominant in the majority of the interactions, but *C.cryptooecium* exhibited a higher probability of overgrowing colonies in frontal encounters. This was suggestive of another pattern in the competitive abilities, namely that some

dominant species may have had a higher probability of overgrowth in terminal sectors. Similar patterns were apparent in interactions between *Alcyonidium* spp. and *C.lineata* (Figs. 4.5.d., 4.8.b.), and *S.unicornis* and *C.lineata* (Figs. 4.8.i., 4.14.b.). *Alcyonidium* spp. and *S.unicornis* were the overall dominant competitors, but, in general, exhibited a higher probability of overgrowing *C.lineata* in terminal sectors.

There were also patterns in the degree of "competitive equivalence" exhibited by pairs of species. For example, *Alcyonidium* spp. and *M.nitida* were approximately equivalent in their competitive abilities (Figs. 4.5.h., 4.13.b.). However, *M.nitida* had a greater probability of winning or tying in frontal sectors, whereas in terminal sectors *Alcyonidium* spp. had a higher probability of overgrowing the former. *M.nitida*, which, in general, was markedly dominant in overgrowth encounters with *C.lineata*, exhibited a higher probability of overgrowth in frontal sectors than *C.lineata*. In terminal sectors, however, the 2 species were more equivalent in the probable outcome of the interactions (Figs. 4.8.h., 4.13.c.).

Several species-pairs interactions indicated a greater probability of a tie in frontal and lateral sectors; for example, interactions between *Alcyonidium* spp. and *C.cryptooecium* (Figs. 4.5.f., 4.10.b.), *Alcyonidium* spp. and *M.nitida* (Figs. 4.5.h., 4.13.b.), *C.lineata* and *E.pilosa* (Figs. 4.8.f., 4.11.b.), *C.lineata*

and *S.unicornis* (Figs. 4.8.i., 4.14.b.), and *C.cryptooecium* and *E.pilosa* (Figs. 4.10.e., 4.11.d.). However, there were also numerous exceptions, including interactions between *Alcyonidium* spp. and *C.lineata* (Figs. 4.5.d., 4.8.b.), *Alcyonidium* spp. and *E.coccinea* (Figs. 4.5.g., 4.12.b.), *C.lineata* and *C.cryptooecium* (Figs. 4.8.e., 4.10.c.), and *C.hyalina* and *E.coccinea* (Figs. 4.9.f., 4.12.e.).

Intraspecific interactions were characterized by ties, and a number of patterns were apparent. For intraspecific interactions among *Alcyonidium* spp. colonies, irrespective of encounter angle, the contact always resulted in a tie (Fig. 4.5.b.). Many species exhibited a greater probability of tying in frontal sectors in encounters between colonies of the same species, with an increased probability of overgrowth in terminal and lateral sectors; e.g. *C.lineata* (Fig. 4.8.c.), *C.hyalina* (Fig. 4.9.d.), *E.coccinea* (Fig. 4.12.h.) and *S. unicornis* (Fig. 4.14.d.). However, *C.cryptooecium* (Fig. 4.10.d.), *E.pilosa* (Fig. 4.11.e.), and *M.nitida* (Fig. 4.13.g.), in general, exhibited greater probabilities of overgrowth in the frontal sectors, and of ties in the terminal sectors; and in *E.pilosa* the only overgrowth recorded occurred in sector 1. Interactions between *M.nitida* colonies differed from other intraspecific interactions in that all 3 outcomes occurred with approximately equal probability; and overgrowth had a greater probability in frontal sectors.

Despite the existence of numerous species' patterns among the probabilities of different outcomes among sectors, other pairs (e.g. *Alcyonidium* spp. and *C.craticula* (Figs. 4.5.c., 4.7.b.), *C.lineata* and *E.pilosa* (Figs. 4.8.f., 4.11.b.), and *C.hyalina* and *E.pilosa* (Figs. 4.9.e., 4.11.c.)) exhibited no pattern of outcome in relation to encounter angle. For many of these, the data sets were too small for valid interpretation of the probabilities, and some were also affected by a marked inequality of sample sizes for each sector (e.g. *Alcyonidium* spp. interacting with *C.cryptooecium* (Figs. 4.5.f., 4.10.b.)). Many of the results had to be interpreted with considerable caution because of the variation in sample sizes between sectors. Most interactions recorded concerned the frontal sectors, with a general decrease in lateral and terminal sectors. The variation in sample sizes meant that, although a species may have exhibited a greater probability of winning in terminal sectors, the species may actually have won more interactions in the frontal sectors. Thus relationships between patterns of probabilities of the different outcomes should be interpreted only as indications as to where differences may have existed, rather than conclusive evidence that actual differences did exist. But statistical significances, implied by the scaled deviances and *t*-tests, lend support to the above conclusions.

A number of species' interactions did not conform to the overall frontal/terminal gradation, and these may be

of especial interest. For example, most observations were in terminal sectors for interactions between *Alcyonidium* spp. and *C.hyalina* (Figs. 4.5.e., 4.9.b.); this arose because *C.hyalina* colonies were frequently almost totally overgrown by *Alcyonidium* spp., which made contacts at the overgrowth margin terminal encounters. A few interactions, for example, those between *C.lineata* and *C.hyalina* (Figs. 4.8.d., 4.9.c.) and *E.coccinea* and *M.nitida* (Figs. 4.12.i., 4.13.f.), did not exhibit marked differences in the sample sizes between frontal and terminal sectors. Also, no clear pattern was apparent in the distribution of the different outcomes among sectors. These results suggested that sector may have played no role in determining the nature of the outcome between these particular species-pairs. This does not, however, necessarily imply that if similar sample sizes were obtained for all the sectors for other species-pairs, the probability of the different outcomes would become variable and apparently independent of sector. The fact remains, that in a random sample of bryozoan interactions, the majority of the encounters observed occurred in frontal sectors. If species exhibit an equal likelihood of contact in any sector, rather than a greater likelihood in frontal sectors, then the outcome of competitive interactions may be independent of encounter angle, but this did not appear to be the case in the present study.

Interpretation of differences between sites and years were complicated because of markedly unequal sample sizes. As a result it was often difficult to determine whether apparent differences in the distribution of the outcome probabilities were sampling effects or due to real differences caused by spatial and/or temporal variations in the competitive ability of the species concerned. For example, 106 interactions being recorded between *E.coccinea* and *Alcyonidium* spp. at Clachan, and only 3 were observed at Cuan. Furthermore, many species were either not observed, or occurred in different abundances at different sites and/or in different years.

Considering the total species' data sets, differences were apparent in the probabilities of the different outcomes, which may have been statistically significant on the basis of the scaled deviances and *t*-tests. For example, *Alcyonidium* spp. exhibited a higher probability of winning in intertidal sites, with a corresponding decline in the probability of a tie at these sites (Fig. 4.5.a.). Similarly , there may have been significant differences between sites in the probability of winning and tying exhibited by *E.coccinea*; this species exhibited an increased probability of winning at Cuan compared to Clachan (Fig. 4.12.a.). *C.cryptooecium* exhibited significant differences in competitive ability between east and west coast sites, and the results suggested a higher probability of winning and a lower probability of tying at east coast sites

compared to west coast sites (Fig. 4.10.a.). Nevertheless, absolute results were still valid irrespective of sample size; for example, *C.aurita* was only observed at Clachan (Fig. 4.6.a.); and *E.coccinea* (Fig. 4.12.a.), *M.nitida* (Fig. 4.13.a.) and *M.ciliata* (Fig. 4.6.c.) were absent from the east coast sites.

Site effects were also apparent among the distribution of the outcome probabilities for specific species-pairs. For those interactions which exhibited no difference in outcome, i.e. the outcome was entirely determinate, then site did not appear to have a bearing on the nature of the interaction outcome (e.g. interactions between *Alcyonidium* spp. and *C.hyalina* (Figs. 4.5.e., 4.9.b.), *E.pilosa* and *E.coccinea* (Figs. 4.11.f., 4.12.g.), and *E.pilosa* and *M.nitida* (Figs. 4.11.g., 4.13.e.)). This may be interpreted as indicating that the overgrown species did not have a "refuge" from overgrowth in sites which were less favourable to the overgrowing species (see Buss, 1979b). Some species' interactions with variable outcomes also appeared to be independent of site. For example, intraspecific *C.lineata* encounters showed similar probabilities of the 3 outcomes irrespective of site (Fig. 4.8.c.). However, there was also evidence that some species-pair interactions exhibited changes in the probability of the different outcomes among the sites. Probabilities for encounters between *Alcyonidium* spp. and *C.lineata* suggested that, in general, at intertidal

sites, the probability of *Alcyonidium* spp. winning decreased, and that of tying increased (Figs. 4.5.d., 4.8.b.). The scaled deviances indicated that site made an important contribution to explaining competition between these species. This was supported by significant *t*-tests indicating that differences existed between the sites. At Clachan all the intraspecific interactions between *C.cryptooecium* colonies resulted in ties, but at intertidal sites there was an increased variability in the outcome of competition (Fig. 4.10.d.). Other species showed evidence of increased "competitive equivalence" at intertidal sites (e.g. interactions between *C.lineata* and *C.hyalina* (Figs. 4.8.d., 4.9.c.)). Conversely, intraspecific *E.pilosa* interactions exhibited a decreased probability of overgrowth at the intertidal sites (Fig. 4.11.e.). There was also evidence for differences in competitive ability between the east and west coast sites. For example, in interactions between *C.lineata* and *E.pilosa*, *C. lineata* was the dominant competitor at the west coast sites but was subordinate at the east coast sites (Figs.4.8.f., 4.11.b.). Both the scaled deviances and *t*-tests indicated this was a statistically significant result. Similarly, *C.cryptooecium* overgrew *S.unicornis* at the east coast sites, but never overgrew *S.unicornis* at Cuan (Figs. 4.10.g., 4.14.c.).

Thus, although the results may have been confounded by difficulties arising from different sample sizes, they suggested that significant differences may have existed between the sites in terms of the probabilities of

different outcomes. As with sector, the nature of the variation was highly dependent on the species involved in the encounter.

Results for the variation in the outcome of competition between the 2 years of the study were even more accentuated by differences in the sample sizes - approximately 3½ times more observations were made in 1984 compared to 1983 and no observations of competition at the east coast sites were made in 1983. Despite this, of all the total data sets for each species examined, only one (*F.hispida* (Fig. 4.6.b.)) was not observed at least once in both years; all the species-pairs examined in detail were recorded in 1983 and 1984. But, as with site, it was difficult to elucidate if the apparent differences between the years were valid and illustrative of significant real differences in the outcome probabilities of competitive interactions, between the 2 years.

However, examination of the total data sets for each species indicated that despite differences in sample sizes, differences in the outcome probabilities between the 2 years may have been significant. For example, *Alcyonidium* spp. exhibited an increased probability of winning and a decreased probability of tying in 1984 compared to 1983 (Fig. 4.5.a.). Conversely, *M.nitida* exhibited a decreased probability of winning and an increased probability of tying in 1984 (Fig. 4.13.a.).

Several of the species (e.g. *C.lineata* (Fig. 4.8.a.) and *E.pilosa* (Fig. 4.11.a.)) showed little difference in their probabilities of the different outcomes between the 2 years.

Similarly, some of the species-pairs interactions, despite sample size differences, exhibited no marked differences in the outcome probabilities, possibly indicating that there was little variation in outcome, at least between the 2 years studied here. Examples included interactions between *C.lineata* and *E.coccinea* (Figs. 4.8.g., 4.12.d.), and intraspecific encounters between *M.nitida* colonies (Fig. 4.13.g.). These results were supported by non-significant scaled deviance values and *t*-tests for observations between the 2 years. Species which exhibited deterministic outcome encounters were apparently not influenced by annual variation (e.g. *Alcyonidium* spp. and *C.hyalina* (Figs. 4.5.e., 4.9.b.), *E.pilosa* and *E.coccinea* (Figs. 4.11.f., 4.12.g.), and *E.pilosa* and *M.nitida* (Figs. 4.11.g., 4.13.e.)). Conversely, many of the interactions did exhibit marked differences in outcome between the years, some of which may have been real rather than simply attributable to differences in the sample sizes. Intraspecific encounters involving *E.pilosa* colonies varied in outcome between the years, only ties were observed in 1984, whereas wins and losses were recorded in 1983 (Fig. 4.11.e.). There was also a similar pattern in the

interactions between *C.hyalina* colonies, greater probabilities of overgrowth interactions occurred in 1983 compared to 1984 (Fig. 4.9.d.). In contrast, *E.coccinea* in competition with *C.hyalina* exhibited increased overgrowth ability in 1984 and a decreased probability of losing and tying (Figs. 4.9.f., 4.12.e.). This species showed a similar increase in competition with *M.nitida* (Figs. 4.12.i., 4.13.f.). *C.hyalina* also exhibited an increase in the probability of winning and a decrease in the probability of losing and tying in competition with *E.pilosa* between 1983 and 1984 (Figs. 4.9.e., 4.11.c.). However, in competition with *M.nitida*, *C.lineata* showed an increase in the probability of wins and ties, with a corresponding decrease in the probability of losing in 1984 (Figs. 4.8.h., 4.13.c.).

Otherwise there appeared to be considerable variability between the years and it was difficult to draw any definitive conclusions (e.g. *Alcyonidium* spp. and *M.nitida* (Figs. 4.5.h., 4.13.b.), *C.lineata* and *S.unicornis* (Figs. 4.8.i., 4.14.b.), and *C.cryptooecium* and *E.coccinea* (Figs. 4.10.f., 4.12.f.)). There was also no evidence of definite trends between years, such as one species exhibiting an improved or deteriorating competitive ability from one year to the next, or an increase or decrease in the degree of "equivalence". Larger, more equal sized samples would have been of value to indicate whether real differences existed in the probabilities of the outcomes among the different years.

Although each part of the above analysis of the data has been considered independently, in fact, as would be expected, they were all complementary to each other. Thus the probabilities of the 3 possible interaction outcomes in terms of the different parameters were those predicted from the scaled deviances and *t*-tests, notwithstanding the limitations of the frequently small data sets. For example, the scaled deviance values for the intraspecific *Alcyonidium* spp. interactions provided statistical evidence that no significant differences existed among the outcomes observed in the different sectors. This was supported by the absence of significant *t*-tests. Examination of the probabilities of the different outcomes illustrated that each sector had no influence on the outcome because all contacts resulted in a tie irrespective of encounter angle.

It must be remembered that the outcomes were considered only in relation to a single parameter, ignoring any within-parameter variation arising through, perhaps, the influence of the other parameters. For example, the importance of the encounter angle might vary from site to site, and in different years species may have different competitive abilities at different sites. Taking the protocol to completion - in the multiple interactions analysis - the variation in the outcomes among sectors, at different sites and in different years

should also be considered. However, at this stage the data sets available are totally inadequate for such a complex analysis.

4.2.4. Summary of the Results:- For those species for which there were adequate data sets, the variation in the outcome of encounters was primarily attributable to the identity of the species against which they were competing; the angle of encounter between the interacting colonies, the site at which the interactions occurred, and the year of the study may also have been of importance. The evidence suggested that any species may have been affected by one or more of these parameters, and possibly, as more data are accumulated for each species all these parameters may be observed to exert some influence on the outcome of many of the interactions. However, a degree of controversy was evident within the data: for some interactions none of the parameters apparently influenced outcome, which must therefore be affected by the multitude of other parameters which are known to influence the outcome of competitive interactions and have not been examined in this study.

4.3. DISCUSSION

The variability and complexity of the outcomes observed among the bryozoan competitive interactions were the most characteristic features of the assemblages examined in this study. This stochasticity probably reflected an absence of absolute differences in the competitive ability of the different species. Thus, each species of an interacting pair won some encounters, and neither consistently overgrew the other. These complexities arose because the species were at least partially balanced in their overgrowth capabilities, which led to the development of frequent reversals in the outcome, and ties or "stand-offs" between competing species. Although the ranking of the competitive abilities of the bryozoan species in this study appeared to be essentially hierarchial in nature, with higher-ranked species exhibiting greater probabilities of overgrowing lower-ranked species, the arrangement did not correspond to the simple linear hierarchy with a single competitive dominant suggested by Jackson and Buss (1975). Equally, the organization of the competitive ability patterns among the bryozoans was not directly analogous with networks mediated by specialized competitive mechanisms, also proposed by Jackson and Buss (1975). Instead, a "network-like" arrangement arose because of the absence of clear competitive dominance in the interactions between species, and this was produced by the high incidence of reversals and ties. The observed competitive relationships more closely resembled

the arrangement proposed by Russ (1982). He suggested that the absence of significant differences in the competitive ability between interacting species led to the production of "back-loops" in the otherwise "hierarchial sequence". Thus, species A > species B > species C, but no significant difference exists in the competitive ability between species C and A. "Back-loops" arise because of a very even balance in the generalized competitive mechanism of overgrowth between species and the absence of clear competitive dominance (Russ, 1982). Similarly, Kay and Keough (1981) stressed the importance of considering species which they designated as being "competitively equivalent", i.e. pairs of species in which neither member wins significantly more often than the other. They considered rankings of competitive ability which contain cases of "competitive equivalences" as important alternatives to the hierarchy or network arrangements of Jackson and Buss (1975).

There is increasing evidence within the literature that a hierarchial or "network-like" arrangement of competitive ability may be too rigid and simplistic for the majority of marine assemblages. Accordingly, many rankings of competitive abilities which are basically hierarchial may have loops, and many networks may have a somewhat hierarchial arrangement of competitive abilities (Russ, 1982). Connell (1976), for example, concluded from an examination of a coral reef community, that interactions between corals did not conform to either the hierarchy or network models of Jackson and Buss (1975).

The species-specific interactions between the lowest- and highest-ranked species, which are necessary for a network arrangement, were scarce. Moreover, all the species ranked below the highest showed some ability to "stand-off" (or tie with) higher-ranked species. The interactions were further complicated by reciprocity between species of equal or similar rank. Similarly, Liddell and Brett (1982), from an examination of overgrowth among epizoans on fossil crinoids, concluded that flexible competitive patterns existed: numerous overgrowth reversals were observed and higher-ranked species were occasionally overgrown by much lower-ranked species. Sebens (1986) suggested that interactions among the species of a subtidal encrusting community were basically hierarchial. However, partial networks, with several species or groups, were produced by reversals within particular species-pairs, rather than by loops in which a subordinate species regularly overgrew a species 2 or more ranks above it in a competitive hierarchy. "Stand-offs", in which there was no change in the border between 2 organisms were also common (Sebens, 1986).

Kay and Keough (1981) concluded that the occurrence of hierarchies and/or networks has not been conclusively demonstrated in the literature, the published data often being inadequate to distinguish between the 2 concepts. Furthermore, Russ (1982) suggested that insufficient data have been provided by Jackson and Buss (1975) to demonstrate clearly the existence of competitive networks. He considered that the loops in hierarchial

sequences - which result in "network-like" arrangements of species competitive abilities - resulted more commonly from the absence of clear dominance in species interactions, rather than from direct "back-loops" formed by specialized or generalized competitive mechanisms. Quinn (1982) also re-examined the data from Buss and Jackson (1979) and concluded that cryptic coral reef communities exhibited an organization close to hierarchial, although there were many species-pairs in which either species may sometimes overgrow the other. There is thus considerable controversy over the competitive ability relationships among marine assemblages; however, it would seem unlikely that any one model will adequately explain the interactions evident in one assemblage, and equally unlikely that a variety of different assemblages will be explained in terms of the same models.

Buss and Jackson (1979) suggested that network formation commonly resulted from interactions between species belonging to different major taxonomic groupings, since these can interact in a greater variety of ways. Several studies have provided results to the contrary, indicating that the variety of interactions within the same group is sufficient to produce a high level of intransitivity. Russ (1982), for example, found that the ranking of the ability of the major taxonomic groups to overgrow others was basically hierarchial. In contrast, the ranking of the competitive abilities of species within the major groups did not form a hierarchy. Because of significant differences in competitive

FIGURE 4.15. Examples of the influence of the encounter angle on the outcome of bryozoan competition:

(a) *Cribrilina cryptooecium* (Cc) extending elongated terminal stolonal outgrowths over *Electra pilosa* (Ep) in a frontal overgrowth interaction. (Scale bar ≙ 0.75mm)

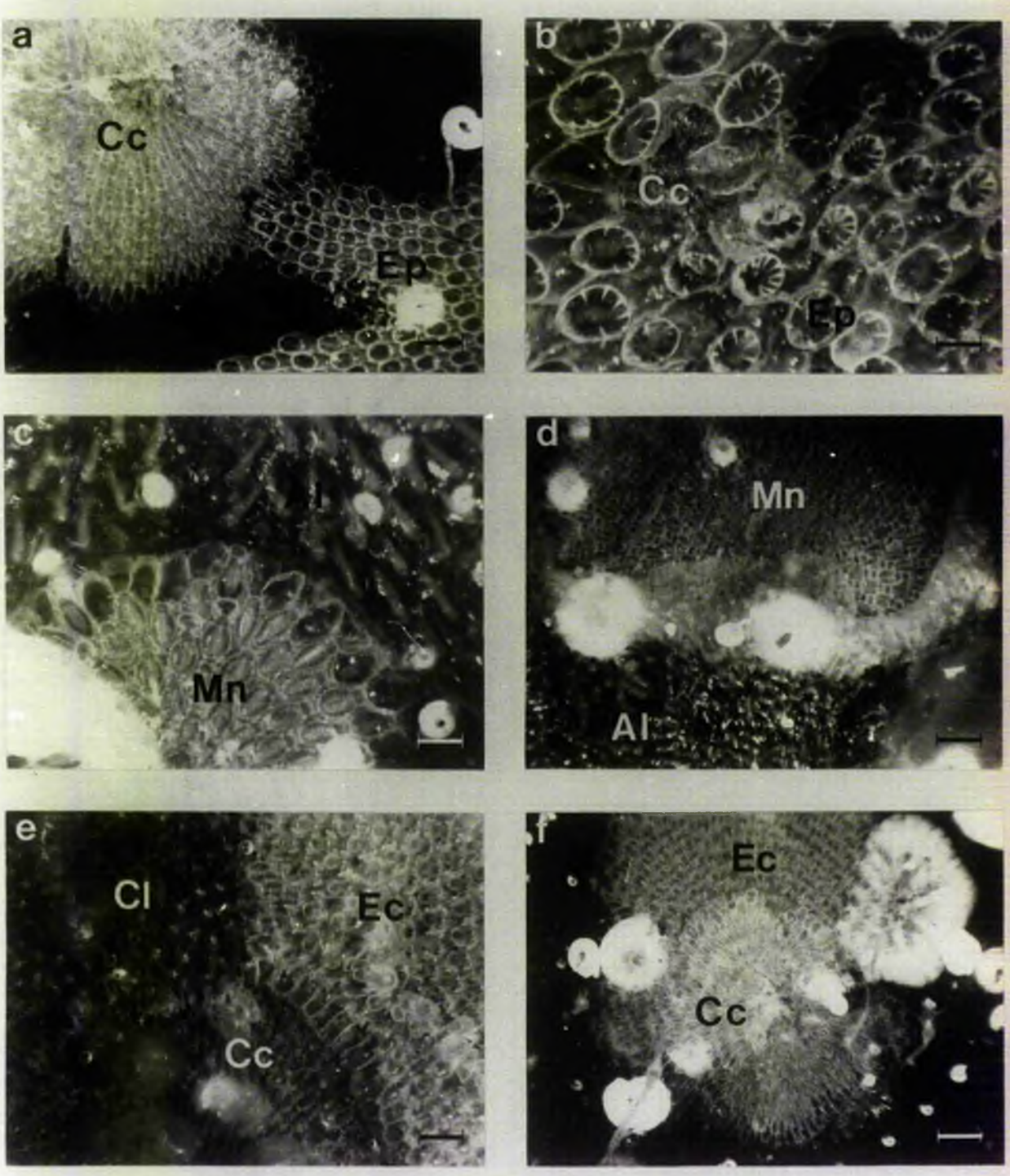
(b) *E.pilosa* overgrowing the ancestrular region of a small *C.cryptooecium* colony in a terminal encounter. (Scale bar ≙ 0.25mm)

(c) The developing zooids of the *Membraniporella nitida* (Mn) colony are beginning to overgrow the *Alcyonidium* sp. (Al) zooids in a predominantly frontal interaction. (Scale Bar ≙ 0.40mm)

(d) *Alcyonidium* sp. overgrowing a *M.nitida* colony in a terminal and lateral encounter. (Scale Bar ≙ 0.90mm)

(e) *Escharoides coccinea* (Ec) overgrowing *C.cryptooecium* (and *Callopora lineata* (Cl)) in a frontal interaction. (Scale bar ≙ 0.85mm)

(f) *C.cryptooecium* overgrowing the ancestrular region of an *E.coccinea* colony in a terminal encounter. (Scale bar ≙ 1.15mm)


a
Cc
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ability, which occurred most frequently between species within the same group, "back-loops" in otherwise hierarchial sequences or networks occurred (Russ, 1982). He concluded that delay/tie situations and reversals of competitive outcome occurred more frequently between colonies having similar abilities in terms of overgrowth. Quinn (1982) suggested that much of the indeterminancy of outcomes observed by Buss and Jackson (1979) was due to observations of bryozoan colonies which were of different ages and which exhibited highly directional growth patterns. Other taxa have less directional and age-specific growth patterns and therefore are more consistent in the outcome of competition (Quinn, 1982). Thus, a high degree of intransitivity may be a predictable characteristic of bryozoan assemblages, and a number of different variables are known to contribute to this intransitivity in competitive outcomes. For example, the size of the individual competing colonies (Buss, 1980; Russ, 1982; Sebens, 1986), the condition of the colony surfaces at the region of contact (Jackson, 1979a; Osman and Haugsness, 1981), spatial heterogeneity (Walters and Wethey, 1986), and the directionality of growth (Jackson, 1979a; Harris and Irons, 1982; Liddell and Brett, 1982; Rubin, 1982).

The results from this study suggested that the encounter angles between encrusting colonies may have had a significant effect on the outcome of bryozoan competitive interactions (see Figure 4.15.). However, marked differences existed between species and between

different species-pairs. For some species (e.g. *E.coccinea* in the present study) there appeared to be a greater probability of successful overgrowth of neighbouring colonies when contact occurred in frontal and lateral sectors. Conversely, for other species (e.g. *Alcyonidium* spp. and *S.unicornis*) there appeared to be a higher probability of overgrowth in terminal and lateral sectors. Of particular significance was the observation that lower-ranked species (e.g. *C.hyalina* and *E.pilosa*) had a greater probability of overgrowing higher-ranked species in terminal sectors. Here, encounter angle may have accounted for a number of the reversals evident among the interactions. Similarly, patterns of "competitive equivalence" between pairs of species varied among the sectors. The results also suggested that the probability of a pair of species tying in an interaction was sector-dependent; in many instances it appeared that the probability of a tie was greatest in the frontal and lateral sectors. Despite the evidence that encounter angle may have influenced the outcome of competition, occasionally no distinct patterns were apparent in the distribution of the different outcomes among the sectors. Thus in some interactions other factors may have been more important in determining outcome.

From a study of overgrowth between 7 cheilostome bryozoans common in the cryptic reef environment, Jackson (1979a) recognized 3 broad categories of overgrowth ability: (i) the clear overgrowth dominants; (ii) those which competed poorly in overgrowth interactions with dominants, as opposed to with lower-ranked species; and

(iii) inferior competitors. No one species won in all interactions, and the outcome of interspecific overgrowth interactions were not always identical; a number of reversals were also evident, where lower-ranked species overgrew higher-ranked species. Jackson (1979a) concluded that these variations in overgrowth interactions were frequently related to the encounter angles between cheilostome colonies and overgrowth competitors. Jackson (1979a) recorded 175 encounter angles for 115 interspecific cheilostome overgrowth interactions, and found 47% involved "frontal" overgrowth, 38% "flank" (or lateral) overgrowth and 15% involved "rear" (or terminal) overgrowth. Although not directly comparable, similar results were obtained in the present study. Considering the results for Clachan (a subtidal site which is more directly comparable with the reef habitat studied by Jackson), 47% of the interactions occurred in the frontal sectors, 32% in lateral sectors and 21% in terminal sectors. Thus in both habitats frontal overgrowth interactions were most frequent, but overgrowths at other angles were also common and thus may have been responsible for the observed variations in the outcome of pair-wise overgrowth interactions. Jackson (1979a) also found significant differences in the effect of encounter angle for different species, and the results were not dissimilar to the patterns identified in the present study. Examination of Jackson's (1979a) W/L ratios (= the number of interactions in which species A overgrew all other cheilostome species ÷ the number of interactions in which other cheilostomes overgrew species

A), shows that higher-ranked species have larger W/L ratios for frontal interactions compared to rear encounters, while lower-ranked species have small W/L ratios for frontal interactions and larger W/L ratios for rear encounters. Thus, high-ranked species overgrew other species most frequently in frontal interactions and were overgrown more often in rear encounters, whereas lower-ranked species overgrew others more often in rear interactions and were most often overgrown in frontal contacts. There was also evidence of variation in the "competitive equivalence" among different encounter angles, for example *Steginoporella* sp. nov. overgrew *Reptadeonella violacea* 11 times in frontal interactions, while the reverse outcome occurred once only. However, in flank and rear overgrowth interactions *Steginoporella* sp. nov. overgrew in 10 interactions and *R.violacea* in 9.

Rubin (1982) also concluded, from a study of encrusting bryozoans on rocks in a shallow off-shore area in south-west England, that there was considerable variability in outcome, and that none of the species won all their interactions. He suggested that the outcome of the competitive encounters between the 12 species considered was largely dependent on the encounter angle formed between the directions of growth of the 2 colonies. He recorded 299 encounters in 3 principal encounter directions, of which 40% were frontal, 35% were lateral and 25% were rear encounters. Rubin (1982) derived an "index of intransitivity" based on the relationship between the probability of species A

overgrowing species B and the probability that species A will be overgrown by B. When the index was determined for encounters between 7 cheilostome species, Rubin (1982) found that, for all the directions combined, the value approximated intransitivity, but for frontal encounters alone it was close to a transitive organization. More detailed study of the principal encounter orientations for 5 of these species showed that intransitivity progressively increased from frontal encounters through to lateral and rear encounters. Similar conclusions applied to some of the species-pair interactions examined in the present study, including interactions between *E.coccinea* and *C.hyalina* or *C.lineata*. Rubin (1982) therefore concluded that, since encounters from all directions are more likely in nature, the underlying pattern of overgrowth in assemblages of encrusting bryozoans will be highly intransitive. Thus the angle of encounter is important in determining the degree of intransitivity that exists within a community. Rubin (1982) explained his results in terms of competition for food: if a normally subordinate species grew over the proximal portion of the zooids of competitors, as would occur in rear encounters, then the lophophore of the subordinate would then be raised up to the same level, or higher, than that of the other colony. This would thereby give rise to a more unpredictable outcome in competition for food particles.

The results were thus very similar among the 3 studies, suggesting that encounter angle may indeed play a consistently significant role in determining the

outcome of bryozoan competitive interactions. Unfortunately Jackson (1979a) and Rubin (1982) did not consider either intraspecific interactions or the third possible outcome ties or "stand-offs", in their appraisal of the influence of encounter angle on the outcome of competition. Jackson (1979a) recorded ties commonly only in intraspecific encounters which were not considered.

Jackson (1979a) considered that the encounter angle between 2 colonies was largely determined by events previous to colony contact. However, Rubin (1982) recorded a particular encounter between *Escharella variolosa* and *Escharoides coccinea*, where along part of the contact margin *E.variolosa* was overgrowing *E.coccinea* from the rear, but elsewhere the youngest zooids of *E.coccinea* were turned through 180° and overgrowth was not occurring. Similar encounters were observed in the present study, specifically involving *E.coccinea* colonies being overgrown in the terminal sectors over the ancestrular region. Newly-developing zooids were observed immediately adjacent to the ancestrula and orientated to produce a frontal encounter with the encroaching competitor; although rarely observed, this zooid arrangement may have deviated from the normal pattern of budding particular to *E.coccinea*.

A number of other studies have briefly considered the importance of encounter angle in influencing the outcome of competitive interactions. Harris and Irons (1982) observed that encrusting bryozoans tended to be overgrown from the rear; thus the bryozoan *Amphiblestrum*

flemingii withstood frontal competition with sponges and *Botryllus schlosseri* , but was readily overgrown from the rear. Liddell and Brett (1982) attributed the low overgrowth ability of the Silurian bryozoan *Berenicea consimilis* to a high proportion of flank encounters. Bryozoans are less able to resist overgrowth by another colony when encountered on a flank, whereas they may be able to resist when encountered at a growing edge. Thus *B.consimilis*, which was unusual among Paleozoic bryozoans in maintaining a fan-shaped colony form, even during later astogeny, was more likely, on a random basis, to encounter competitors on colony flanks (Liddell and Brett, 1982).

The results from this study also suggested that the competitive ability of different species varied among the sites and between the years of study. The bryozoan species did not settle equally abundantly at all 4 sites studied, some species were restricted to subtidal sites, others to intertidal sites and some species were more abundant at west or east coast sites. These represented absolute differences and led to quite distinct assemblages at the various sites. Particularly noteworthy were *E.coccinea* and *S.unicornis* , both relatively high-ranked competitors, which displayed almost inverse patterns of abundance between the sites. The sites differed in a number of characteristics, but especially in exposure to wave action and the periods of immersion between low tides, and it was unlikely that all the bryozoan species would be equally well adapted to all

the sites. Ryland (1962b) has tabulated the habitat preferences of a number of bryozoans among the mid-intertidal and subtidal zones, and Todd and Turner (1986) have presented data on the "preferences" of a number of bryozoan species at both Clachan and Cuan on the west coast. Different species may, therefore, be expected to exhibit different competitive abilities at the various sites. Thereby, a predominantly sublittoral species, perhaps settling at lower intertidal sites, may be expected to differ in competitive ability compared to colonies in more optimal habitats. However, *E.coccinea*, which was rarely observed at Cuan (the intertidal site) but was more frequent at the subtidal site, Clachan (Todd and Turner, 1986; see also Ryland, 1962b), exhibited a higher probability of winning in intertidal sites compared to subtidal sites. *Alcyonidium* spp. which are abundant throughout the mid-intertidal and subtidal zones (Ryland, 1962b) also exhibited a higher probability of winning at intertidal sites and a lower probability of tying, compared to the subtidal sites where it was most abundant. Nonetheless, interactions involving *Alcyonidium* spp. have probably been complicated by the inclusion of results for 2 or 3 species within the single group. Conversely, *S.unicornis*, a principally intertidal species (Todd and Turner, 1986), exhibited a decreased probability of winning interactions at sites with increasing periods of aerial exposure during low tide. There were also differences in competitive abilities under different conditions of wave exposure; *C.cryptooecium*, for example, exhibited a greater

probability of winning and a lower probability of losing at the more exposed east coast sites. Differences in competitive ability may have been mediated by various habitat-related adaptations, but variability in growth rates between different sites may have been of particular significance. Buss (1979a) considered that overgrowth involved differential growth rates along interspecific colony margins, with the fastest growing species overgrowing its competitor.

The majority of studies of competitive interactions in marine assemblages have considered the spatial relationships at only the one site, (e.g. Jackson, 1979a; Keen and Neill, 1980; Kay and Keough, 1981; Rubin, 1982). Quinn (1982), however, examined competitive overgrowth interactions on the open rock low intertidal zones of 3 sites in Washington State and Alaska, which he considered were representative of the full range of conditions to be found on the open coast of the north-west Pacific. His essential conclusion was that the outcomes were consistent from location to location. However, Quinn's (1982) observations applied to a somewhat restricted habitat of very exposed outcroppings, and some of the organisms examined were substantially more abundant in other intertidal habitats or were found primarily subtidally. As he himself suggested, it is likely that the situation on open intertidal surfaces may have little to do with general adaptations to the problems of space competition. Therefore, he concluded that the competitive processes may indeed differ between habitats. He further considered that reversals among species of

similar rank may occur and may be habitat-specific (i.e. due to varying competitive environments). For example, the high-ranking species *Aplidium* spp. (ascidian), *Dendrobeania lichenoides* (bryozoan) and *Codium setchellii* (macroalga) were observed overgrowing all the other encrusting species encountered, but the 3 were found in somewhat different habitats and not observed interacting. Thus, in other habitats, specific reversals may occur in some outcomes and habitat reversals may prove to be generally common. Sebens (1986) examined the spatial relationships among encrusting marine organisms at 2 subtidal sites in New England which differed in their exposure to ocean swell. Although the species composition at the 2 sites differed, the same species accounted for most of the interactions at both sites. Sebens (1986) derived 4 indices of spatial interaction to describe each species' or groups' competitive ability and its importance to the community as a whole, and found a number of significant differences between the sites. Several species exhibited differences in the overgrowth index between the sites (e.g. bryozoans had high overgrowth indices at the exposed site) and in terms of the effect on the entire assemblage, different species or groups accounted for more overgrowth at protected or exposed sites. Similarly, differences existed among species or groups at different sites in terms of growth rates and resistance to overgrowth. Bryozoans, for example, showed higher growth rates and were also overgrown to a greater extent at the exposed site. Sebens (1986) recorded 4 instances where competitive

superiority of a species-pair switched between sites and 2 cases where the outcome was much less predictable at one of the sites. However, none of these involved bryozoans.

In the present study competition in the bryozoan assemblages was examined in 2 successive years, 1983 and 1984, and the results suggested that there were significant between-year differences in the probabilities of the different outcomes. *M.ciliata*, for example, was a dominant competitor in 1983, but subordinate in 1984. Similarly, *E.coccinea* and *M.nitida* exhibited lower probabilities of winning and a corresponding increase in the probability of tying in 1984 versus 1983. As with differences in competitive abilities between sites, so differences between the years may have been mediated by differences in growth rates. Jebram (1973) found that the development of different colony forms of *Conopeum seurati* was dependent on growth rate, which itself was influenced by colony size, food, temperature, salinity and possibly other factors. Similarly, Winston (1976, cited in Buss 1979b), investigating the influence of nutrition on the colony morphology of *Conopeum tenuissimum*, found that as the nutritional value of the available food decreased, the colony morphologies became increasingly "runner-like" in character; under suitable dietary conditions, however, buds developed distally and laterally to fill the spaces between the branches. "Sheet-like" and "runner-like" growth forms differ fundamentally in their competitive ability, with the

latter being generally inferior (Buss, 1979b). Therefore subtle yearly variation in a number of environmental parameters might alter the growth and hence the competitive abilities of the different species.

The majority of studies of competition among marine assemblages are based upon static observations over a short period of time, e.g. Jackson, 1979a; Quinn, 1982; Rubin, 1982 and Russ, 1982. As already stated the present study has considered competitive interactions that developed in 2 separate, but successive, years. But most information on the results and mechanisms of competitive encounters can be obtained from time-series studies, relatively few of which have been carried out. Kay and Keough (1981), studied overgrowth interactions over extended time periods and recorded a number of observations where one colony overgrew another, but the initially overgrown species eventually won. Quinn (1982) recognized that departures from strict hierarchial arrangements may occur if reversals of outcomes developed, and suggested, despite an absence of evidence, that differences in competitive ability may vary seasonally, for any pair of intertidal competitors. Schoener (1983), in a review of the relevant literature, concluded that temporal variability in competition was especially rare in most marine systems; conversely, Connell (1983) concluded that the incidence of competition varied considerably from year to year (and place to place). Conclusive evidence that the competitive abilities of species may vary seasonally is provided by Sebens (1986) who studied interactions

between encrusting species in 2 seasons, and found marked differences among the 4 competitive indices applied. For example, bryozoans had higher overgrowth indices in warm compared to cold months, and made a larger contribution to the effect on the entire assemblage in the warm months; additionally, bryozoan resistance to overgrowth was very low during the warm months when superior competitors grew faster. Sebens (1986) recorded one case where the competitive superiority of a species switched between seasons and 5 cases where the outcome was much less predictable.

In general, the results from the present study and evidence in the literature, suggest that competitive outcomes vary both among sites and between years. For any given species these differences may be due to variation in one or more of the 4 competitive attributes recognized by Sebens (1986): (i) its ability to overgrow other species; (ii) its ability to prevent itself being overgrown; (iii) its own frequency and the frequencies of each potential competitor in the community; (iv) its potential growth rate. Sebens (1986) concluded that these change somewhat with habitat, season and other species in the assemblage.

The influence of only 3 variables, encounter angle, site and year, on the incidence of the 3 possible outcomes, win, lose and tie, have been analysed in detail. In reality, however, the competitive interactions between the bryozoan colonies were complicated by a multitude of other variables which are known to influence

the outcome of competition. Thus in only very few instances would encounter angle, site and year be the critical variables influencing the outcome. Very few of the competing colonies were identical in size, either in terms of their vertical relief or total surface area, both of which may influence competitive ability (see Buss, 1980; Russ, 1982; Sebens, 1986). Colony size may have a further influence on competition because as colony surface area increases, contact with other colonies is also likely to increase; similarly, as the circumference of a colony in direct contact with the substratum increases so does the probability of contact with other sessile organisms (Jackson, 1979b). The question therefore arises whether the outcome of competition is influenced by the extent of total competition along the growing margin. Stebbing (1973a) found that in competition between *Alcyonidium hirsutum* and *Flustrellidra hispida*, overgrowth only occurred when the overgrowing colony was surrounded by others and growth could not be redirected. Conversely, Sebens (1986) suggested that "stand-offs" between colonies arose when growth was occurring along other borders. The outcome of competition was further complicated because numerous instances were observed where one species was being overgrown by a competing species at one region of the growth margin, and elsewhere along the colony border the outcome was reversed in an encounter with a different colony of the same competing species. A number of the observed competitive reversals may also have been attributable to a normally lower-ranked species

overgrowing a surface irregularity, such as a spirorbid tube, and thereby gaining a height advantage before overgrowing a normally higher-ranked species (see Walters and Wethey, 1986). The physiological condition of the competing colonies may also have influenced the outcome of competition. For example, *Alcyonidium* spp. colonies which were deteriorating and disintegrating, but with functional zooids still present, were observed to be overgrown by previously subordinate species. Seasonal variations in the growth patterns of species, for example in relation to reproductive activity, may also have produced variation in the outcome of competitive encounters. Todd and Turner (1988) found evidence that for unconstrained (i.e. not overgrown by colonial ascidians) *Schizoporella unicornis* colonies, there was a reduction and cessation of growth during the summer following establishment, which they suggested arose as a result of the onset of reproductive activity. *S.unicornis* might, therefore, predictably be an inferior competitor for space during periods of reproductive activity. The degree of colony fouling is also known to influence the competitive outcome (see Jackson, 1979a; Osman and Haugsness, 1981).

Intra- and interspecific bryozoan competition for space is a complex sequence of events, the outcome of which is highly variable. The variability of outcome was found in the current study to be attributable to variation in the encounter angle between competing colonies, and also the site being studied and the year

during which competition occurred. The relative importance of such sources of variability in competitive intransitivity remains, as yet, unresolved (Karlson, 1985).

5. THE INFLUENCE OF HERBIVOROUS MOLLUSCAN GRAZERS ON EPIFAUNAL ASSEMBLAGES

5.1. INTRODUCTION

Traditionally, community theory has been concerned with competitive processes, and it is predicted that competition will invariably eliminate all but a few species, and that often only one will effectively utilize the resource and will come to dominate the community (Paine and Levin, 1981). However, in a review of the evidence for the occurrence of competition in natural communities, Connell (1975) concluded that many species seldom reached population densities sufficiently great for resource competition to become important, because either physical extremes or predation eliminated or suppressed them. Thus, the competitive processes are precluded, and the monopolization of the limiting resource by the competitive dominants prevented. Such local disruptions or disturbances render a limiting resource available to a pool of potential invaders (Levin and Paine, 1974). In many marine assemblages space is considered to be a primary limiting resource, and Ayling (1981), for example, estimated that in a subtidal area of high *Evechinus chloroticus* (urchin) density approximately 82% of the surface was released annually as free space due to the grazing activities of this species. Local disruptions or disturbances appear to be important factors in structuring a diverse array of assemblages, and Dethier (1984) concluded that disturbance is a major stochastic process generating variability, and an integral, even necessary, factor in ecosystem function,

playing a major ecological role in controlling the structure of assemblages.

White and Pickett (1985, p.7) defined a "disturbance" as "...any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment". However, no 2 disturbance events are alike, and any definition must allow for the fact that disturbance is relative to the spatial and temporal dimensions of the system (Pickett and White, 1985). Disturbances vary markedly in areal extent, intensity and frequency; these features comprise the "disturbance regime" and a number of important correlations are evident among the individual characteristics (Sousa, 1985). For example, smaller, less intense disturbances generally occur relatively frequently, whilst large intense disturbances occur less frequently. The "disturbance regime" will influence the effect on the community concerned; however, the responses of the natural communities to disturbance depends not only on the "disturbance regime", but also on the characteristics and life-histories of the resident species (see, for example, Sousa, 1980; Connell and Keough, 1985; Pickett and White, 1985). There is, therefore, no uniform way in which disturbances influence the community.

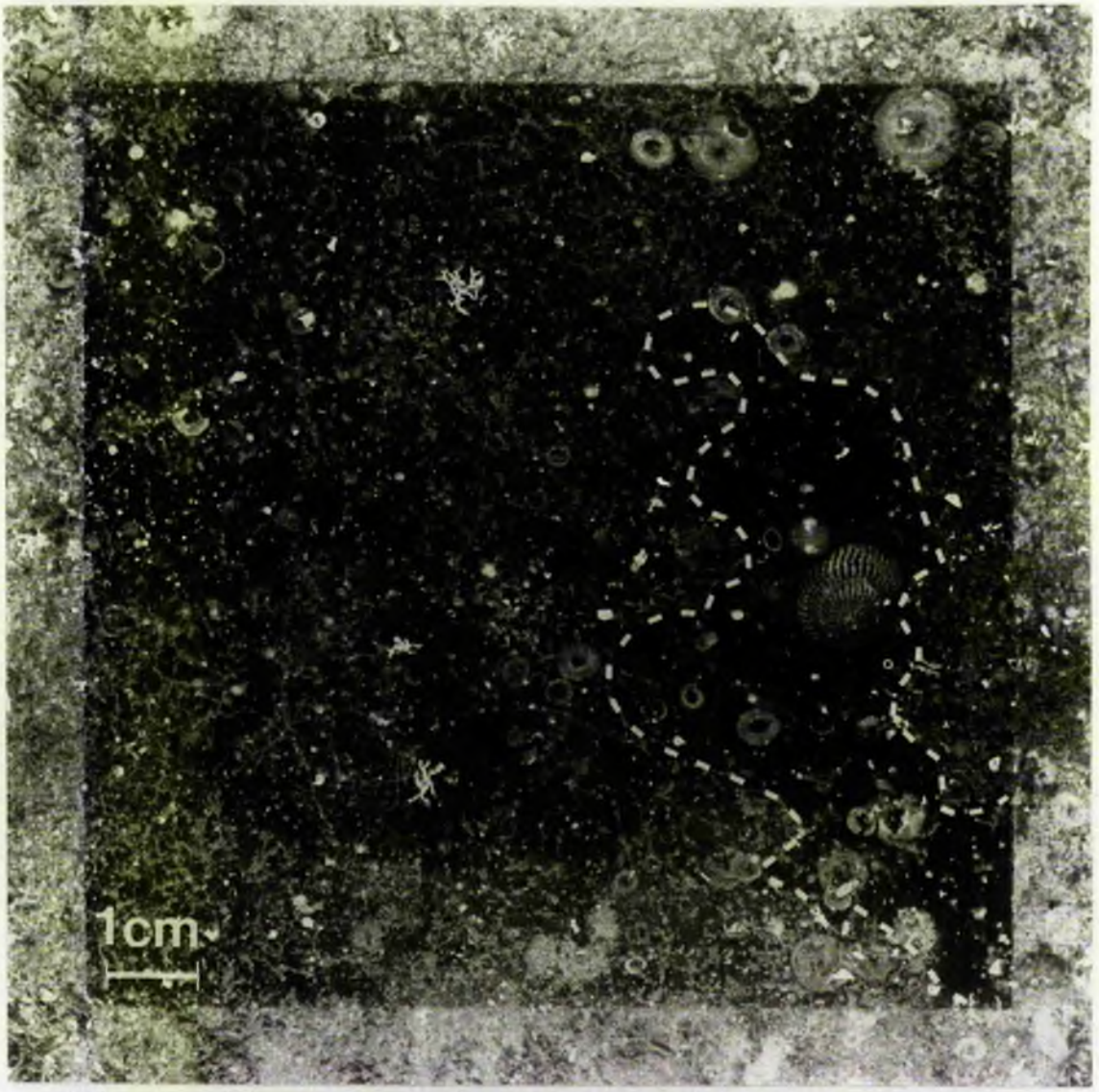
Generally, disturbances of (i) biological and (ii) physical origins are distinguishable:

(i) Menge (1982, p. 522) defined "biotic disturbance" as the "disruption of habitat or organisms caused by the non-trophic activities of organisms which usually leads directly or indirectly to mortality". Sousa (1985), however, considered biological disturbance to encompass everything from singular acts of predation, that free space occupied by the prey individuals killed, to non-predatory acts that inadvertently kill or displace other organisms. Note, however, that Connell (1972) has disputed the tendency to regard the activities of predators and grazers as disturbances. Many examples of biological disturbance can be found in the literature (e.g. Connell, 1961a; Dayton, 1971; Paine, 1974; Peterson, 1979; Ayling, 1981; Mook, 1981b).

(ii) Menge (1982, p.522) defined "physical disturbance" as the "disruption of habitat or organisms caused by the physical environment which usually leads directly or indirectly to mortality". It generally acts on a larger spatio-temporal scale than the principal agents of biological disturbance (Paine and Levin, 1981). There are numerous examples of physical disturbance in the literature (e.g. Dayton, 1971; Osman, 1977; Sousa, 1979, 1980; Paine and Levin, 1981; Davis and Wilce, 1987; see also, chapters in Pickett and White, 1985).

Biological and physical disturbances do not, however, act independently. Menge (1978a), for example, found that predators in harsh habitats had no controlling influence on the community structure, while at more benign localities they exerted a strong controlling

FIGURE 5.1. The effects of *Gibbula cineraria* grazing activities on a developing panel assemblage; the grazed area is enclosed by the white dashed line. The panel substratum is natural Cumberland slate and the square area is stained dark blue (see Todd and Turner, 1986).


1cm

effect on the community. He suggested that the lack of influence of relatively dense populations of *Thais (=Nucella) lapillus* on the mussel and barnacle communities at exposed headlands was a consequence of the severe restriction of the foraging range of the snail by the high probability of being dislodged by waves. Conversely, Moran (1980) concluded that fish predation was more important in structuring fouling communities at exposed sites, and he suggested that predation may be more severe in physically controlled environments since the adaptive priority of the organisms must be to the physical regime. Pickett and White (1985) have, furthermore, suggested that 2 agents of disturbance may act synergistically.

An examination of the development of certain epifaunal assemblages on the west coast of Scotland (see Todd and Turner, 1986, 1988, in press) suggested that the grazing activities of *Gibbula cineraria* (L.) may have an important influence on the assemblages (see Figure 5.1.). In the present study the "biological disturbance" examined was that mediated by the grazing activities of *G.cineraria* on developing epifaunal assemblages. A number of studies have demonstrated an indirect effect of grazing gastropods on sessile organisms (e.g. Dayton, 1971; Bertness, 1984; Underwood, 1985; Petraitis, 1987). The effect is indirect in the sense that the grazers do not apparently require the epifaunal material as a specific component of their diet (Underwood, 1979).

The intertidal prosobranch gastropod *G.cineraria* is abundant on hard substrata in St.Andrews Bay (Laverack and Blackler, 1974), and was frequently observed under rocks and in pools around the study sites, and on the panels within the experimental frames (personal observations). *G.cineraria* is a grazing rhipidoglossan mollusc, feeding predominantly on microscopic epiphytes and small algae (see Steneck and Watling, 1982). The snails feed by lightly brushing their marginal teeth over the substratum in broad grazing strokes, using the median and lateral teeth as food collectors (Steneck and Watling, 1982; Hawkins and Hartnoll, 1983). Because the marginal teeth are long, the force exerted by each tooth against the substratum is not great; furthermore, because none of the radula teeth are hardened with iron compounds and the buccal mass is not very robust, rhipidoglossan grazers are less capable of grazing very tough substrata and are unable to remove pieces of material from the substratum itself (Steneck and Watling, 1982). They are thus distinct from taenioglossan and docoglossan molluscs which exhibit scraping or rasping modes of feeding, enabling utilization of tougher substrata in the diet (Steneck and Watling, 1982).

The influence of 2 other species, the predatory muricacean prosobranch gastropod *Nucella lapillus* (L.), and the carnivorous asteroid *Asterias rubens* L. were also examined. They are both generally abundant between the tide-marks in St.Andrews Bay (Laverack and Blackler, 1974; personal observations). *N.lapillus* is generally

considered to prey almost exclusively on *Balanus* spp. and *Mytilus* spp. (Connell, 1961a,b; Menge, 1978a,b); however, Largen (1967), from his own experiments and a review of the literature, concluded that *N.lapillus* preys upon a number of species, including other prosobranchs (e.g. *Patella vulgata*, *Gibbula umbilicalis*, *G.cineraria*, *Littorina littorea*, *L.littoralis* and *Monodonta lineata*) and bivalves (e.g. *Cardium edule* and *Anomia ephippium*). *A.rubens* is a generalist and opportunistic predator, feeding upon bivalves (e.g. *Mactra*, *Donax*, *Pecten*, *Mytilus*, *Venus*, *Cardium* and *Chlamys*), gastropods (e.g. *Littorina*, *Rissoa* and *Crepidula)*, chitons, and crustaceans (isopods, amphipods, hermit crabs and barnacles) (see Jangoux, 1982). *A.rubens* is also a facultative scavenger, feeding on moribund fish and molluscs (Jangoux, 1982). *N.lapillus* and *A.rubens* may thus be expected to have minimal influences on the initial development of the epifaunal assemblages examined in this study, their predatory activities being restricted to barnacles and *Anomia* spp. on the artificial substrata. Neither *Anomia* spp. nor barnacles were observed to recruit very abundantly at the study site (the lower intertidal site in St.Andrews Bay; see Chapter 3).

As well as being predators on some of the epifaunal species, *N.lapillus* and *A.rubens* provided a 'control' for the *G.cineraria* component of the study. The deleterious effects of grazing herbivores on epifaunal assemblages

may arise because the settled larvae are rasped-off with the radula (even though they may not constitute important food items) as the grazers browse across the substratum. However, the effects may also be attributable to the movement of relatively large mobile species across the surface; of especial significance may be the attrition of their shells against the substratum and/or the mucus trails left by the organisms as they move across the surface. If either of the latter have important deleterious effects on the assemblages then similar results would be expected for panels exposed to the activities of *G.cineraria*, *N.lapillus*, and/or *A.rubens*; conversely, if the settled larvae are being rasped-off, incidental to the feeding activities of the grazing *G.cineraria*, then the presence of *N.lapillus* or *A.rubens* would not be expected to markedly affect the assemblages.

Connell (1975) suggested that the effect of predation in preventing competitive exclusion may occasionally be reduced, and one principal situation when this may arise is when the prey grow too large to be successfully attacked. These "refuges" are facilitated by spatial and temporal irregularity in predation, and are normally dependent on an unpredictable event, for example, a short period of severe weather. Such events may lead to a reduction in the populations of natural predators and thus allow the prey a period of enhanced growth and survival. Once an individual or group survives to a size at which attack by the predator is much less probable, it will continue to grow and retain

more resources, and thereby exclude or displace other organisms. Connell (1975) cited, as an example, his work on the population dynamics of the barnacle *Balanus cariosus*, the juveniles of which were normally eaten by predatory snails. In rare instances, however, some individuals survived for 2 years, by which time they were invulnerable to all the common predators except the starfish *Pisaster ochraceus*. Similarly, Dayton (1971) recorded an escape in growth by *B.cariosus* and *Mytilus californianus* from *Thais* spp. predation. Sebens and Lewis (1985) observed, during the summer of 1982, an abundance of large (20-25mm diameter) *Semibalanus cariosus* at sites in the San Juan Islands. They attributed this peak in the population size frequency distributions to the heavy mortality of *Thais* spp. during the severe winter of 1968-1969 recorded by Dayton (1971), which led to the enhanced initial survival of the 1970 settlement of *S.cariosus*. Sebens and Lewis (1985) concluded that this chance "size-escape", which enabled more individuals to reach sizes increasingly immune to predation, has structured the *S.cariosus* population for more than a decade. At one site they estimated that as much as 50% of the large barnacles present in 1982 were survivors from the cohort that settled during the period of low *Thais* spp. activity. Conversely, Ayling (1981) suggested that, in general, large size did not provide an escape from predation for the encrusting organisms in the community he studied, however, for sponges such as *Polymastia fusca* and *Ancorina alata*, the intensity and

regularity of disturbance was reduced with an increase in size. The present study examined whether the epifaunal species characteristic of the developing assemblages were able to 'escape' the influence of non-predatory grazers by attaining a relatively large size during 2 months exclusion from the grazing activities of *G.cineraria*.

5.2. RESULTS

The results of the analyses of the grazing experiments are given in Figures 5.2.-5.13.. The numbers of recruits and mortalities recorded on the panels from different 'treatments' (where the 'treatment' represents the numbers of *G.cineraria*, *N.lapillus* or *A.rubens* enclosed in the nets) were analysed with a one-way ANOVA, and the non-significant ranges were identified with a Student-Newman-Keuls test (hereafter referred to as 'S-N-K'). In the diagrammatic representation of the results of the 'S-N-K' tests, any 2 means not underscored by the same line are considered to be significantly different, and any 2 underscored by the same line are not significantly different at the 5% level. Although the 'S-N-K' test practically never contradicts the *F*-test (Keuls, 1952), it is more conservative than ANOVA and it is therefore possible to reject the overall null hypothesis of the original analysis, but to have no evidence of differences among the means in the 'S-N-K' test (Underwood, 1981). Such instances arose, for example, in the results for hydroid recruitment onto the *G.cineraria* panels in the 'J-A85' sampling period (Fig. 5.6.e.), and those for ctenostome mortality in the 'O-F86' grazer introduction sampling period (Fig. 5.12.e). The converse situation was also observed; for example, in the results for serpulid mortality in the *N.lapillus* and *A.rubens* 'J-S85' data set (Fig. 5.11.b.).

Considerable seasonality of recruitment was evident in the results. In general, recruitment was most abundant during the summer months, but there were differences among the taxonomic groups; for example, anomiids and ctenostomes recruited in greatest abundance during the winter periods, whereas serpulids, barnacles and ascidians were most abundant in the summer months. Thus, by repeating the experiments at 2 or 4 month intervals throughout the year it was possible to examine the influence of *G.cineraria*, *N.lapillus* and *A.rubens* activities on different assemblages of species, of varying abundance, through the year. As well as a periodicity in larval recruitment, the interpretation of the results may be further complicated by a seasonality in the activity of *G.cineraria*, *N.lapillus* and *A.rubens*. A number of studies have demonstrated that these 3 species (or a related species in the case of *G.cineraria*) may exhibit seasonal variation in their feeding activities. Williams (1964) observed that the related *G.umbilicalis* was largely confined to rock pools during the winter months and that the snails made very few feeding excursions. Similarly, Connell (1961b) concluded that *N.lapillus* spent a smaller proportion of time feeding in winter than in summer, and that mature *N.lapillus* may cease feeding altogether. Briggs (1980) found that the numbers of *A.rubens* feeding in a subtidal area increased during the spring and summer months but declined in late September.

FIGURE 5.2. Results for the *G.cineraria* grazing experiment immersed between July and September 1984. The graphs illustrate the mean (+1 standard error) number of recruits (= unshaded) and mortalities (= shaded) recorded in the different treatments. On the right of the diagram are the results of the statistical analyses. The results from the 'S-N-K' tests are represented diagrammatically, the treatment means are ranked in order of increasing size from left to right; means underscored by the same line are asserted to be homogeneous and means not underscored by the same line are heterogeneous.

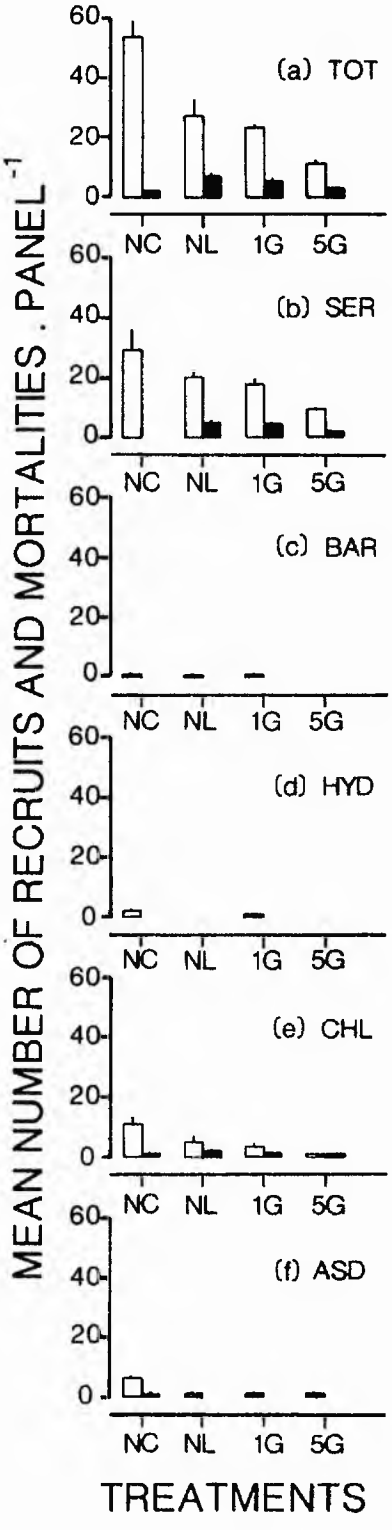
Key: NC = Net Control; NL = Netless Control; 1G = One *G.cineraria*.panel^{-1}; 3G = Three *G.cineraria*.panel^{-1}; 5G = Five *G.cineraria*.panel $^{-1}$.

F = the analysis of variance; C = Cochran's test for the homogeneity of the variances; (i) = the result from Bartlett's test for homogeneity of the variances differs in significance from that of Cochran's test.
* = $p<0.05$; ns = Not Significant.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Hydroids;
(e) Cheilostome bryozoans;
(f) Ascidians.

Note: the 3G treatment panels were not immersed during this period and the results for the 5G treatment are derived from only 2 of the replicates, the *G.cineraria* were lost from the third.



	RECRUITMENT	MORTALITY
(a) TOT	F = 19.38 * C = ns 5G 1G NL NC	F = 7.33 * C = ns NC 5G 1G NL
(b) SER	F = 3.63 ns C = 0.82 * (i) 5G 1G NL NC	F = 40.46 * C = ns NC 5G 1G NL
(c) BAR	F = 0.32 ns C = ns 5G 1G NL NC	NO MORTALITIES
(d) HYD	F = 6.89 * C = ns 5G NL 1G NC	NO MORTALITIES
(e) CHL	F = 4.87 * C = ns 5G 1G NL NC	F = 0.44 ns C = ns 5G 1G NC NL
(f) ASD	F = 16.71 * C = ns 5G 1G NL NC	F = 3.39 ns C = 1.00 * (i) 5G 1G NL NC

FIGURE 5.3. Results for the *G.cineraria* grazing experiment immersed between September 1984 and February 1985. See Figure 5.2. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Anomiids;
(d) Hydroids;
(e) Ctenostome bryozoans;
(f) Cheilostome bryozoans;
(g) Ascidians.

Note: the results for the 3G and 5G treatments are derived from 2 of the replicates, only 2 *G.cineraria* were present on the third replicate in each treatment.

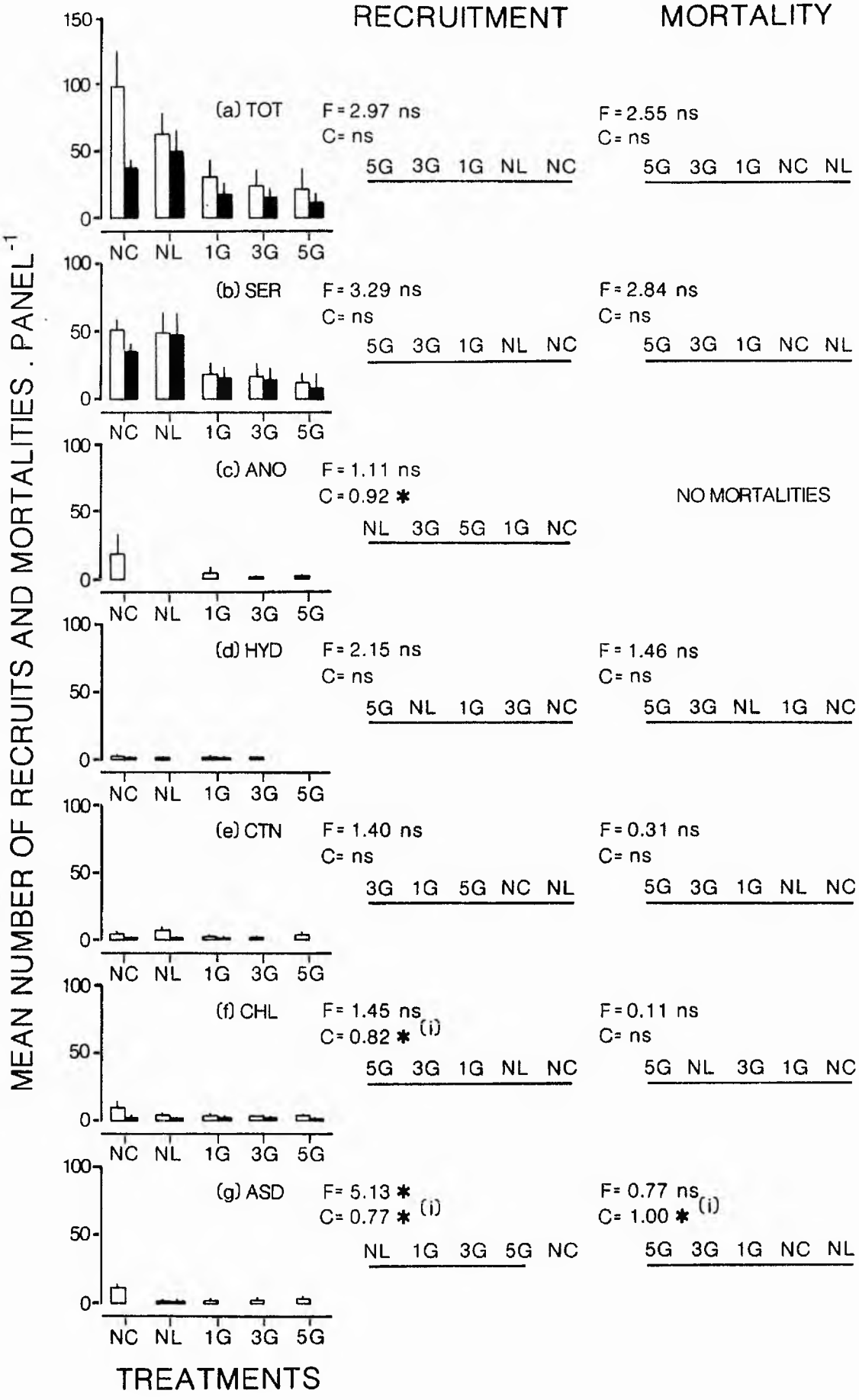

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL -1
150
100
50
0
NC NL 1G 3G 5G
(a) TOT
F = 2.97 ns
C = ns
5G 3G 1G NL NC
F = 2.55 ns
C = ns
5G 3G 1G NC NL
(b) SER
F = 3.29 ns
C = ns
5G 3G 1G NL NC
F = 2.84 ns
C = ns
5G 3G 1G NC NL
(c) ANO
F = 1.11 ns
C = 0.92 *
NL 3G 5G 1G NC
NO MORTALITIES
(d) HYD
F = 2.15 ns
C = ns
5G NL 1G 3G NC
F = 1.46 ns
C = ns
5G 3G NL 1G NC
(e) CTN
F = 1.40 ns
C = ns
3G 1G 5G NC NL
F = 0.31 ns
C = ns
5G 3G 1G NL NC
(f) CHL
F = 1.45 ns
C = 0.82 * (i)
5G 3G 1G NL NC
F = 0.11 ns
C = ns
5G NL 3G 1G NC
(g) ASD
F = 5.13 *
C = 0.77 * (i)
NL 1G 3G 5G NC
F = 0.77 ns (i)
C = 1.00 *
5G 3G 1G NC NL
TREATMENTS

FIGURE 5.4. Results for the *G.cineraria* grazing experiment immersed between February and April 1985. See Figure 5.2. for further details.

Recruitment and mortality results for:
(a) Total numbers;
(b) Hydroids;
(c) Ctenostome bryozoans;
(d) Cheilostome bryozoans.

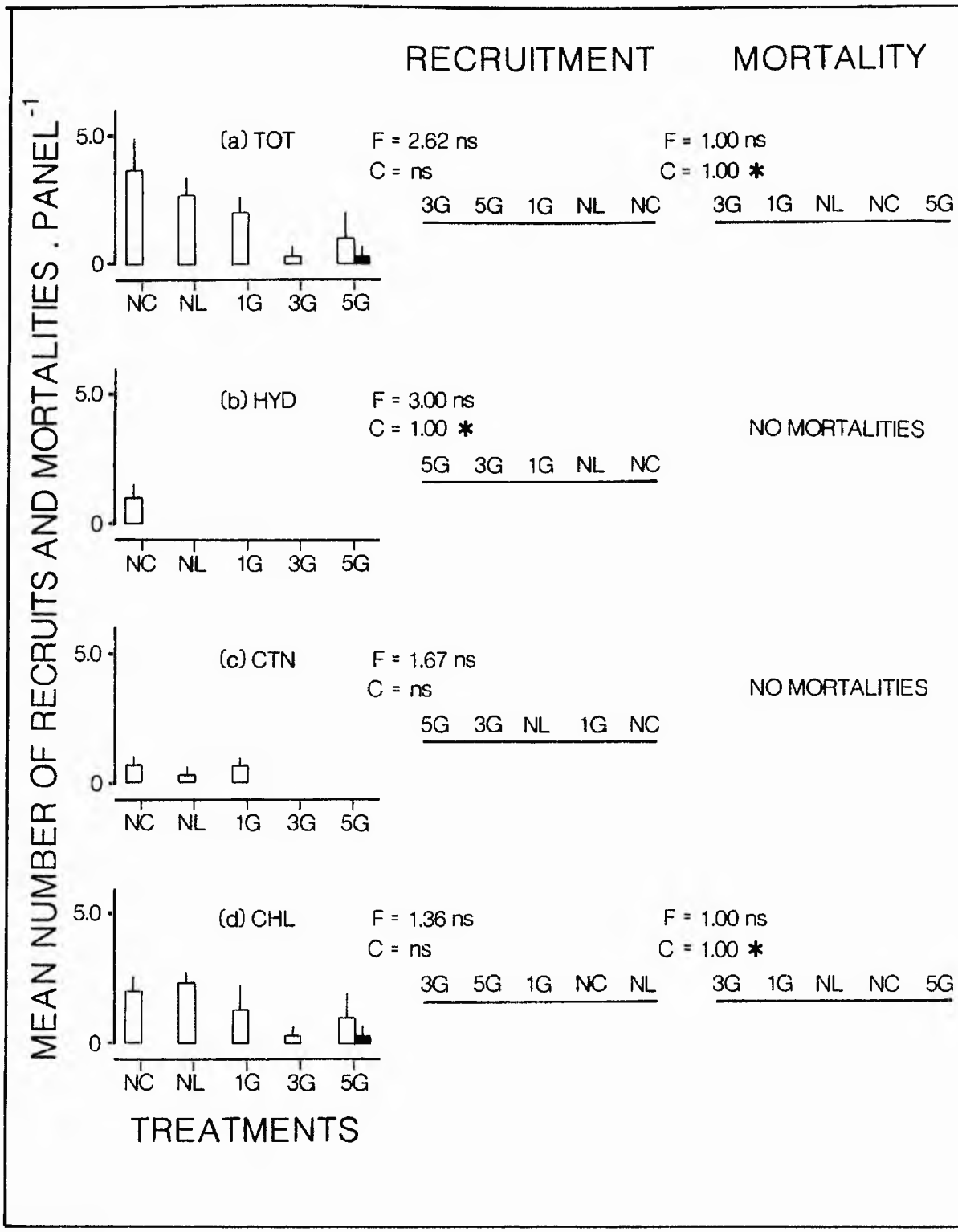

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL -1
(a) TOT
F = 2.62 ns
C = ns
3G 5G 1G NL NC
F = 1.00 ns
C = 1.00 *
3G 1G NL NC 5G
(b) HYD
F = 3.00 ns
C = 1.00 *
5G 3G 1G NL NC
NO MORTALITIES
(c) CTN
F = 1.67 ns
C = ns
5G 3G NL 1G NC
NO MORTALITIES
(d) CHL
F = 1.36 ns
C = ns
3G 5G 1G NC NL
F = 1.00 ns
C = 1.00 *
3G 1G NL NC 5G
5.0
0
NC NL 1G 3G 5G
TREATMENTS

FIGURE 5.5. Results for the *G.cineraria* grazing experiment immersed between April and June 1985. See Figure 5.2. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Hydroids;
(e) Ctenostome bryozoans;
(f) Cheilostome bryozoans;
(g) Ascidians.

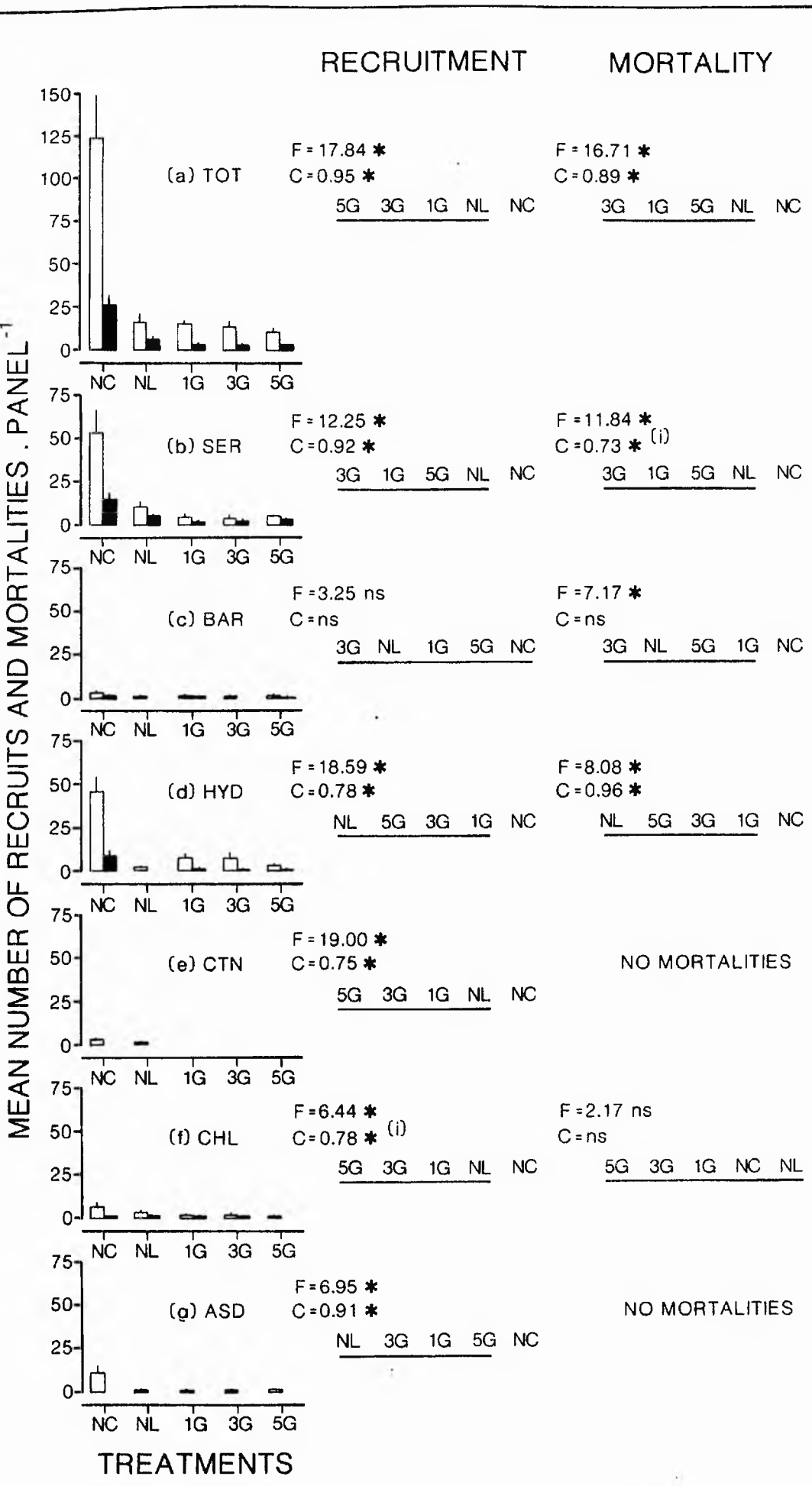
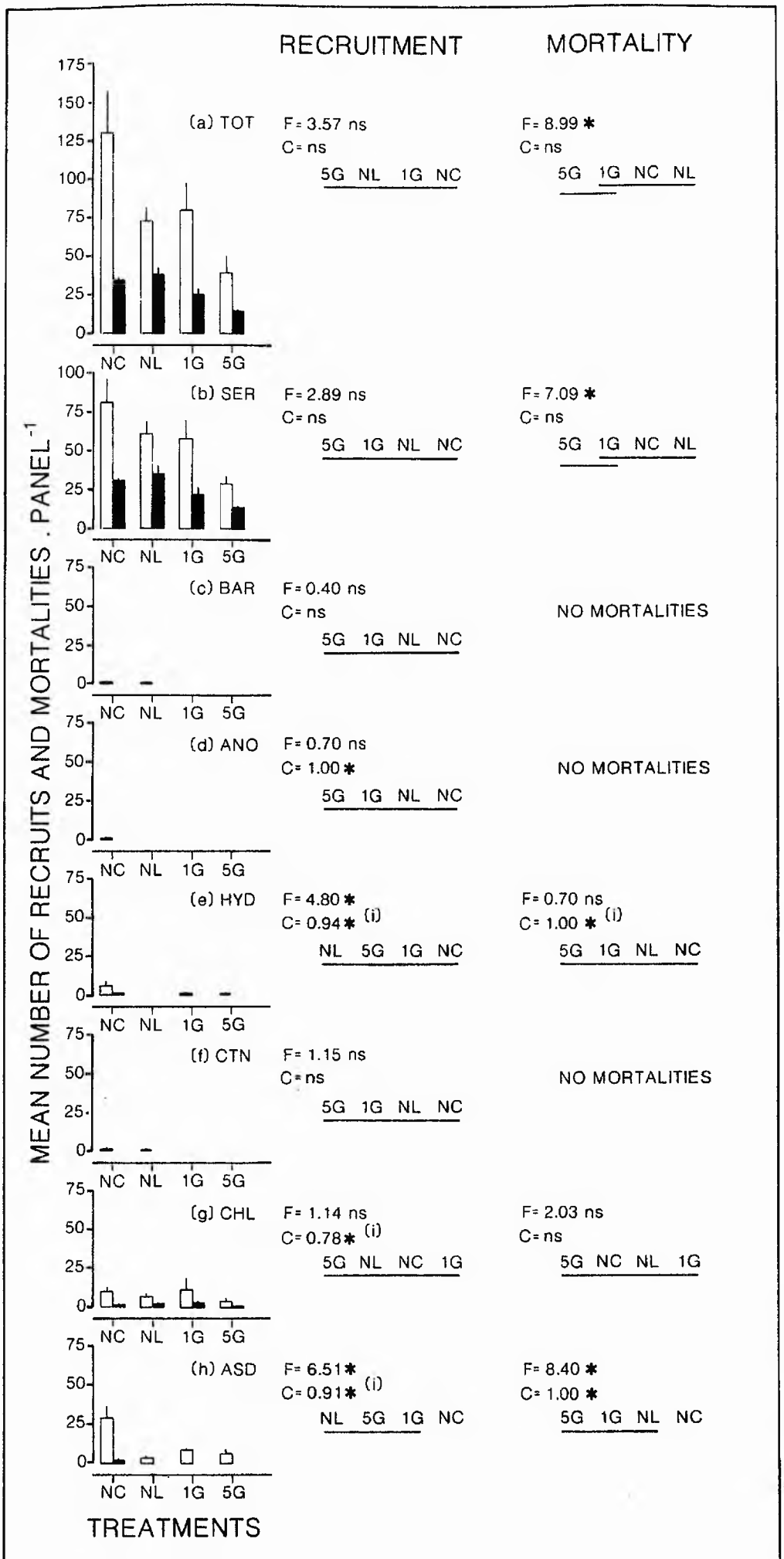

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL^{-1}
(a) TOT
F = 17.84 *
C = 0.95 *
5G 3G 1G NL NC
F = 16.71 *
C = 0.89 *
3G 1G 5G NL NC
(b) SER
F = 12.25 *
C = 0.92 *
3G 1G 5G NL NC
F = 11.84 *
C = 0.73 * (i)
3G 1G 5G NL NC
(c) BAR
F = 3.25 ns
C = ns
3G NL 1G 5G NC
F = 7.17 *
C = ns
3G NL 5G 1G NC
(d) HYD
F = 18.59 *
C = 0.78 *
NL 5G 3G 1G NC
F = 8.08 *
C = 0.96 *
NL 5G 3G 1G NC
(e) CTN
F = 19.00 *
C = 0.75 *
5G 3G 1G NL NC
NO MORTALITIES
(f) CHL
F = 6.44 *
C = 0.78 * (i)
5G 3G 1G NL NC
F = 2.17 ns
C = ns
5G 3G 1G NC NL
(g) ASD
F = 6.95 *
C = 0.91 *
NL 3G 1G 5G NC
NO MORTALITIES
0 25 50 75 100 125 150
NC NL 1G 3G 5G
TREATMENTS

FIGURE 5.6. Results for the *G.cineraria* grazing experiment immersed between June and August 1985. See Figure 5.2. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Anomiids;
(e) Hydroids;
(f) Ctenostome bryozoans;
(g) Cheilostome bryozoans;
(h) Ascidians.

Note: the results for the 1G and 5G treatments are derived from only 2 of the replicates, 1 *G.cineraria* was lost from the third replicate in each case; no data were available for the 3G treatment because no *G.cineraria* remained on 2 of the replicates and 1 was lost from the third replicate. Several of the nets were extensively damaged during this period, this was possibly attributable to the high number of crabs (*Carcinus maenas* (L.)) observed in the frames at this time.


RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL^{-1}
(a) TOT
F= 3.57 ns
C= ns
5G NL 1G NC
F= 8.99 *
C= ns
5G 1G NC NL
(b) SER
F= 2.89 ns
C= ns
5G 1G NL NC
F= 7.09 *
C= ns
5G 1G NC NL
(c) BAR
F= 0.40 ns
C= ns
5G 1G NL NC
NO MORTALITIES
(d) ANO
F= 0.70 ns
C= 1.00 *
5G 1G NL NC
NO MORTALITIES
(e) HYD
F= 4.80 *
C= 0.94 * (i)
NL 5G 1G NC
F= 0.70 ns
C= 1.00 * (i)
5G 1G NL NC
(f) CTN
F= 1.15 ns
C= ns
5G 1G NL NC
NO MORTALITIES
(g) CHL
F= 1.14 ns
C= 0.78 * (i)
5G NL NC 1G
F= 2.03 ns
C= ns
5G NC NL 1G
(h) ASD
F= 6.51 *
C= 0.91 * (i)
NL 5G 1G NC
F= 8.40 *
C= 1.00 *
5G 1G NL NC
NC NL 1G 5G
TREATMENTS

It is important to note that the present results represent the final overall effect of 2 or 4 months of *G.cineraria*, *N.lapillus* or *A.rubens* activity or exclusion; there is no information available on the numbers of recruits that have settled and have been lost in the interim, leaving no trace, prior to the sampling date.

As in the study on the influence of panel 'age' on larval recruitment (Chapter 3) the effects of the pre-emption of space by the previously recruited individuals and colonies, on the rates of subsequent larval attachment were considered to be of minor significance. Recruits, in general, probably did not occupy sufficient space, even on panels protected from grazers for 2 to 4 months during the periods of peak recruitment and greatest growth, to markedly inhibit further recruitment.

5.2.1. <u>The Influence of *Gibbula cineraria* Grazing on Epifaunal Assemblages</u>:- (see Figures 5.2.-5.6.)

(a) <u>Total Recruitment and Mortality</u>:- (See Fig. 5.2.a.; 5.3.a.; 5.4.a.; 5.5.a.; 5.6.a.)

Among all 5 data sets most recruitment was recorded on the net control panels, but only for the 'J-S84' and 'A-J85' sampling periods was the observed recruitment on these panels significantly greater than in the other treatments (F = 19.38, $P<0.05$; F = 17.84, $P<0.05$ (Cochran and Bartlett's (hereafter referred to as 'C & B'), $P<0.05$), respectively). Otherwise there were no significant differences among the treatments, although

a number of patterns were evident. With the exception of the 'J-A85' period, the netless controls were the second highest-ranked in terms of the numbers of recruits recorded. Among the *G.cineraria* panels there was a tendency for the panels grazed by high *G.cineraria* densities (e.g. 5 *G.cineraria*.panel^{-1} to have fewer recruits than those grazed by low *G.cineraria* densities (e.g. 1 *G.cineraria*.panel^{-1}). However, none of these differences were statistically significant.

When the numbers of mortalities were considered, the results were characterized by considerable variability among the different data sets, and patterns in the significant differences and the rankings of each treatment mean were less consistent. Overall, the *G.cineraria* panels were lower-ranked, in terms of the numbers of mortalities recorded, than the controls. However, there were no significant differences between the numbers of mortalities on the grazed panels; the only differences noted were between the grazed panels and the controls, or between the 2 controls. There were significant differences among the treatments for the 'J-S84' (F = 7.33, P<0.05), 'A-J85' (F = 16.71, P<0.05 ('C & B', P<0.05)) and 'J-A85' (F = 8.99, P<0.05) sampling periods. No significant differences were evident during the periods of low recruitment (i.e. 'S-F85' and 'F-A85'). For the 'F-A85' period, mortalities were recorded only on the high density *G.cineraria* panels.

(b) Serpulid Recruitment and Mortality:- (see Fig. 5.2.b.; 5.3.b.; 5.5.b.; 5.6.b.)

The greatest serpulid recruitment was recorded on the net control panels, but the only statistically significant result was for the 'A-J85' (F = 12.25, P<0.05 ('C & B', P<0.05)) period, where more recruits were observed on the net controls than in the other treatments. Although none of the other differences between the numbers of serpulid recruits in each treatment were significant, a number of patterns were evident. The netless control panels were the second highest-ranked, and, in general, among the *G.cineraria* panels fewer recruits were recorded on the panels of high grazer density.

There was considerable variability among the significant differences and the rankings of the mean numbers of mortalities recorded for each treatment. However, in general, the controls were more highly-ranked than the *G.cineraria* panels, and the high grazer density panels were lower-ranked than the low grazer density panels. Significant differences among the grazed panels, between the grazed panels and the controls and/or among the controls were recorded in the 'J-S84' (F = 40.46, P<0.05), 'A-J85' (F = 11.84, P<0.05) and 'J-A85' (F = 7.09, P<0.05) sampling periods; the only non-significant result was for treatments immersed during the 'S-F85' period.

(c) Barnacle Recruitment and Mortality:- (see Fig. 5.2.c.; 5.5.c.; 5.6.c.)

The interpretation of the results for barnacle recruitment and mortality was complicated by the very low numbers of barnacles that recruited to the panels. None of the differences between the treatments were statistically significant, in any of the sampling periods, but the net control panels were always the highest-ranked in terms of the numbers of recruits recorded. In the 'J-S84' and 'J-A85' periods, where barnacle recruitment was lowest and very few recruits were observed on the *G.cineraria* panels, the netless treatments were second highest-ranked.

Mortalities were recorded only in the 'A-J85' period, during which the greatest numbers of barnacle recruits were also observed. Significantly more mortalities were recorded on the net controls than the netless controls and grazed panels, among which no significant differences were evident ($F = 7.17$, $P<0.05$).

(d) Anomiid Recruitment and Mortality:- (see Fig. 5.3.c.; 5.6.d.)

Anomiids recruited in abundance during the 'S-F85' sampling period, but none of the differences between the treatments were statistically significant. They were recorded most frequently on the net control panels, and were not observed on the netless controls. Among the *G.cineraria* panels most anomiid recruits occurred on the

low grazer density panels. Anomiids also recruited during the 'J-A85' period but were only recorded on the net control panels, and the differences between the treatments were not statistically significant.

No anomiid mortalities were observed.

(e) Hydroid Recruitment and Mortality:- (see Fig. 5.2.d.; 5.3.d.; 5.4.b.; 5.5.d.; 5.6.e.)

The greatest numbers of hydroid recruits were recorded on the net control panels, and during the 'F-A85' period they were observed exclusively on these panels. However, the numbers of hydroid recruits on the net controls were significantly different from the other treatments in only the 'J-S84' ($F = 6.89$, $P<0.05$) and 'A-J85' ($F = 18.59$, $P<0.05$ ('C & B', $P<0.05$) periods. For the 'J-A85' data a significant ANOVA was obtained ($F = 4.80$, $P<0.05$) but no differences were detected by the 'S-N-K' test between the treatment means. No significant differences existed between the numbers of recruits that occurred among the other treatments, and there were no distinct patterns among the ranking of the netless controls and grazed panels. However, in general, the low grazer density panels had more hydroid recruits than the high grazer density panels. Unlike the other taxonomic groups discussed so far, the netless control panels frequently had fewer hydroid recruits than the grazed panels.

Few hydroid mortalities were observed and none were recorded in the 'J-S84' and 'F-A85' sampling periods. Only low numbers of mortalities were recorded during the 'S-F85' and 'J-A85' periods, and they were almost entirely restricted to the net control treatments. None of the differences between the mean numbers of hydroid mortalities recorded for the different treatments were statistically significant. Most mortalities were observed on the panels with the greatest number of recruits (i.e. during the 'A-J85' period) where significantly more mortalities were recorded on the net control panels than in the other treatments (F = 8.08, $P<0.05$ ('C & B', $P<0.05$)). The low numbers, or total absence of records, of mortalities for species such as hydroids, as well as ctenostomes and ascidians, was largely a result of the lack of a persistent exoskeleton (cf. spirorbids and barnacles).

(f) <u>Ctenostome Recruitment and Mortality</u>:- (see Fig. 5.3.e.; 5.4.c.; 5.5.e.; 5.6.f.)

Ctenostome recruits were observed in only low numbers on the panels and were frequently absent from those grazed by *G.cineraria* (e.g. during the 'F-A85' and 'A-J85' immersion periods). In the majority of cases the net and netless controls were more highly-ranked than the grazed panels, in terms of the numbers of recruits recorded. The only significant difference was for the 'A-J85' data set, where there were significantly more

recruits on the net control panels than for any other treatment (F = 19.00, P<0.05 ('C & B', P<0.05)).

Very few mortalities were recorded (see section 5.2.e.), and none were observed during the 'F-A85', 'A-J85' and 'J-A85' periods. There were no significant differences among the treatments for the 'S-F85' data set, but no ctenostome mortalities were recorded on the more intensely grazed panels.

(g) Cheilostome Recruitment and Mortality:- (see Fig. 5.2.e.; 5.3.f.; 5.4.d.; 5.5.f.; 5.6.g.)

In the 'J-S84', 'S-F85' and 'A-J85' sampling periods, the net control panels were the highest-ranked in terms of the numbers of cheilostome recruits recorded, with the netless controls ranked second; low grazer density treatments were higher-ranked than panels with high grazer densities. However, only during the 'A-J85' period were the net control panels significantly different from all the other treatments (F = 6.44, P<0.05), and in the 'J-S84' period they were significantly different only from the high *G.cineraria* density treatment (F = 4.87, P<0.05). Otherwise no significant differences were evident among the treatments. The results for the 'F-A85' and 'J-A85' periods were less well-defined, and there were no statistically significant differences between the various treatments. The lowest numbers of recruits were recorded on the more intensely grazed panels. However,

netless control or *G.cineraria* panels were higher-ranked than the net controls.

Conclusions regarding the cheilostome mortalities were restricted by the small data sets. Mortalities were recorded in the majority of the treatments during all the sampling periods, but patterns were difficult to discern, other than a general tendency for high *G.cineraria* density panels to be lower-ranked, and for the controls to be higher-ranked. The primary exception was during the 'F-A85' period, where mortalities were recorded only on the high grazer density panels. No statistically significant differences were evident among any of the treatments in any of the sampling periods.

(h) Ascidian Recruitment and Mortality:- (see Fig. 5.2.f.; 5.3.g.; 5.5.g.; 5.6.h.)

In all the sampling periods where ascidian recruitment occurred, significantly greater numbers of ascidian recruits were observed on the net control panels than for the other treatments ('J-S84': $F = 16.71$, $P<0.05$; 'S-F85': $F = 5.13$, $P<0.05$; 'A-J85': $F = 6.95$, $P<0.05$ ('C & B', $P<0.05$); 'J-A85': $F = 6.51$, $P<0.05$). *G.cineraria* grazing activities thus appeared to have a significant effect on the ascidians in all the sampling periods where recruitment occurred, and, correspondingly, very low numbers of recruits were generally observed on the grazed panels. Excluding the 'J-S84' period, where low numbers of recruits were observed, the general

pattern among the results was for the netless control panels to be lowest-ranked, with more recruits being recorded on the *G.cineraria* panels. However, none of these differences were statistically significant. Among the *G.cineraria* panels more ascidian recruits were observed on either the high or the low grazer density panels.

Very few ascidian mortalities were observed (see section 5.2.e.) and those that were, occurred only on the control panels, and primarily on the net controls. The only significant difference occurred in the 'J-A85' period, where significantly more mortalities were recorded on the net control panels than in the other treatments (F = 8.40, $P<0.05$ ('C & B', $P<0.05$)). No mortalities were recorded on the *G.cineraria* panels.

(i) Summary of the Results:-

The results indicated that the grazing activities of *G.cineraria* may have had marked effects on the assemblages that became established on the panels. However, it should be noted that there is no direct evidence on the nature of the mechanism by which the *G.cineraria* influenced settling larvae; no statement can be made as to whether or not grazer activities inhibited larval settlement or caused an increase in post-settlement mortality. In general, for all the taxonomic groups examined, fewer recruits were recorded on the grazed panels (including the netless controls) compared

to the numbers on the net control panels, at the end of the period of immersion. The netless controls were accessible to all grazers and predators while the net control panels excluded these. Furthermore, lower numbers of recruits were, in general, recorded on the intensely grazed panels compared to the less intensely grazed panels. However, none of the differences between the grazed treatments were statistically significant, possibly indicating that 1 *G.cineraria* was able to graze a 16 x16 cm panel as effectively as 3 or 5 *G.cineraria*, and suggesting that it might be profitable to repeat the experiments on larger substrata to better examine the effect of grazer density on epifaunal assemblages.

The numbers of mortalities recorded were characterized by greater variability among the different treatments, taxonomic groups and the periods of immersion. Although the greatest numbers of mortalities were frequently recorded on the un-grazed panels, those recorded on the grazed panels generally represented a larger fraction of the total recruitment. For example, consider the total recruitment and mortality observed for the 'J-A85' immersion period: the numbers of mortalities represented 26% of the total recruitment observed on the net controls, 31% on the low-density *G.cineraria* panels, 37% on the high-density *G.cineraria* panels, and 52% on the netless controls. The relatively low numbers of mortalities observed on the *G.cineraria* panels may have been attributable to grazer activity dislodging the dead remains of recruits which may have

otherwise been evident, and recordable, for prolonged periods on the protected net control panels.

The effect of *G.cineraria* grazing activity was also evident in the range of colony sizes attained by the species that were recorded on the panels at the end of the immersion periods. For example, *Schizoporella unicornis* colonies recruiting during the 'J-S84' period attained sizes between A-A+6(4) zooids (where A = ancestrula, 6 = number of functional zooids, and (4) = number of developing zooids) on the net control panels, compared to maximum colony sizes of A-A+1 zooids on grazed panels. Similarly, *Electra pilosa* recruiting during the 'S-F85' period attained sizes between A+2(2)-A+14(3) zooids on the net controls and A-A+5(5) zooids on grazed panels. These results should not be taken as indicative of differences in growth rates between the treatments, but rather that on protected panels growth progressed without interruption, so that colonies attained a larger size than on grazed panels. In the latter cases, colonies were presumably damaged or destroyed by grazer activity before growth could proceed very far.

Some of the differences observed between the sampling periods may have been attributable to seasonal variation in the grazing activities of *G.cineraria*. A notable feature of the results was the virtual absence of significant differences between the treatments in the 'S-F85' and 'F-A85' immersion periods (i.e. the winter

FIGURE 5.7. Results for the *N.lapillus* and *A.rubens* experiments immersed between August and October 1984. The graphs illustrate the mean (+1 standard error) number of recruits (= unshaded) and mortalities (= shaded) recorded in the different treatments. On the right of the diagram are the results of the statistical analyses. The results from the 'S-N-K' tests are represented diagrammatically, the treatment means are ranked in order of increasing size from left to right ; means underscored by the same line are asserted to be homogeneous and means not underscored by the same line are heterogeneous.

Key: NC = Net Control; NL = Netless Control; 1A = One *A.rubens*.panel^{-1}; 1N = One *N.lapillus*.panel^{-1}; 3N = Three *N.lapillus*.panel^{-1}.

F = the analysis of variance; C = Cochran's test for the homogeneity of the variances; (i) = the result from Bartlett's test for the homogeneity of the variances differs in significance from that of Cochran's test.

* = $p<0.05$; ns = Not significant.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Hydroids;
(e) Cheilostome bryozoans;
(f) Ascidians.

Note: the 1N and 3N treatments were not immersed during this period.

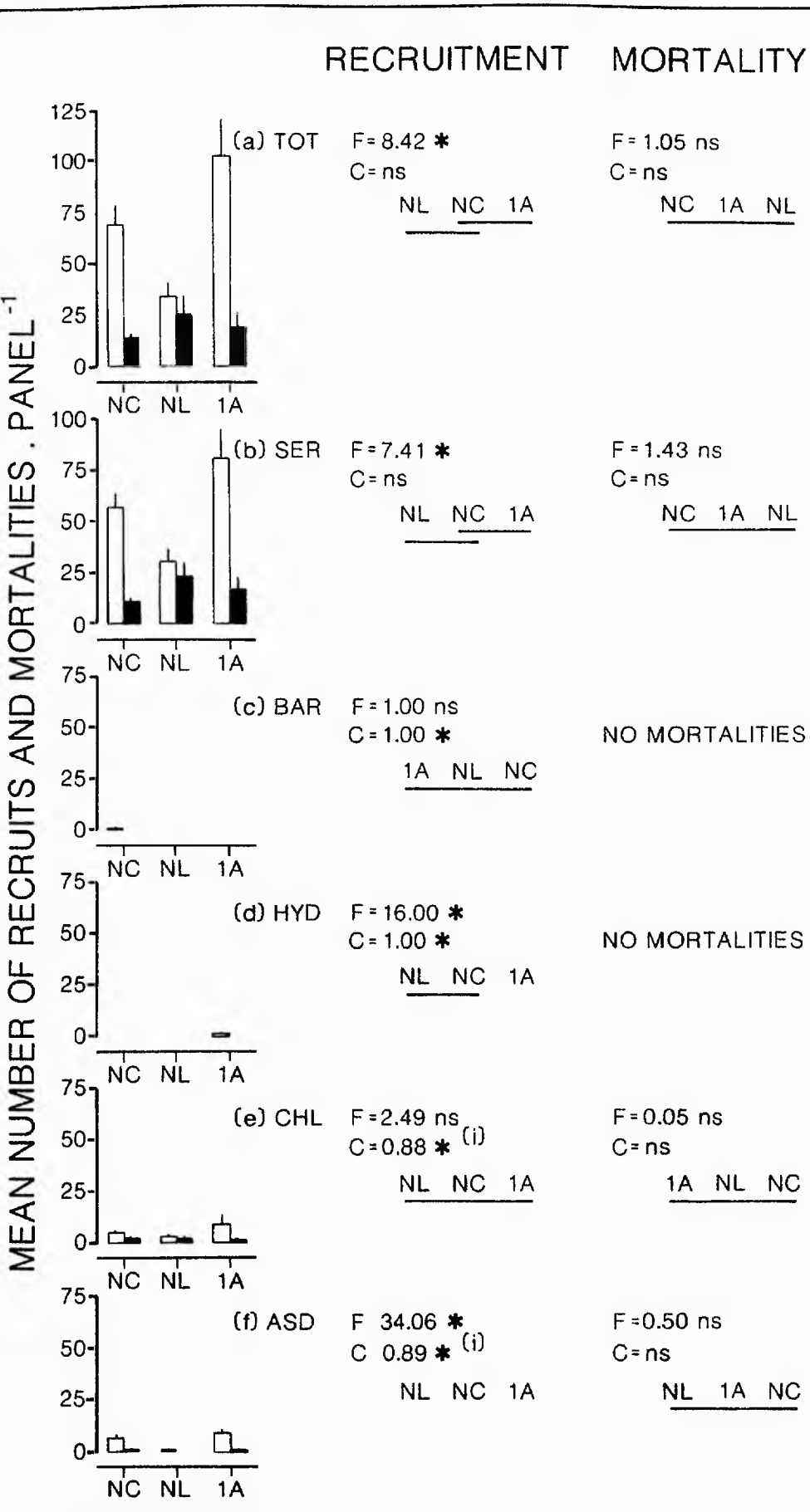

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL -1
125
100
75
50
25
0
(a) TOT
F = 8.42 *
C = ns
NL NC 1A
F = 1.05 ns
C = ns
NC 1A NL
NC NL 1A
100
75
50
25
0
(b) SER
F = 7.41 *
C = ns
NL NC 1A
F = 1.43 ns
C = ns
NC 1A NL
NC NL 1A
75
50
25
0
(c) BAR
F = 1.00 ns
C = 1.00 *
1A NL NC
NO MORTALITIES
NC NL 1A
75
50
25
0
(d) HYD
F = 16.00 *
C = 1.00 *
NL NC 1A
NO MORTALITIES
NC NL 1A
75
50
25
0
(e) CHL
F = 2.49 ns
C = 0.88 * (i)
NL NC 1A
F = 0.05 ns
C = ns
1A NL NC
NC NL 1A
75
50
25
0
(f) ASD
F 34.06 *
C 0.89 * (i)
NL NC 1A
F = 0.50 ns
C = ns
NL 1A NC
NC NL 1A
TREATMENTS

FIGURE 5.8. Results for the *N.lapillus* and *A.rubens* experiments immersed between October 1984 and March 1985. See Figure 5.7. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Anomiids;
(e) Hydroids;
(f) Ctenostome bryozoans;
(g) Cheilostome bryozoans;
(h) Ascidians.

Note: the results for the 3N treatment are derived from 2 of the replicates, only 1 *N.lapillus* was present on the third replicate.

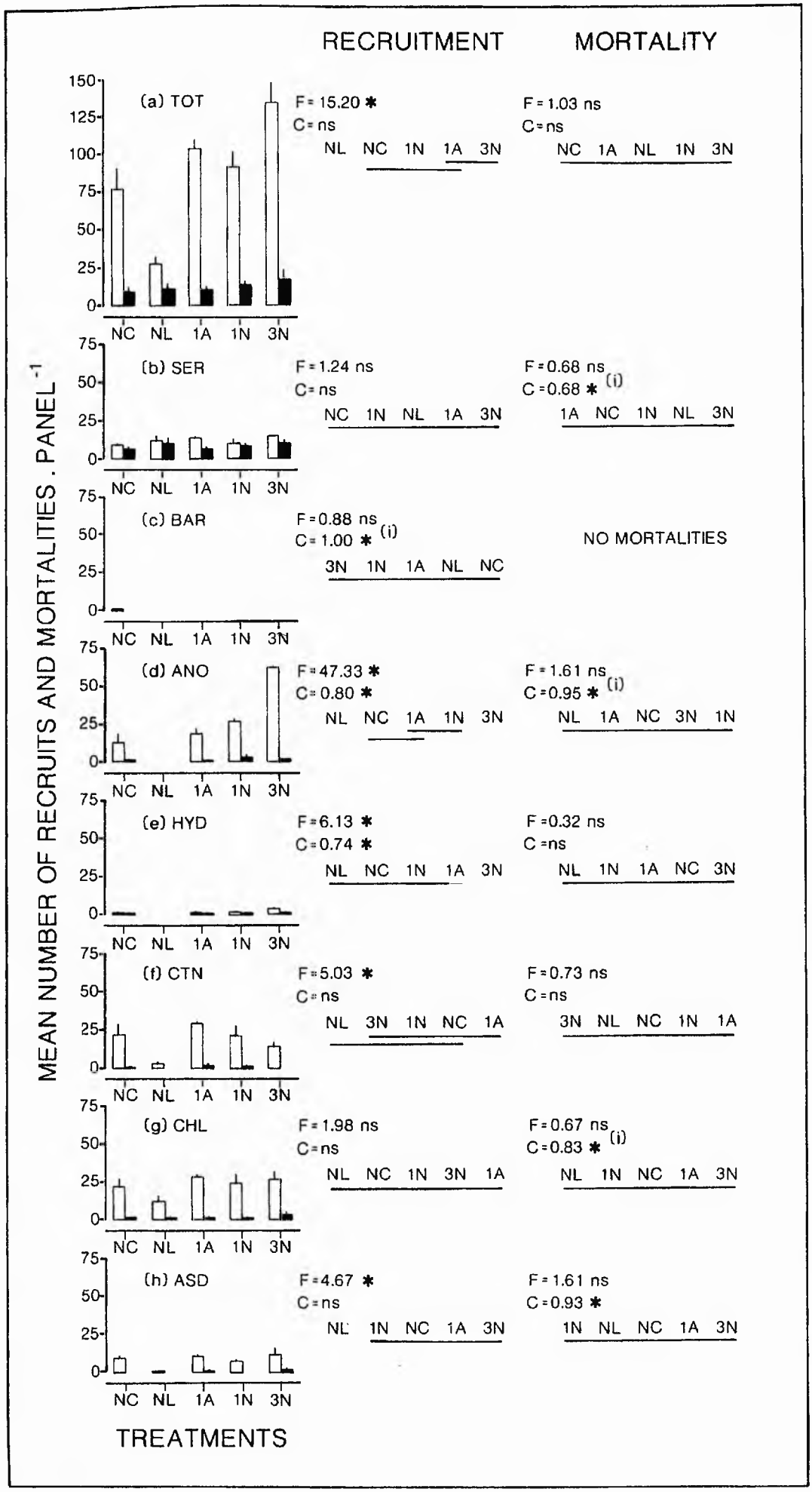

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL -1
(a) TOT
F = 15.20 *
C = ns
NL NC 1N 1A 3N
F = 1.03 ns
C = ns
NC 1A NL 1N 3N
(b) SER
F = 1.24 ns
C = ns
NC 1N NL 1A 3N
F = 0.68 ns
C = 0.68 * (i)
1A NC 1N NL 3N
(c) BAR
F = 0.88 ns
C = 1.00 * (i)
3N 1N 1A NL NC
NO MORTALITIES
(d) ANO
F = 47.33 *
C = 0.80 *
NL NC 1A 1N 3N
F = 1.61 ns
C = 0.95 * (i)
NL 1A NC 3N 1N
(e) HYD
F = 6.13 *
C = 0.74 *
NL NC 1N 1A 3N
F = 0.32 ns
C = ns
NL 1N 1A NC 3N
(f) CTN
F = 5.03 *
C = ns
NL 3N 1N NC 1A
F = 0.73 ns
C = ns
3N NL NC 1N 1A
(g) CHL
F = 1.98 ns
C = ns
NL NC 1N 3N 1A
F = 0.67 ns
C = 0.83 * (i)
NL 1N NC 1A 3N
(h) ASD
F = 4.67 *
C = ns
NL 1N NC 1A 3N
F = 1.61 ns
C = 0.93 *
1N NL NC 1A 3N
0 25 50 75 100 125 150
NC NL 1A 1N 3N
TREATMENTS

FIGURE 5.9. Results for the *N.lapillus* and *A.rubens* experiments immersed between March and May 1985. See Figure 5.7. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Anomiids;
(e) Hydroids;
(f) Ctenostome bryozoans;
(g) Cheilostome bryozoans;
(h) Ascidians.

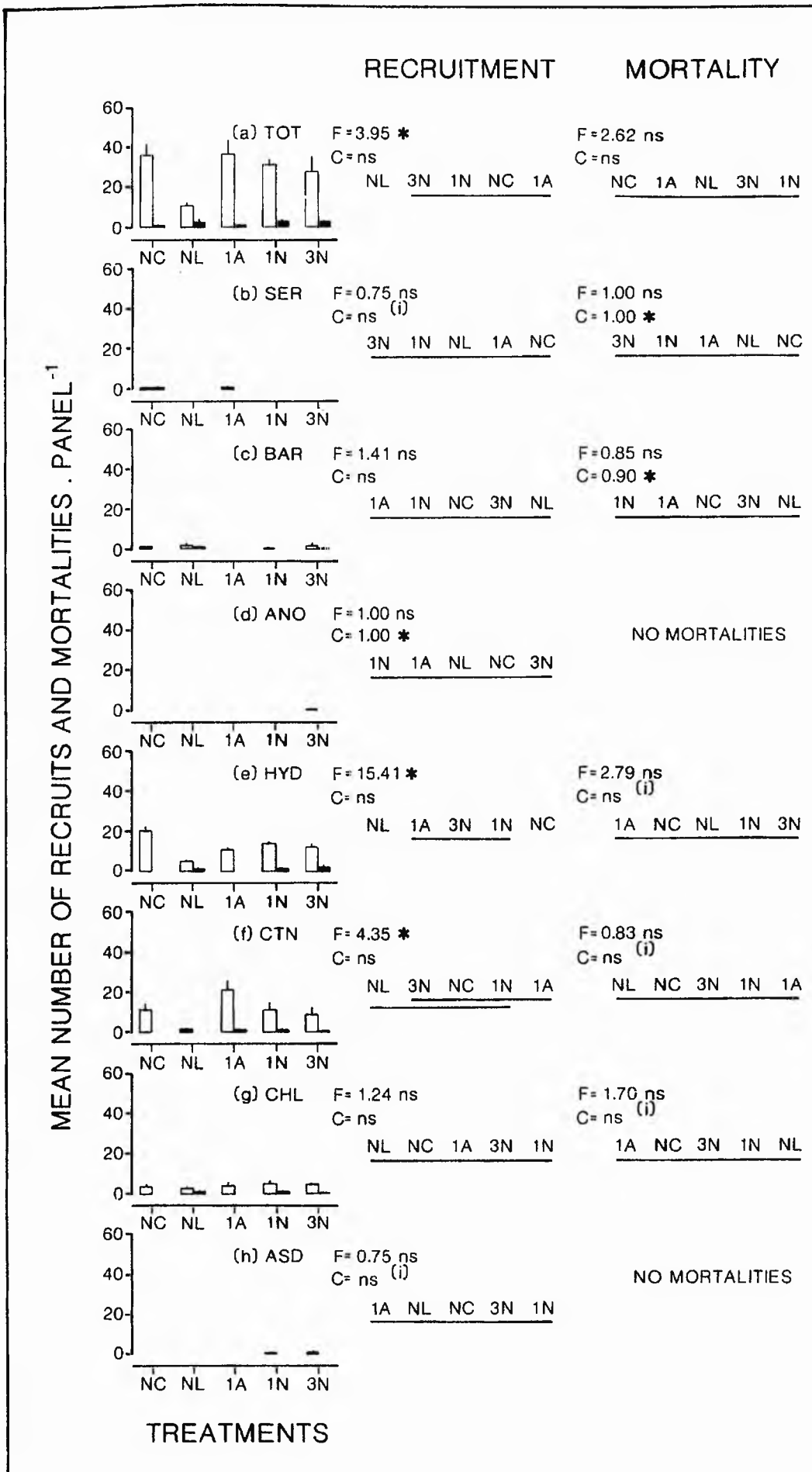

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL-1
(a) TOT
F = 3.95 *
C = ns
NL 3N 1N NC 1A
F = 2.62 ns
C = ns
NC 1A NL 3N 1N
(b) SER
F = 0.75 ns
C = ns (i)
3N 1N NL 1A NC
F = 1.00 ns
C = 1.00 *
3N 1N 1A NL NC
(c) BAR
F = 1.41 ns
C = ns
1A 1N NC 3N NL
F = 0.85 ns
C = 0.90 *
1N 1A NC 3N NL
(d) ANO
F = 1.00 ns
C = 1.00 *
1N 1A NL NC 3N
NO MORTALITIES
(e) HYD
F = 15.41 *
C = ns
NL 1A 3N 1N NC
F = 2.79 ns
C = ns (i)
1A NC NL 1N 3N
(f) CTN
F = 4.35 *
C = ns
NL 3N NC 1N 1A
F = 0.83 ns
C = ns (i)
NL NC 3N 1N 1A
(g) CHL
F = 1.24 ns
C = ns
NL NC 1A 3N 1N
F = 1.70 ns
C = ns (i)
1A NC 3N 1N NL
(h) ASD
F = 0.75 ns
C = ns (i)
1A NL NC 3N 1N
NO MORTALITIES
0 20 40 60
NC NL 1A 1N 3N
TREATMENTS

FIGURE 5.10. Results for the *N.lapillus* and *A.rubens* experiments immersed between May and July 1985. See Figure 5.7. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Anomiids;
(e) Hydroids;
(f) Ctenostome bryozoans;
(g) Cheilostome bryozoans;
(h) Ascidians.

Note: the results for the 3N treatment are derived from 2 of the replicates, only 1 *N.lapillus* was present on the third replicate.

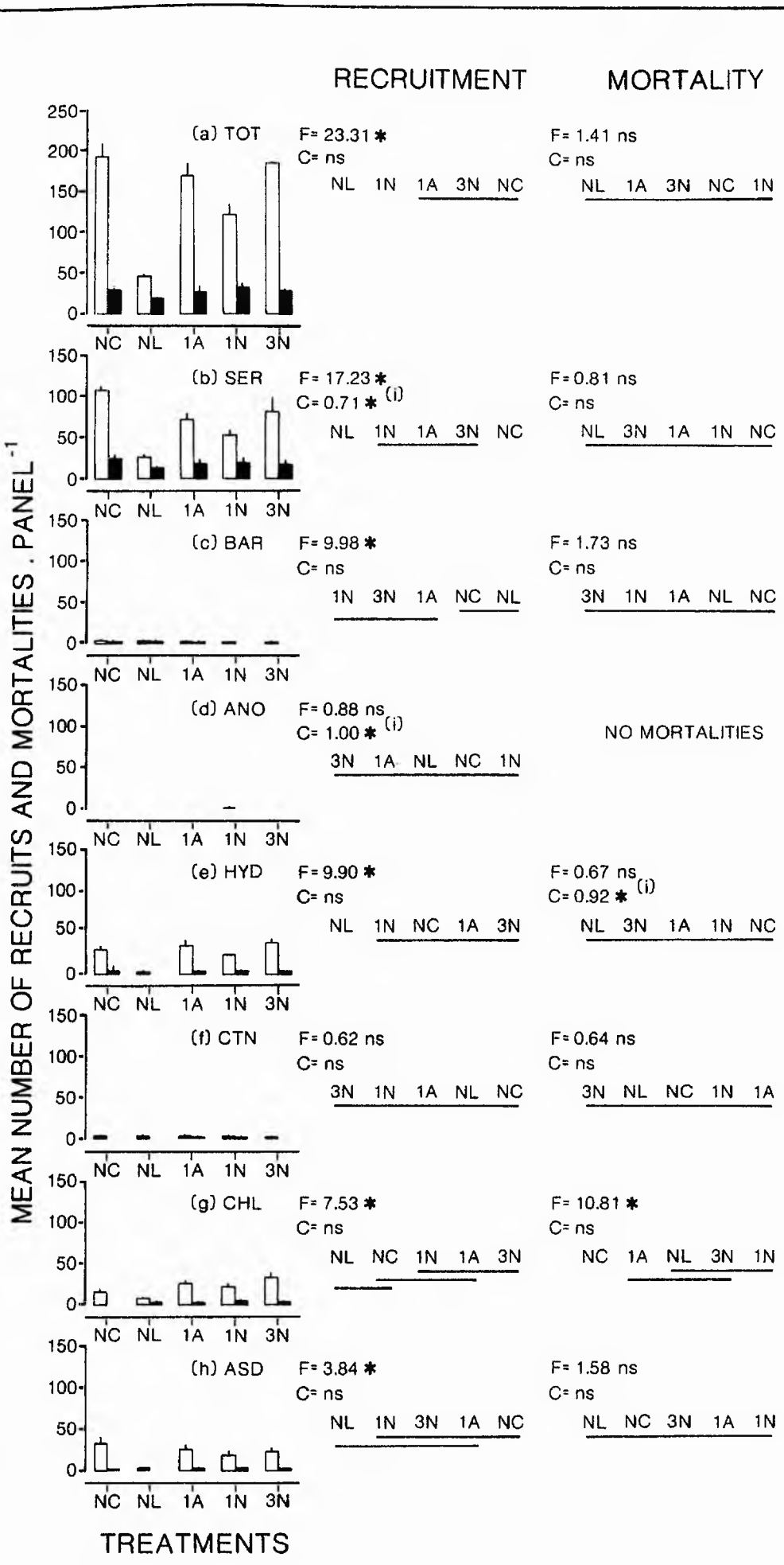
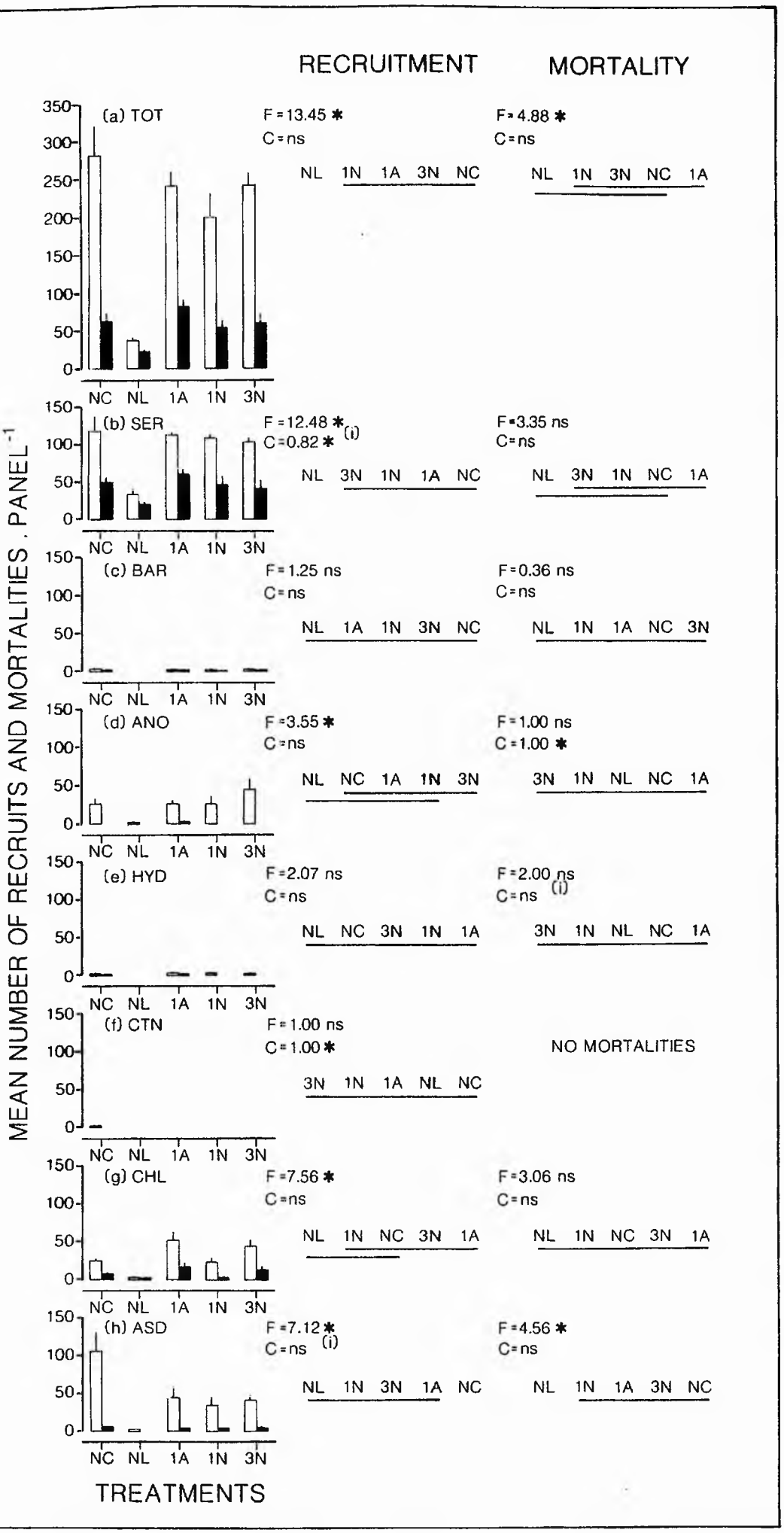

RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL^{-1}
(a) TOT
F= 23.31 *
C= ns
NL 1N 1A 3N NC
F= 1.41 ns
C= ns
NL 1A 3N NC 1N
(b) SER
F= 17.23 *
C= 0.71 * (i)
NL 1N 1A 3N NC
F= 0.81 ns
C= ns
NL 3N 1A 1N NC
(c) BAR
F= 9.98 *
C= ns
1N 3N 1A NC NL
F= 1.73 ns
C= ns
3N 1N 1A NL NC
(d) ANO
F= 0.88 ns
C= 1.00 * (i)
3N 1A NL NC 1N
NO MORTALITIES
(e) HYD
F= 9.90 *
C= ns
NL 1N NC 1A 3N
F= 0.67 ns
C= 0.92 * (i)
NL 3N 1A 1N NC
(f) CTN
F= 0.62 ns
C= ns
3N 1N 1A NL NC
F= 0.64 ns
C= ns
3N NL NC 1N 1A
(g) CHL
F= 7.53 *
C= ns
NL NC 1N 1A 3N
F= 10.81 *
C= ns
NC 1A NL 3N 1N
(h) ASD
F= 3.84 *
C= ns
NL 1N 3N 1A NC
F= 1.58 ns
C= ns
NL NC 3N 1A 1N
250
200
150
100
50
0
NC NL 1A 1N 3N
TREATMENTS

FIGURE 5.11. Results for the *N.lapillus* and *A.rubens* experiments immersed between July and September 1985. See Figure 5.7. for further details.

Recruitment and mortality results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Anomiids;
(e) Hydroids;
(f) Ctenostome bryozoans;
(g) Cheilostome bryozoans;
(h) Ascidians.


RECRUITMENT
MORTALITY
MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL^{-1}
(a) TOT
F = 13.45 *
C = ns
NL 1N 1A 3N NC
F = 4.88 *
C = ns
NL 1N 3N NC 1A
(b) SER
F = 12.48 * (i)
C = 0.82 *
NL 3N 1N 1A NC
F = 3.35 ns
C = ns
NL 3N 1N NC 1A
(c) BAR
F = 1.25 ns
C = ns
NL 1A 1N 3N NC
F = 0.36 ns
C = ns
NL 1N 1A NC 3N
(d) ANO
F = 3.55 *
C = ns
NL NC 1A 1N 3N
F = 1.00 ns
C = 1.00 *
3N 1N NL NC 1A
(e) HYD
F = 2.07 ns
C = ns
NL NC 3N 1N 1A
F = 2.00 ns (i)
C = ns
3N 1N NL NC 1A
(f) CTN
F = 1.00 ns
C = 1.00 *
3N 1N 1A NL NC
NO MORTALITIES
(g) CHL
F = 7.56 *
C = ns
NL 1N NC 3N 1A
F = 3.06 ns
C = ns
NL 1N NC 3N 1A
(h) ASD
F = 7.12 *
C = ns (i)
NL 1N 3N 1A NC
F = 4.56 *
C = ns
NL 1N 1A 3N NC
NC NL 1A 1N 3N
TREATMENTS

months), compared to the greater incidence of significant differences between treatments in the other sampling periods (i.e. the summer months) when *G.cineraria* was predictably most active. These conclusions can only be tentative, and are complicated by the low levels of recruitment that occurred during the winter months when grazing activity might have had least effect on the assemblages.

5.2.2. The Influence of *Nucella lapillus* and *Asterias rubens* on Epifaunal Assemblages:- (see Figures 5.7.-5.11.)

(a) Total Recruitment and Mortality:- (see Fig. 5.7.a.; 5.8.a.; 5.9.a.; 5.10.a.; 5.11.a.)

The most striking feature of the results was the low numbers of recruits recorded on the netless control panels compared to the other treatments. In the 'A-O84' period, the netless controls had similar numbers of recruits to the net control panels, but had significantly fewer recruits than were recorded on the *A.rubens* panels ($F = 8.42$, $P<0.05$). In the other data sets, 'O-M85', 'M-M85, 'M-J85' and 'J-S85', there were significantly fewer recruits on the netless controls than all the other treatments ('O-M85': $F = 15.20$, $P<0.05$; 'M-M85': $F = 3.95$, $P<0.05$; 'M-J85': $F = 23.31$, $P<0.05$; and 'J-S85': $F = 13.45$, $P<0.05$). Among the other treatments there were a number of significant differences and several patterns were evident. During the autumn/winter sampling

periods (i.e. 'A-O84' and 'O-M85') the net control panels were the second lowest-ranked in terms of the numbers of recruits recorded, greater numbers of recruits were observed in the *N.lapillus* and *A.rubens* treatments. Some of the differences among these treatments were statistically significant; for example, the net controls had significantly fewer recruits than the high-density *N.lapillus* panels in the 'O-M85' data set. Conversely, where recruits were more abundant in the 'M-J85' and 'J-S85' periods, the greatest numbers were observed on the net control panels. However, with the exception of the 'M-J85' period, where the low-density *N.lapillus* panels had significantly fewer recruits than the other treatments (excluding the netless controls), differences between these treatments were not significant.

The results for the numbers of mortalities recorded were more variable among the different sampling periods, and no well-defined patterns in the rankings of the treatment means were evident. There were no significant differences between the various treatments, except in the 'J-S85' period where the netless control panels had significantly fewer mortalities than were recorded on the *A.rubens* panels ($F = 4.88$, $P<0.05$).

(b) **Serpulid Recruitment and Mortality**:- (see Fig. 5.7.b.; 5.8.b.; 5.9.b.; 5.10.b.; 5.11.b.)

During the periods of low serpulid recruitment (i.e. the 'O-M85' and 'M-M85' sampling periods) there were no

significant differences in the numbers of recruits recorded on the different treatment panels. In the 'M-M85' period, recruits were observed only on the net control and *A.rubens* panels. Conversely, during the periods of greatest serpulid recruitment, the smallest numbers of recruits were recorded on the netless control panels, and in the 'M-J85' and 'J-S85' periods significantly fewer recruits occurred on these panels than in the other treatments (F = 17.23, $P<0.05$; F = 12.48, $P<0.05$, respectively). In the 'A-O84' period there were no significant differences between the net and netless controls, but significantly fewer recruits were recorded on the netless controls than on the *A.rubens* panels (F = 7.41, $P<0.05$). In the 'M-J85' and 'J-S85' sampling periods the greatest numbers of recruits were observed on the net controls, and in the 'M-J85' period these panels had significantly more recruits than were recorded for the other treatments; otherwise there were no significant differences among the treatments. Similarly, in the 'J-S85' period there were no significant differences between the net control, *A.rubens* and *N.lapillus* panels.

Considering the serpulid mortalities, the only significant difference observed was in the 'J-S85' period where there were significantly fewer mortalities on the netless control panels than were observed on the *A.rubens* panels (but note that, F = 3.35, $P>0.05$). Otherwise there were no significant differences between the

treatments, and it was difficult to discern any pattern in the ranking of the mean numbers of mortalities in the different treatments among the sampling periods.

(c) Barnacle Recruitment and Mortality:- (see Fig. 5.7.c.; 5.8.c.; 5.9.c.; 5.10.c.; 5.11.c.).

During the periods of low barnacle recruitment (i.e. the 'A-O84' and 'O-M85' sampling periods) barnacles were recorded only on the net control panels, but there were no significant differences among the treatments. Similarly, there were no significant differences among the treatments in the 'M-M85' and 'J-S85' periods, and no pattern in the ranking of the treatment means was discernible. Barnacles were not recorded on panels in all the treatments. The only significant difference was recorded in the 'M-J85' data set, where the control panels had significantly more barnacle recruits than were observed on the *N.lapillus* and *A.rubens* panels ($F = 9.98$, $P<0.05$).

Low numbers of barnacle mortalities were recorded, and none were observed in the 'A-O84' and 'O-M85' periods. In the sampling periods where mortalities were observed, they did not occur in all the treatments, and none of the differences were statistically significant. It was also difficult to determine any pattern in the ranking of the mean numbers of mortalities among the different treatments.

(d) Anomiid Recruitment and Mortality:- (see Fig. 5.8.d.; 5.9.d.; 5.10.d.; 5.11.d.)

In the'M-M85' and 'M-J85' sampling periods, where low numbers of anomiid recruits were observed, anomiids were recorded only on the *N.lapillus* panels, but the differences among all the treatments were not statistically significant. Similarly, in the 'O-M85' and 'J-S85' periods most anomiid recruits were observed on the *N.lapillus* and *A.rubens* panels, especially on the high-density panels of the former. In the 'O-M85' data set there were significantly more recruits recorded on the high-density *N.lapillus* panels than in the other treatments (F = 47.33, P<0.05 ('C & B', P<0.05)). None of the differences, in the numbers of anomiid recruits recorded, between the *N.lapillus* and *A.rubens* treatments were statistically significant in the 'J-S85' data set. Relatively few anomiid recruits were observed on the control panels during these sampling periods. In the 'O-M85' data set significantly fewer recruits were observed on the netless controls than in the other treatments, and the net control panels had significantly fewer recruits than were recorded on the *N.lapillus* panels. In the 'J-S85' data set the netless controls had significantly fewer anomiid recruits than the high-density *N.lapillus* panels (F = 3.55, P<0.05); there were no other significant differences between the net control, *N.lapillus* and *A.rubens* treatments.

Few anomiid mortalities were recorded; none were observed on panels during the periods of low anomiid recruitment, and mortalities were not recorded on panels in all the treatments during the other sampling periods. Most mortalities were observed on the *N.lapillus* panels of the 'O-M85' data set, but none of the differences between the numbers of anomiid mortalities observed in the different treatments were statistically significant. Consequently, it was difficult to discern any pattern in the ranking of the treatment means.

(e) Hydroid Recruitment and Mortality:- (see Fig. 5.7.d.; 5.8.e.; 5.9.e.; 5.10.e.; 5.11.e.)

During periods of low hydroid recruitment (i.e. the 'A-O84', 'O-M85' and 'J-S85' sampling periods) the greatest numbers of recruits were recorded on the *N.lapillus* and *A.rubens* panels. In the 'A-O84' period, hydroids were recorded only on the *A.rubens* panels and in significantly greater numbers than on the control panels ($F = 16.00$, $P<0.05$, ('C & B', $P<0.05$)). In the 'O-M85' period most hydroid recruits were observed on the *N.lapillus* and *A.rubens* panels, and the high-density *N.lapillus* treatments had significantly more recruits than the other treatments ($F = 6.13$, $P<0.05$ ('C & B', $P<0.05$)). Although the differences among the 'J-S85' period treatments were not statistically significant, most hydroid recruits were observed on the *N.lapillus* and *A.rubens* panels. In all 3 of these sampling periods no recruits occurred on the netless controls, which,

together with the net controls, were always lowest-ranked in terms of the numbers of hydroid recruits. Low numbers of recruits were also observed on the netless control panels in the periods of more abundant hydroid recruitment, and in both the 'M-M85' and 'M-J85' sampling periods the netless controls had significantly fewer recruits than the other treatments ($F = 15.41$, $P<0.05$; $F = 9.90$, $P<0.05$, respectively). In the 'M-M85' period significantly more recruits were recorded on the net control panels than in the other treatments, but there were no significant differences between the numbers of recruits on the *N.lapillus* and *A.rubens* panels. In the 'M-J85' period, however, most recruits were recorded on the *N.lapillus* and *A.rubens* panels, but there were no significant differences between these and the net control panels.

Generally, few hydroid mortalities were observed and none of the differences between the treatments were significant, and it was difficult to discern any pattern in the rankings of the mean treatment mortalities among the different sampling periods.

(f) Ctenostome Recruitment and Mortality:- (see Fig. 5.8.f.; 5.9.f.; 5.10.f.; 5.11.f.)

Relatively few ctenostome recruits were recorded in the 'M-J85' and 'J-S85' sampling periods, and none of the differences between the treatments were significant. The greatest numbers of recruits were observed on the controls; in the 'J-S85' period, ctenostome recruits

were recorded only on the net controls. During periods of more abundant ctenostome recruitment (i.e. the 'O-M85' and 'M-M85' periods) 2 consistent patterns were evident, with most recruits recorded on the *A.rubens* panels and the lowest numbers on the netless controls. In both data sets the differences between these treatments were significant ($F = 5.03$, $P<0.05$; $F = 4.35$, $P<0.05$, respectively); none of the other differences between the treatments were significant, although more ctenostomes were recorded on the low-density *N.lapillus* panels than the high-density panels.

Few ctenostome mortalities were observed, but were most frequent in the *N.lapillus* and *A.rubens* treatments. However, none of the differences in the numbers of mortalities recorded were significant.

(g) Cheilostome Recruitment and Mortality:- (see Fig. 5.7.e.; 5.8.g.; 5.9.g.; 5.10.g.; 5.11.g.)

During the months when cheilostome recruits were least abundant (i.e. the 'A-O84' and 'M-M85' sampling periods) no significant differences were evident among the treatments. However, fewer recruits occurred on the controls, and greater numbers were recorded on the *N.lapillus* and *A.rubens* panels. Similarly, in the 'O-M85' period, where more cheilostome recruits were recorded, there were no significant differences among the treatments, but more recruits were observed on the *N.lapillus* and *A.rubens* panels. A number of significant differences were evident between treatments in the

periods of most abundant cheilostome recruitment. The greatest numbers of recruits were observed on the *N.lapillus* and *A.rubens* panels, but there was a variable pattern among the rankings of the different treatment means in the different periods. In the 'M-J85' sampling period the high-density *N.lapillus* treatment had significantly more recruits than the controls, but not the other *N.lapillus* and *A.rubens* treatments ($F = 7.53$, $P<0.05$); there were no significant differences between the net controls and the *A.rubens* and low-density *N.lapillus* panels. For the 'J-S85' period, however, there were no significant differences between the net controls and any of the *N.lapillus* and *A.rubens* treatments. The lowest numbers of recruits were observed on the netless controls, and in the 'M-J85' period the numbers of recruits recorded on these panels were significantly different from all the other treatments except the net controls. Similarly, for the 'J-S85' period ($F = 7.56$, $P<0.05$), where there was also no significant difference between the numbers of recruits observed on the netless controls and the low-density *N.lapillus* panels.

Low numbers of cheilostome mortalities were observed in the 'A-O84', 'O-M85' and 'M-M85' sampling periods, and there were no significant differences between the treatments. In general, the rankings of the mean mortalities observed in the different treatments were highly variable. There were also no significant

differences between the treatments during the 'J-S85' period, when more cheilostome mortalities were observed. There were significant differences recorded between the treatments only in the 'M-J85' sampling period, where there were fewer mortalities observed on the net control panels compared to the other treatments (F = 10.81, P<0.05). There was also a significant difference between the numbers of mortalities recorded on the *A.rubens* and low-density *N.lapillus* panels.

(h) Ascidian Recruitment and Mortality:- (see Fig. 5.7.f.; 5.8.h.; 5.9.h.; 5.10.h.; 5.11.h.)

The only non-significant result for differences in the numbers of ascidian recruits among the treatments occurred in the 'M-M85' sampling period, where recruitment was only recorded on the *N.lapillus* panels. Among all the other periods significant differences were evident between the numbers of ascidians that recruited to panels in different treatments. The netless controls had the lowest numbers of ascidian recruits, and in the 'A-O84' and 'O-M85' sampling periods, significantly fewer ascidians recruited to the netless control panels than the other treatments (F = 34.06, P<0.05; F = 4.67, P<0.05, respectively). In the 'M-J85' and 'J-S85' periods the netless controls had significantly fewer recruits than were observed on the net control panels (F = 3.84, P<0.05; F = 7.12, P<0.05, respectively), but there were no significant differences between the numbers of recruits that occurred on the netless controls and the

other treatments. In the periods of low ascidian recruitment (i.e. 'A-O84' and 'O-M85') more recruits were observed on the *N.lapillus* and *A.rubens* panels compared to the net controls. In the 'O-M85' period all these treatments were statistically equivalent in terms of the numbers of ascidian recruits, and in the 'A-O84' period the *A.rubens* panels had significantly more recruits than the controls. However, where ascidian recruitment was more abundant (i.e. the 'M-J85' and 'J-S85' periods) the greatest numbers of ascidian recruits were observed on the net control panels, and during the 'J-S85' period significantly more recruits were recorded on these panels than for any of the other treatments. Conversely, in the 'M-J85' period there were no significant differences between the net controls and the *N.lapillus* and *A.rubens* panels. Within both these sampling periods, although there were no significant differences between the *N.lapillus* and *A.rubens* panels, most recruits occurred on the *A.rubens* panels and lowest numbers were recorded on the low-density *N.lapillus* panels.

Very few ascidian mortalities were observed, and none were recorded in the 'M-M85' sampling period, during which the lowest numbers of ascidian recruits occurred. No significant differences were evident among the numbers of mortalities recorded for each treatment in the 'A-O84', 'O-M85' and 'M-J85' sampling periods; and there were no distinct patterns among the rankings of the treatment means, other than that no mortalities were

observed on the netless control panels. In the 'J-S85' period significantly fewer ascidian mortalities were observed on the netless controls compared to the other treatments (F = 4.56, P<0.05); otherwise there were no significant differences between the treatments.

(i) Summary of the Results:-

The predatory activities of *N.lapillus* and *A.rubens*, whose principal prey items either occurred in relatively low numbers, or not at all, on the experimental substrata, appeared to have negligible deleterious effects on the developing epifaunal assemblages. This suggested, therefore, that the movement of a shell across the substratum and/or the effects of mucus, were not, apparently, deleterious to the settled larvae. For all the taxonomic groups examined, and in all the sampling periods, in the majority of instances there were no significant differences between the numbers of recruits observed in the net control, *N.lapillus* and *A.rubens* treatments. Furthermore, significantly more recruits were frequently observed on these panels than on the netless controls which were accessible by all grazers and predators. Contrary to a deleterious effect, the results suggested that the presence of *N.lapillus* and *A.rubens* may have enhanced recruitment onto the panels by some taxonomic groups (e.g. anomiids), because more recruits were observed on these panels than on the net controls.

FIGURE 5.12. Results for the *G.cineraria* introduction experiment immersed between October 1985 and February 1986. The graphs illustrate the mean (+1 standard error) number of recruits (= unshaded) and mortalities (= shaded) recorded in the different treatments. On the right of the diagram are the results of the statistical analyses. The results for the 'S-N-K' tests are represented diagrammatically, the treatment means are ranked in order of increasing size from left to right; means underscored by the same line are asserted to be homogeneous and means not underscored by the same line are heterogeneous.

Key: NC = Net Control; NL = Netless Control; 1N = One *N.lapillus*.panel^{-1}; 1NI = One *N.lapillus*.panel^{-1} introduced after 2 months; 1G = One *G.cineraria*.panel^{-1}; 1GI = One *G.cineraria*.panel^{-1} introduced after 2 months; 3G = Three *G.cineraria*.panel^{-1}; 3GI = Three *G.cineraria*.panel^{-1} introduced after 2 months; 5G = Five *G.cineraria*.panel^{-1}; 5GI = Five *G.cineraria*.panel^{-1} introduced after 2 months.

F = the analysis of variance; C = Cochran's test for the homogeneity of the variances; (i) = the result from Bartlett's test for the homogeneity of the variances differs in significance from that of Cochran's test.
* = $P<0.05$; ns = Not Significant.

Recruitment (= R) and mortality (= M) results for:

(a) Total numbers;
(b) Serpulids;
(c) Anomiids;
(d) Hydroids;
(e) Ctenostome bryozoans;
(f) Cheilostome bryozoans;
(g) Ascidians.

Note: the results for the 1G, 3G and 5G treatments are derived from 2 of the replicates, 1 of the *G.cineraria* was dead on the third replicate in each treatment.

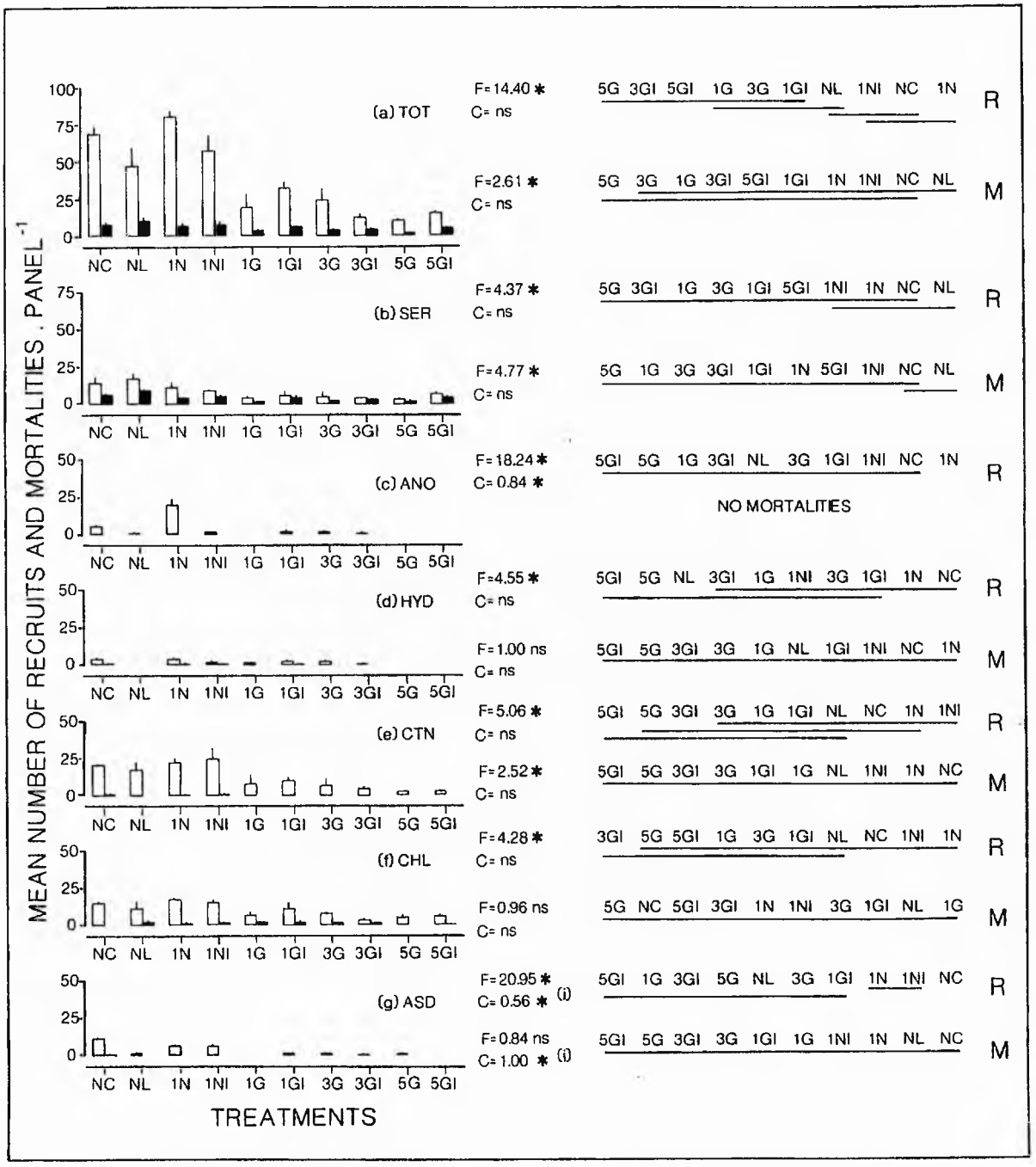
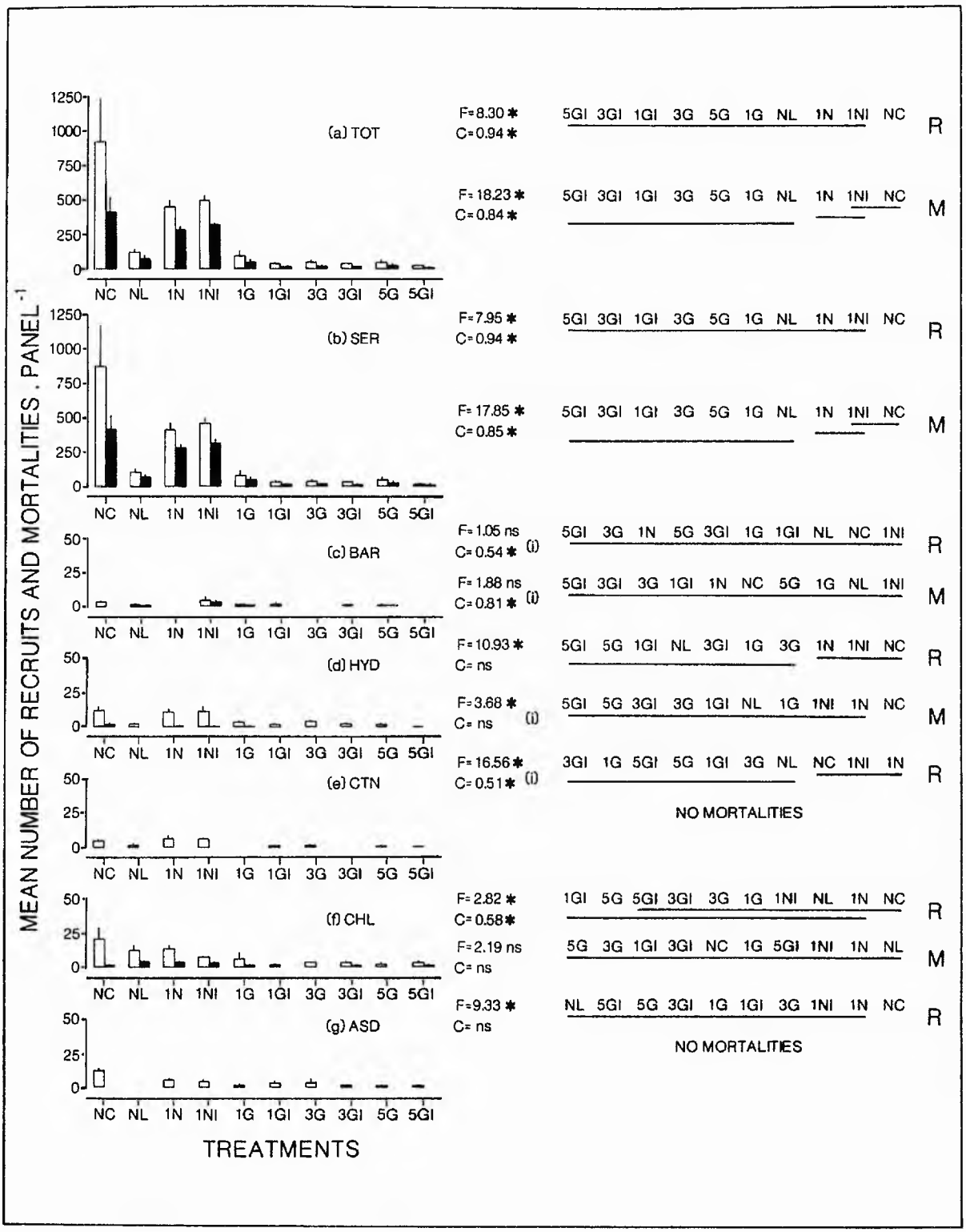

MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL^{-1}
(a) TOT
(b) SER
(c) ANO
(d) HYD
(e) CTN
(f) CHL
(g) ASD
NC NL 1N 1NI 1G 1GI 3G 3GI 5G 5GI
TREATMENTS
F=14.40 * C= ns
5G 3GI 5GI 1G 3G 1GI NL 1NI NC 1N R
F=2.61 * C= ns
5G 3G 1G 3GI 5GI 1GI 1N 1NI NC NL M
F=4.37 * C= ns
5G 3GI 1G 3G 1GI 5GI 1NI 1N NC NL R
F=4.77 * C= ns
5G 1G 3G 3GI 1GI 1N 5GI 1NI NC NL M
F=18.24 * C= 0.84 *
5GI 5G 1G 3GI NL 3G 1GI 1NI NC 1N R
NO MORTALITIES
F=4.55 * C= ns
5GI 5G NL 3GI 1G 1NI 3G 1GI 1N NC R
F=1.00 ns C= ns
5GI 5G 3GI 3G 1G NL 1GI 1NI NC 1N M
F=5.06 * C= ns
5GI 5G 3GI 3G 1G 1GI NL NC 1N 1NI R
F=2.52 * C= ns
5GI 5G 3GI 3G 1GI 1G NL 1NI 1N NC M
F=4.28 * C= ns
3GI 5G 5GI 1G 3G 1GI NL NC 1NI 1N R
F=0.96 ns C= ns
5G NC 5GI 3GI 1N 1NI 3G 1GI NL 1G M
F=20.95 * C= 0.56 * (i)
5GI 1G 3GI 5G NL 3G 1GI 1N 1NI NC R
F=0.84 ns C= 1.00 * (i)
5GI 5G 3GI 3G 1GI 1G 1NI 1N NL NC M

FIGURE 5.13. Results for the *G.cineraria* introduction experiment immersed between February and June 1986. See Figure 5.12. for further details.

Recruitment (= R) and mortality (= M) results for:

(a) Total numbers;
(b) Serpulids;
(c) Barnacles;
(d) Hydroids;
(e) Ctenostome bryozoans;
(f) Cheilostome bryozoans;
(g) Ascidians.

Note: the results for the 3G treatment are derived from only 2 of the replicates, 1 of the *G.cineraria* on the third replicate was dead.


MEAN NUMBER OF RECRUITS AND MORTALITIES . PANEL -1
(a) TOT
(b) SER
(c) BAR
(d) HYD
(e) CTN
(f) CHL
(g) ASD
NC NL 1N 1NI 1G 1GI 3G 3GI 5G 5GI
TREATMENTS
F=8.30 * C=0.94 * 5GI 3GI 1GI 3G 5G 1G NL 1N 1NI NC R
F=18.23 * C=0.84 * 5GI 3GI 1GI 3G 5G 1G NL 1N 1NI NC M
F=7.95 * C=0.94 * 5GI 3GI 1GI 3G 5G 1G NL 1N 1NI NC R
F=17.85 * C=0.85 * 5GI 3GI 1GI 3G 5G 1G NL 1N 1NI NC M
F=1.05 ns C=0.54 * (i) 5GI 3G 1N 5G 3GI 1G 1GI NL NC 1NI R
F=1.88 ns C=0.81 * (i) 5GI 3GI 3G 1GI 1N NC 5G 1G NL 1NI M
F=10.93 * C=ns 5GI 5G 1GI NL 3GI 1G 3G 1N 1NI NC R
F=3.68 * C=ns (i) 5GI 5G 3GI 3G 1GI NL 1G 1NI 1N NC M
F=16.56 * C=0.51 * (i) 3GI 1G 5GI 5G 1GI 3G NL NC 1NI 1N R
NO MORTALITIES
F=2.82 * C=0.58 * 1GI 5G 5GI 3GI 3G 1G 1NI NL 1N NC R
F=2.19 ns C=ns 5G 3G 1GI 3GI NC 1G 5GI 1NI 1N NL M
F=9.33 * C=ns NL 5GI 5G 3GI 1G 1GI 3G 1NI 1N NC R
NO MORTALITIES

Mortalities among the different treatments were less predictable, varying within and among the taxonomic groups and the different sampling periods.

5.2.3. The Effect of Initial Grazer Exclusion on Assemblage Development:- (see Figures 5.12. and 5.13.)

(a) Total Recruitment and Mortality:- (see Fig. 5.12.a.; 5.13.a.)

A greater number of recruits were recorded during the 'F-J86' immersion period compared to the 'O-F86' period. In both sampling periods there were no significant differences between the total numbers of recruits recorded on any of the *G.cineraria* panels - either those which were grazed throughout or panels with *G.cineraria* introduced after 2 months. Furthermore, in general, fewer recruits were recorded on the high-density *G.cineraria* panels and on panels with *G.cineraria* introduced after a 'grazer-free' period, than on the low-density grazer panels. The netless controls were not significantly different from the grazed panels in terms of the total numbers of recruits, in the 'F-J86' period. Furthermore, these controls were significantly different only from the high-density *G.cineraria* panels in the 'O-F86' period (F = 14.40, $P<0.05$). Generally, more recruits were recorded on the *N.lapillus* and net control panels than on the *G.cineraria* panels, and most of the significant differences that arose in the analyses were between the controls and the *N.lapillus* panels, and

between these treatments and the *G.cineraria* panels. The only significant difference between the treatments in the 'F-J86' period was that a greater number of recruits were observed on the net controls, compared to all the other treatments (F = 8.30, P<0.05 ('C & B', P<0.05)). For the 'O-F86' period there were no significant differences among the *N.lapillus* and net control panels, but these had significantly more recruits than were recorded on the *G.cineraria* panels.

Very few mortalities were observed among the treatments in the 'O-F86' period, the only significant difference was between the netless controls and the high-density, constantly grazed panels (F = 2.61, P<0.05). The overall pattern was, however, for more mortalities to be recorded on the controls and the *N.lapillus* panels, with fewer observed on constantly grazed *G.cineraria* panels. During the 'F-J86' period more mortalities were observed; as in the 'O-F86' period relatively low numbers of mortalities were recorded on the *G.cineraria* and netless control panels, and there were no significant differences between these treatments. However, significantly fewer mortalities were recorded on the grazed and netless control panels than occurred on the *N.lapillus* and net control panels (F = 18.23, P<0.05 ('C & B', P<0.05)). Among these, the net controls had significantly more mortalities than the treatment with *N.lapillus* present throughout the study period.

(b) Serpulid Recruitment and Mortality:- (see Fig. 5.12.b.; 5.13.b.)

The lowest numbers of serpulid recruits were recorded on the *G.cineraria* panels, and in the 'F-J86' period fewer recruits were recorded on the introduced grazer panels than on the constantly grazed panels. In both sampling periods more serpulid recruits were observed on the *N.lapillus* and control panels. However, in the 'O-F86' period the numbers of recruits recorded on the *N.lapillus* and net control panels were not significantly different from the numbers on the *G.cineraria* treatments, but the netless controls had significantly more recruits than the *G.cineraria* panels ($F = 4.37$, $P<0.05$). There were no significant differences between the controls and the *N.lapillus* panels. In the 'F-J86' period the net controls had significantly more serpulid recruits than all the other treatments ($F = 7.95$, $P<0.05$ ('C & B', $P<0.05$)).

Considering the numbers of serpulid mortalities, in both sampling periods the *G.cineraria* panels generally had fewer mortalities than were observed on the controls and *N.lapillus* panels. In the 'O-F86' period significantly more mortalities were observed on the netless controls than in all the other treatments except the net controls ($F = 4.77$, $P<0.05$); there were no significant differences between the 2 controls or between the *G.cineraria* and *N.lapillus* panels. In the 'F-J86' period all the *G.cineraria* and netless control panels,

among which there were no significant differences, had significantly fewer mortalities than the other treatments (F = 17.85, $P<0.05$ ('C & B' $P<0.05$)). Among the net control and the *N.lapillus* panels the only significant difference was between the net control and the treatment with *N.lapillus* constantly present.

(c) Barnacle Recruitment and Mortality:- (see Fig. 5.13.c.)

Barnacles occurred only during the 'F-J86' sampling period and in relatively low numbers. Most recruits were observed on the *N.lapillus* and control panels, although none were recorded in the treatment where *N.lapillus* was constantly present. Fewer recruits were observed on the *G.cineraria* panels, and on a number of these no recruits were recorded. None of the differences between the treatments were statistically significant.

Barnacle mortalities were observed in only a few treatments, and none of the differences were significant. The greatest numbers of barnacle recruits were observed on the net controls and the introduced *N.lapillus* panels, both of which were excluded from the activities of grazers and *N.lapillus* for the duration of the study or the initial 2 months of immersion, respectively. Furthermore, the greatest numbers of barnacle mortalities were recorded on the introduced *N.lapillus* panels, possibly indicating that the barnacles achieved an adequate size during the 2 month 'predation-free'

period to become suitable prey for the introduced *N.lapillus*.

(d) Anomiid Recruitment and Mortality :- (see Fig. 5.12.c.)

Anomiids only recruited to the panels during the 'O-F86' sampling period and recruits were not recorded in all the treatments, in particular no anomiids were observed on a number of the *G.cineraria* panels. There were significantly more anomiid recruits on the panels with *N.lapillus* constantly present compared to the other treatments, among which there were no further significant differences (F = 18.24, $P<0.05$ ('C & B', $P<0.05$)).

There were no anomiid mortalities.

(e) Hydroid Recruitment and Mortality:- (see Fig. 5.12.d.; 5.13.d.)

Hydroids recruited to the panels during both study periods, but in relatively low numbers in the 'O-F86' period. However, the general pattern among the treatments was similar in both cases; most recruits occurred on the controls and *N.lapillus* panels and fewer on the *G.cineraria* panels, among which more recruits occurred on the low-density grazer panels than the high-density grazer panels. In the 'O-F86' period no recruits were observed on the netless controls or the most heavily grazed panels, which were significantly different from the highest-ranked treatments, i.e. the net control

panels and those with *N.lapillus* present throughout (F = 4.55, $P<0.05$). Otherwise there were no significant differences among the treatments. The results were better defined in the 'F-J86' period, during which more hydroid recruits were observed. The low-ranked *G.cineraria* and netless control panels had significantly fewer recruits than were observed on the net control and *N.lapillus* panels (F = 10.93, $P<0.05$); there were no further significant differences among the treatments in these 2 groups.

Very few hydroid mortalities were recorded, in particular on the *G.cineraria* and netless control panels; most were observed on the net controls and *N.lapillus* panels. However, in the 'O-F86' sampling period none of the differences between the treatments were significant; and during the 'F-J86' period the only significant difference was between the net controls and the other treatments, with significantly more mortalities observed on the former (F = 3.68, $P<0.05$).

(f) Ctenostome Recruitment and Mortality:- (see Fig. 5.12.e.; 5.13.e.)

Ctenostomes recruited in greater numbers during the 'O-F86' study period; fewer recruits were observed in the 'F-J86' period, and recruits were entirely absent from a number of the *G.cineraria* panels. In general, fewer recruits were recorded on the more heavily grazed *G.cineraria* panels, and more on the less intensely grazed

panels; the greatest numbers of recruits were recorded on the controls and the *N.lapillus* panels. There were a number of significant differences between these treatments. In the 'O-F86' period the *N.lapillus* and net control treatments had significantly more ctenostome recruits than the high-density *G.cineraria* panels (F = 5.06, $P<0.05$), but were not significantly different from the low-density *G.cineraria* panels. In the 'F-J86' period the results were better defined; all the *G.cineraria* and netless control panels had significantly fewer recruits than were recorded on the net controls and the *N.lapillus* panels (F = 16.56, $P<0.05$). In both sampling periods there were no significant differences between the numbers of ctenostome recruits observed on the *G.cineraria* and netless control panels, or between the *N.lapillus* and net control panels.

Ctenostome mortalities were recorded in the 'O-F86' sampling period only, and were restricted to the ungrazed *N.lapillus* and net control panels. However, there were no significant differences among any of the treatments, on the basis of the 'S-N-K' test (but note that, F = 2.52, $P<0.05$).

(g) <u>Cheilostome Recruitment and Mortality</u>:- (see Fig. 5.12.f.; 5.13.f.)

Cheilostomes recruited in similar numbers during the 2 study periods and the overall pattern of ranking among the treatment means was similar. The greatest

numbers of cheilostome recruits were recorded on the controls and the *N.lapillus* panels, with fewer recruits recorded on the *G.cineraria* panels. A number of significant differences existed between the numbers of cheilostome recruits recorded in the different treatments. In the 'O-F86' period the lowest-ranked *G.cineraria* introduction treatment had significantly fewer recruits than were recorded on the *N.lapillus* and net control panels ($F = 4.28$, $P<0.05$). In the 'F-J86' period similar significant differences existed between the low-ranked *G.cineraria* panels and the net controls ($F = 2.82$, $P<0.05$ ('C & B', $P<0.05$)). No other differences between the treatments, in either sampling period, were significant.

Very few cheilostome mortalities were observed and none of the differences between the treatments were significant. There was no readily discernible pattern in the ranking of the mean mortalities for each sampling period.

(h) Ascidian Recruitment and Mortality:- (see Fig. 5.12.g.; 5.13.g.)

Similar numbers of ascidians recruited to the panels in both periods, and, in both, the greatest numbers of recruits were observed on the net controls and *N.lapillus* panels, and fewer recruits were recorded on the netless controls and the *G.cineraria* panels. Significant differences existed between the numbers of recruits

recorded in the different treatments; in both periods there were significantly more recruits recorded on the net control panels than in any of the other treatments ('O-F86': $F = 20.95$, $P<0.05$; 'F-J86': $F = 9.33$, $P<0.05$). In the 'F-J86' period there were no further significant differences among the *G.cineraria* panels, the *N.lapillus* panels and the netless controls. However, in the 'O-F86' period the *G.cineraria* and netless treatments (among which there were no significant differences) had significantly fewer ascidian recruits than were observed on the *N.lapillus* panels. These latter were statistically equivalent in terms of the numbers of ascidian recruits observed.

The only ascidian mortalities recorded were on the net control panels in the 'O-F86' sampling period, but there were no significant differences between the treatments.

(i) Summary of the Results:-

The results indicated that none of the taxonomic groups examined were able to achieve an 'escape-in-size' during the 2 months exclusion from the influence of *G.cineraria* grazing activities on the experimental substrata. There were no significant differences between the *G.cineraria* panels, either those that were constantly grazed or those with *G.cineraria* introduced after a period of 2 months. If the epifaunal species had been able to achieve a sufficient size to make them less

susceptible to the non-predatory grazing activities of *G.cineraria* then, at the end of the experimental period, a greater number of recruits would predictably have occurred on the panels from which the grazers were initially excluded, than on the constantly grazed panels. The other conclusions from this part of the study were essentially the same as those drawn from the first part, *viz.* that *G.cineraria* grazing activity had a markedly deleterious effect on the developing assemblages, and this effect may have been dependent on the intensity of the grazing activity (i.e. the density of *G.cineraria* per panel). The predatory activities of *N.lapillus* appeared to have had no, or limited, influence on the developing assemblages; similar numbers of recruits as recorded on the net controls were frequently observed in the presence of *N.lapillus*.

5.3. DISCUSSION

It is well established that herbivorous grazing is a major determinant of both algal distributions and the overall algal community structure in marine environments (Hawkins and Hartnoll, 1983). Hawkins and Hartnoll (1983) suggested that molluscan grazers were of particular significance in the intertidal, where they feed primarily on algal films and sporelings. There are numerous examples of the importance of herbivorous molluscs in structuring algal communities, for example, Bertness *et al.* (1983), Bertness (1984), Jara and Moreno (1984), Fletcher (1987), Petraitis (1987) and Van Tamelen (1987). There is also substantial evidence that the grazing activities of herbivorous molluscs may have numerous indirect effects on the epifauna. Bertness *et al.* (1983), for example, suggested that by influencing the cover of algal crusts (e.g. *Ralfsia verrucosa* and *Hildenbrandia rubra*), which inhibited the settlement of *Balanus balanoides*, *Littorina littorea* foraging may have indirectly influenced barnacle settlement by providing crust-free space. Similarly, the herbivorous limpets *Fissurella virescens*, *F.longifissa*, *Siphonaria maura* and *S.palmata*, by eliminating foliose algae, enhanced the recruitment of *Balanus inexpectatus*, which virtually never recruited to algal turfs; conversely, grazing of the foliose algae inhibited recruitment of *Chama echinata* which recruited best to algal turfs (Menge *et al.*, 1986). Van Tamelen (1987) similarly concluded that the herbivorous limpets (*Collisella pelta*, *C.scabra* and

C.digitalis) and the chitons (*Mopalia* spp. and *Nuttallina californica*) facilitated the recruitment of barnacles, primarily *Chthamalus* spp., by controlling the micro- and macroalgal abundances, both of which inhibited the recruitment of barnacles by interfering with their settlement.

Herbivorous grazers may have significant impacts on diatom abundances and are capable of causing major reductions in the resource base (Castenholz, 1961; Nicotri, 1977). Although Castenholz (1961) concluded that the diatoms in ungrazed and grazed areas were similar and that no selective grazing by *Littorina scutulata* was occurring; Nicotri (1977), in a study of the grazing effects of 4 species of intertidal gastropods, provided evidence that 3 diatom species were strongly selected for, i.e. they were conspicuously reduced or were totally absent from the grazed areas. Nicotri (1977) suggested that this "selectivity" was a passive type of selection, arising primarily from differences in the diatom morphology and accessibility, rather than the grazers actively choosing the diatom species. However, this "preference" had drastic effects on the microalgal community structure, in that the dominant "canopy" species of the diatom mat were removed. Nicotri (1977) considered that this resulted in a considerable alteration of the microclimate, which might influence the settlement and growth of algal sporelings. Similar effects may be applicable to the establishment of epifaunal assemblages (see Chapter 3 for a discussion of

the importance of microbial and microalgal films in larval settlement).

Bertness *et al.* (1983), Bertness (1984), and Petraitis (1987) have all suggested that the grazing of *L.littorea* on sheltered shores may have a further effect on the epifaunal organisms, in that the foraging activities of the snails prevented sediment accumulation. In *L.littorea* removal treatments sediment accumulated and inhibited barnacle settlement, or smothered any barnacles that did settle.

A number of studies have also reported incidental effects of grazer activity, similar to those observed here, on the distribution and abundances of epifaunal organisms. Dayton (1971) found that limpet (*Acmaea* spp.) grazing was an important factor in reducing the settlement and establishment of barnacles, principally *Balanus glandula* and *B.cariosus*, and to a lesser extent *Chthamalus dalli*. The mechanisms by which limpets interfered with barnacle recruitment involved eating, pushing and dislodging (the "bulldozing" effect) of the cyprids or newly metamorphosed barnacles from the substratum. Underwood and his co-workers (see Underwood, 1985) found a similar effect of the grazing activities of the limpet *Cellana tramoserica* on the settlement and subsequent survival of the barnacle *Tesseropora rosea*. At natural densities the limpets had deleterious effects due to their crushing and bulldozing the spat, however, at low-densities, limpets had a

positive effect on the settlement of barnacles because they removed algal species that would otherwise pre-empt the space, and thus make it unavailable for settlement. Underwood (1985) concluded that the effects of limpets on settlement and survival of barnacles would be variable (spatially and temporally), depending on the rates of recruitment and growth of competitors for space. Similarly, Menge *et al.* (1986) concluded that the recruitment of *B.inexpectatus* was inhibited by the grazing activities of the limpets *F.virescens*, *F.longifissa*, *S.maura* and *S.palmata*.

Petraitis (1987) found that *L.littorea* inadvertently ingested *Semibalanus balanoides*, and furthermore, suggested that by reducing the densities of barnacles *L.littorea* indirectly depressed the establishment of *Mytilus edulis*. Bertness (1984) found that *L.littorea* grazing hindered the settlement of the bryozoans *Schizoporella errata*, *Cryptosula pallasiana* and *Conopeum reticulum*, because snail removal had a significant positive effect on the recruitment of these encrusting bryozoans. Bryozoans were recorded on 50-60% of the snail removal rocks sampled, compared to 5-10% of the control rocks - however, most of the bryozoans that successfully settled were adversely affected by the sediment that accumulated in the absence of *L.littorea* grazing activities.

Ayling (1981) suggested that the herbivorous gastropods *Cellana stellifera*, *Cantharidus purpureus*,

Trochus viridis, *Cookia sulcata* and *Micrelenchus sanguineus* may influence the encrusting animals by removing newly settled larvae, although this effect was not properly documented. Young and Chia (1984) found that juveniles of the ascidians *Corella inflata*, *Boltenia villosa* and probably also *Styela gibbsii* showed significantly higher survival in the absence of the grazing gastropod *Margarites pupillus*. They concluded that *M.pupillus* killed juvenile ascidians, either by rasping them off with the radula, or by dragging the shell across them. However, the former was probably more common because the juveniles were apparently unharmed by the mucus trails left by the snails as they passed over, the ascidians opened their siphons and resumed normal pumping behaviour within a few minutes (Young and Chia, 1984). Conversely, Stocker and Bergquist (1987) examined the influence of grazing by the gastropod *C.sulcata* and the sea-urchin *Evechinus chloroticus* on the recruitment of the subtidal colonial ascidian *Pseudodistoma novaezelandiae* and concluded that the grazers had no significant effect.

There is, therefore, considerable evidence in the literature that the grazing activities of a number of herbivorous molluscs may have indirect and direct, incidental effects on the settlement or recruitment and survival of epifaunal organisms. The results from this study suggested that the grazing activities of *G.cineraria* may have had similar effects on the

assemblages of epifaunal organisms developing on the artificial substrata. Although the significance levels have to be interpreted cautiously where the assumption of homogeneity of the variances was violated, and for a number of taxonomic groups the results were confounded by small data sets, in general, fewer recruits were recorded, at the end of each period of immersion, on the *G.cineraria* grazed panels than on the controls. For the majority of the taxonomic groups, in all the seasons, the greatest numbers of recruits were observed on the net control (i.e. the grazer exclusion) panels, and in all the statistical analyses where significant differences were evident, these were between the net controls and the *G.cineraria* grazed panels. Although none of the differences between the *G.cineraria* grazed panels were statistically significant, the results further suggested that more recruits were observed on the low-density grazed panels compared to the high-density grazed panels.

No attempt was made in this study to examine the effects of nets, either on larval settlement or the activities of the *G.cineraria*, *N.lapillus* or *A.rubens*. Instead, it was accepted that artefacts probably were present, and any differences in the abundance of larval recruits between panels enclosed in nets or between those enclosed and not enclosed, were considered to be attributable to the grazing or predatory activities of varying densities of the enclosed organisms (see Keough, 1984b). There was, however, evidence in the results that

enclosing the *G.cineraria* on panels within nets may have affected their foraging behaviour, because in many instances in the present study, greater numbers of recruits were recorded on the netless control panels than on the *G.cineraria* grazed panels, which may be indicative of more intense grazing by the experimental densities of *G.cineraria*, than would be experienced under natural grazer densities. Similar results have been obtained in other studies, Connell (1961b), for example, suggested that such restriction may result in more intense limpet grazing inside cages than on the open shore, and Nicotri (1977) found that grazed areas within cages usually contained less microalgae than similar uncaged areas, which he attributed to an increase in the available foraging time for the caged limpets, due to increased moisture retention by the cages. Keough and Butler (1979) suggested that caging predators artificially increased their densities and was thus likely to lead to an overestimation of the effects of the predators on the community.

A comparison of the numbers of recruits recorded on panels from which grazers were totally excluded for 2 months, and then exposed to *G.cineraria* grazing activities for 2 months, with panels that were grazed throughout the 4 month period, suggested that the grazing activities of *G.cineraria* led to the removal of the established epifauna. If this were not the case, it would be predicted that, at the end of the 4 month immersion period, more recruits would have been

consistently recorded on the introduced grazer panels than on the constantly grazed panels, due to the fact that those organisms that settled on the panels during the grazer-free period should have remained if unaffected by grazer activity. However, although the results of the statistical analyses were less well-defined, there were no significant differences among the numbers of recruits observed on the constantly grazed and introduced grazer panels - often fewer recruits were observed in the latter treatment. Thus, a temporary 'refuge' from grazer activity, possibly enabling, for example, a greater size to be attained, did not appear to have decreased the effects of the grazing *G.cineraria* on the epifaunal assemblages. These results indicated that it was the grazing activities *per se* of the *G.cineraria* that were directly influencing the epifaunal organisms, rather than the herbivores affecting larval settlement by, for example, altering the surface microclimate through their grazing activities (cf. Nicotri, 1977). If the latter were occurring, those organisms which settled prior to grazer introduction, which presumably leads to a decline in the conditions favourable to settlement (as indicated by the low numbers of recruits recorded on the grazed panels) would have remained at the end of the immersion period. There would have been at least some evidence of their settlement, even if they had died on the introduction of the grazers, because of a deterioration in the conditions favourable to their survival. *G.cineraria*, thus, appeared to be an essentially non-

selective grazer in terms of its effect on the epifauna, effectively treating the panels as homogeneous surfaces, with a corresponding adverse influence on the post-settlement survival of the epifauna.

The present study considered only the effects of *G.cineraria* grazing on panels from which grazers were excluded for 2 months and then introduced for 2 months. It may be that if the recently settled epifauna were 'protected' from herbivorous grazers for longer periods and/or the panels were immersed during the periods of greatest growth then some individuals or colonies may have been able to achieve an 'escape-in-size'. No data are available on the sizes of the organisms present on the initially 'protected' panels immediately prior to grazer introduction. However, data on colony sizes obtained from the first part of the study, where panels were terminated after 2 months immersion, are available and suggested that over the periods examined colonies would have attained only relatively small sizes. For example, on the net control panels immersed between February and April 1985 (i.e. approximately the same period of grazer exclusion as in the 'F-J86' experiment) the largest *Alcyonidium* spp. colonies observed were only 1(+3) zooids in size and only *E.pilosa* ancestrulae were recorded. There are no similar data available for the first 2 months of the 'O-F86' experiment because panels immersed the previous October were not examined until 4 months had elapsed because severe weather conditions

prevented access to the frames after 2 months immersion. Conversely, on panels initiated between April and August 1985 relatively large colony sizes were recorded on the net control panels after 2 months immersion. For example, *Alcyonidium* spp. colonies varied in size between 1 and 75(+56) zooids, *E.pilosa* colonies between A and >A+42(18) zooids, *S.unicornis* colonies between A and A+23(5) zooids, and colonies of *B.leachii* and *T.tenerum* of up to 26 and 11 zooids, respectively, were observed. Thus, before definitive conclusions can be drawn as to whether or not epifaunal species can attain an 'escape-in-size' from the effects of herbivorous grazer activity, it would be necessary to examine the influence of *G.cineraria* on larger-sized individuals and colonies.

Breitburg (1985) found that both the numbers of individuals or colonies, and the area covered by the abundant sessile invertebrates, were significantly reduced by grazing, on plates protected by cages for 21 weeks prior to exposure to large grazers. After 14 weeks exposure to grazer activity, *Tubulipora* spp. and encrusting bryozoans were almost entirely absent from the plates, compared to a mean number of 58 *Tubulipora* spp. colonies, 24 *Rhynchozoon rostratum*, 11 *Cauloramphus spinifera* and 9 *Microporella* spp. colonies per plate at 21 weeks, just prior to exposing the experimental plates to grazers. The percent substratum cover of *Tubulipora* spp. and encrusting bryozoans declined from 3.7% and 3.4% respectively, to 0.2% over the same period. Breitburg (1985) thus concluded that grazers were able to remove

established invertebrate individuals and colonies. Contrary to these results, Dayton (1971) found that although limpet activity reduced barnacle recruitment, some barnacles did metamorphose and escape the limpet disturbance. He concluded that within 10-20 days after metamorphosis, the barnacles were sufficiently large that they were not killed by the limpets.

N.lapillus and *A.rubens* did not appear to have similarly deleterious effects on the epifaunal assemblages, as did the grazing activities of *G.cineraria*. Patterns in the results were less well-defined and there was more variability within and among the different taxonomic groups and seasons. In many instances, however, the lowest numbers of recruits were observed on the netless controls, and often this difference was statistically significant. There were comparatively few significant differences among the *N.lapillus* and *A.rubens* treatments, or between these and the net controls, suggesting that similar numbers of recruits were recorded both in the presence or absence of *N.lapillus* and *A.rubens*. This lack of significant effect on the assemblages is not unexpected, considering the relative paucity of the major dietary components of the essentially carnivorous *N.lapillus* and *A.rubens* (see Largen (1967) and Jangoux (1982), respectively). However, Largen (1967) cited evidence that young *N.lapillus* may feed on *Spirorbis* spp.; similarly, Hawkins and Hartnoll (1983) noted that juvenile asteroids were

capable of extruding their stomachs over the substratum, thereby feeding on the film of detritus, microalgae and microfauna. A number of other studies have recorded incidences of *A.rubens* feeding on species characteristic of epifaunal assemblages. Nair (1962), for example, observed *A.rubens* feeding on *Pomatoceros triqueter*; Gulliksen and Skjaeveland (1973) recorded heavy predation by *A.rubens* on the ascidian *Ciona intestinalis*; Briggs (1980) recorded *P.triqueter* and unidentified "substrate" as the main prey species of *A.rubens*; and Jangoux (1982) included *Spirorbis* spp. and *Serpula vermicularis* as potential food items of *A.rubens*. However, there did not appear to be any evidence of similar predation on any of the major taxonomic groups of epifaunal organisms examined in this study. Keough and Butler (1979) found similar results in an examination of the predatory roles of 4 asteroid species in the organization of a sessile community. Although the asteroids preyed upon potential competitors for space (e.g. ascidians, bryozoans and sponges) the results suggested that none of the predators greatly influenced the composition of the sessile fauna. They estimated that predation by asteroids accounted for only 9% of the changes in individual patches of sessile species, and they attributed most of the changes to seasonal increases and decreases.

Herbivorous gastropods may thus have a potentially significant effect on the development of epifaunal assemblages. Although the experimental methodology and

densities of *G.cineraria* utilized, may have overestimated the effect, the low numbers of recruits recorded on unprotected panels and the abundance of *G.cineraria*, both on the experimental substrata and on the undersides of boulders on the shore, suggest that *G.cineraria* may play a significant role in structuring natural epifaunal assemblages. (Note, however, that the experiments did not distinguish the potential effects of other grazers which may have had access to panels and rock undersides, but were not observed during the study).

6. THE INTERACTION OF ECOLOGICAL PROCESSES

Three important ecological processes (larval recruitment, competition and herbivorous grazing) operating in marine epifaunal assemblages have been examined. Although these studies have indicated the importance of these processes in the assemblages, the processes did not act independently of each other, and their interactions may have had important influences on the assemblages concerned. Buss (1986), for example, has suggested that spatial and temporal variability in larval settlement, along with variations in the relative distributions of settled colonies on substrata, may result in asymmetrical competitive encounters, i.e. at different sizes, encounter angles, etc.. Since intra- and interspecific competitive ability is known to vary as a function of such encounter asymmetries, Buss (1986) suggested that competitive ability may be adapted to exploit particular classes of settlement-induced encounter asymmetries. Competitive intransitivity, thus, may ultimately reflect adaptations of organisms to variations in the timing and location of settlement, such that the various proximate patterns in competitive rankings result from the interaction of particular settlement patterns with post-settlement processes (Buss, 1986). Similarly, the activities of grazing herbivores may determine which species will interact and/or may influence the competitive abilities of competing species. Menge *et al.* (1986) concluded that the determination of the relative importance and impact of each process is

impossible, unless all the factors are studied in the same experiment.

A number of studies have, for example, investigated the manner in which competition and predation may interact to produce patterns of distribution and abundance of organisms. Predation is generally, considered to be directly related to the prevention of resource monopolization. Buss (1986) has suggested that predation appears to interact with competition in 2 different ways to produce patterns in community organization:- (i) predation reduces or precludes the occurrence of competition by reducing densities of prey species to levels at which competition fails to arise, i.e. predation and competition are mutually exclusive processes; e.g. Paine (1974) and Lubchenco (1978); (ii) predation acts to maintain the occurrence of competition, principally in systems with intransitive competitive rankings; e.g. Paine (1984). Physical disturbance may interact with competition in a similar manner as predation, maintaining non-equilibrium conditions under which competition is reduced and exclusion unlikely (Branch, 1984). A wide range of largely unpredictable events can achieve this; e.g. battering by logs (Dayton, 1971), and the overturning of boulders (Osman, 1977; Sousa, 1979, 1980; and Davis and Wilce, 1987).

A number of models have been proposed based on the premise that interactions between these ecological processes are of primary importance in assemblages.

Connell (1975), for example, suggested that many species seldom reached population densities great enough to compete for resources, because either physical extremes or predation eliminated or suppressed them in their young stages. In intermediate conditions, or where the species attained a large-size, the species may reach high population densities and compete for resources. Menge and Sutherland (1976) considered that the relative importance of competition and predation depended on the trophic level considered and the overall trophic complexity in a community. They hypothesized that competition is relatively more important in maintaining high diversity at higher trophic levels, because of the absence of other controlling factors, and also in communities with fewer trophic levels. Conversely, predation was considered to be important as an organizing factor at lower trophic levels, and in trophically complex communities. The "intermediate disturbance hypothesis" (Connell, 1978, 1979) predicts that moderate levels of disturbance to communities reduces competition and prevents resource monopolization by the competitive dominant, and thus allows species coexistence. At the extremes, however, low disturbance allows monopolization and therefore reduces diversity; conversely, high continuous disturbance generates extinctions and thus also reduces diversity.

Most of these models of mechanisms determining the characteristics of marine assemblages implicitly assume that the important interactions are those that occur

among the adult organisms (i.e. the post-settlement processes). Settlement, and subsequent early survival of juveniles, are assumed to be nearly uniform spatially and temporally; and any stochasticity that does arise is considered to be artefactual and thus generally ignored. Until recently little attention has been paid to the importance of larval recruitment; however, a number of workers have concluded that settlement rate may play a role as important as post-settlement processes in determining assemblage structure (e.g. Jensen and Morse, 1984; Keough, 1984b; Underwood and Denley, 1984; Caffey, 1985; Connell, 1985; Gaines and Roughgarden, 1985; Underwood, 1985; Roughgarden, 1986). There is increasing evidence that competition can be mediated by larval recruitment patterns (e.g. Keen and Neill, 1980; Buss, 1981; Grosberg, 1981; Young and Chia, 1981; Rubin, 1985; and Grosberg and Quinn, 1986). The same may be true for predation (e.g. Keough, 1984c).

There is, thus, an increasing realization that variation in settlement and recruitment should be explicitly incorporated in the development of models for assemblages; the variable input and early survival of settled larvae may play a large role in setting the initial but variable conditions under which post-settlement processes occur (Caffey, 1985; Gaines and Roughgarden, 1985; Young, 1985). Sammarco (1982) in a study of the effects of *Diadema antillarum* grazing on algal diversity and community structure, found that

diversity was not necessarily maximized at intermediate grazing pressures, as predicted by the "intermediate disturbance hypothesis". Instead, the control of diversity was influenced primarily by the lack of growth and recruitment of the potentially dominant alga. He concluded that this variable recruitment appeared to play just as important a role in determining the response of algal diversity to grazing pressure, as the interplay between food preferences of the herbivore and the competitive abilities of the algae (see Lubchenco, 1978). Gaines and Roughgarden (1985) and Roughgarden (1986) have suggested that a tacit assumption in the "intermediate disturbance hypothesis" is that of high settlement. They concluded that if settlement rates were so low that extensive contact failed to develop among the space occupiers, then there would be no opportunity for a hierarchy of competitive overgrowths to be expressed, and that under these circumstances diversity and disturbance would be inversely related. Roughgarden (1986) proposed that the "intermediate disturbance principle" may be a special case of a broader co-dependence of species diversity on disturbance and settlement rate; species diversity peaks at intermediate disturbance only for sufficiently high settlement rates. Similarly, Connell (1985) has re-evaluated his 1975 model and suggested that such a model may not be applicable in situations where the densities of both competitors or of predators are reduced sufficiently by low rates of settlement. The species that occupies the most space may be the one which

happened to settle more abundantly, rather than being the superior competitor, as predicted by the model (Connell, 1985). Underwood and Denley (1984) concluded that generalizations about competition and predation are weak and of very limited predictive value if the numbers of prey or potential competitors are themselves unpredictable.

Thus, the patterns of distribution and abundance of marine organisms on hard substrata result from the interactions between larval settlement, competition, predation (including herbivory) and physical disturbance - no one factor or process is likely to independently structure an assemblage. However, none of these processes are important if larval settlement is insufficient. "The structure of intertidal communities is not a simple function of characteristic interactions of predation and competition. The functions are likely to be complex because of enormous temporal and spatial heterogeneity in the abundances of interacting species, a direct result of the dispersive phase of their life histories" (Underwood and Denley, 1984, p. 172).

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APPENDIX 1

The format of the instructions required in the analysis of bryozoan competition using the GLIM 3.77 statistical package:

$UNITS 546$
(defines an array with 546 cells)

$CALCULATE OUTCOME=%GL(3,1)$
(rearranges the data sets into a format acceptable by GLIM)

$FACTOR SP1 1 SP2 18 SITE 4 SEASON 2 SECTOR 12 OUTCOME 3$
(defines the variables as categories and defines the number of categories in each case)

$DATA SP1 SP2 SITE SEASON SECTOR COUNT$

$DINPUT$
(informs the system that the data is to be read from an external file (containing only data) into the vectors specified by the DATA statement)

$CALCULATE W=(SP2==4)$
(calculation of the weight vector, W, to restrict fitting to a subset of the data, in this case only the interactions with species 4 are considered)

$YVARIATE COUNT$
(declaration of the dependent or y-variable, which in this model is the cell COUNT)

$ERROR POISSON$
(defines the error term in the model as a Poisson distribution; log link is declared by default)

$WEIGHT W$
(declaration of the weight variate)

$FIT OUTCOME$
(the model is set up and it is now possible to fit models to the data)

$DISPLAY E R$
(requests output of the coefficients and residuals of the model).

APPENDIX 2

TABLE A2.1. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each major taxonomic group examined, at each sampling date for the panels initiated, at the upper site, in April 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
APRIL 1984 (UPPER SITE) INITIATED: 20/4/84																			
1/5/84	11	1.000 (±0.577)	0	0	0	0	0	0.333 (±0.333)	0	0	0	0.667 (±0.333)	0	0	0	0	0	0	0
17/5/84	27	0.333 (±0.333)	0	0	0	0	0	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0
31/5/84	41	232.7 (±12.2)	0	0	0	0	0	227.0 (±12.5)	0	0	0	4.333 (±0.667)	0	1.333 (±0.333)	0	0	0	0	0
27/6/84	68	389.3 (±29.4)	13.33 (±2.19)	0	0	2.333 (±0.333)	0	362.3 (±26.8)	8.333 (±2.33)	0	0	17.67 (±4.33)	4.000 (±1.00)	5.333 (±2.33)	1.000 (±0.577)	0.333 (±0.333)	0	1.333 (±0.882)	0
28/7/84	99	116.7 (±5.93)	92.30 (±19.0)	6.000 (±3.06)	0	86.00 (±7.55)	14.33 (±9.87)	1.000 (±0.577)	55.00 (±13.7)	0	0	2.333 (±1.20)	16.00 (±4.62)	0.333 (±0.333)	5.000 (±2.65)	4.333 (±1.33)	0.333 (±0.333)	16.67 (±3.18)	1.667 (±0.667)
30/8/84	132	20.33 (±1.45)	570.0 (±34.1)	0	5.667 (±2.85)	4.333 (±1.86)	56.67 (±1.20)	6.000 (±0.577)	481.3 (±33.8)	0	0	0.667 (±0.667)	5.000 (±1.53)	0	1.000 (±1.00)	4.667 (±0.333)	4.667 (±1.20)	4.000 (±1.00)	15.67 (±3.71)

TABLE A2.2. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in May 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
MAY 1984 (LOWER SITE) INITIATED: 4/5/84																			
17/5/84	13	1.000 (±0)	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0	0.333 (±0.333)	0	0.333 (±0.333)	0	0	0
1/6/84	28	25.00 (±3.00)	0.667 (±0.333)	0	0	10.33 (±2.40)	0.333 (±0.333)	2.667 (±0.882)	0.333 (±0.333)	0	0	4.000 (±1.53)	0	6.667 (±2.03)	0	1.333 (±0.882)	0	0	0
14/6/84	41	36.33 (±3.48)	4.333 (±0.882)	0	0	9.333 (±2.19)	0.667 (±0.333)	1.333 (±0.333)	0	0	0	9.000 (±2.52)	1.333 (±0.333)	15.67 (±1.33)	1.667 (±0.333)	1.000 (±0)	0.667 (±0.667)	0	0
3/7/84	60	41.67 (±0.333)	33.00 (±4.62)	0	0	8.000 (±2.08)	3.333 (±0.882)	0	0.333 (±0.333)	0	0	6.000 (±0.577)	6.667 (±2.03)	15.00 (±2.00)	19.67 (±2.19)	6.333 (±1.76)	3.000 (±0.577)	6.333 (±0.667)	0
29/7/84	86	240.7 (±50.7)	53.67 (±5.17)	5.667 (±3.48)	0	150.7 (±21.7)	17.67 (±4.18)	0.333 (±0.333)	0	0	0	2.333 (±0.667)	9.333 (±1.76)	7.667 (±3.48)	14.33 (±0.882)	27.33 (±6.01)	5.667 (±1.33)	46.67 (±16.5)	6.667 (±0.882)
14/8/84	102	45.33 (±8.57)	91.70 (±25.9)	2.667 (±1.33)	5.333 (±3.18)	8.333 (±1.45)	12.67 (±2.60)	0	0.667 (±0.667)	0	0	0.333 (±0.333)	2.667 (±1.45)	0	7.667 (±3.18)	7.333 (±2.67)	18.33 (±4.67)	26.67 (±5.36)	44.33 (±14.7)
27/9/84	146	52.00 (±26.1)	200.7 (±33.8)	0	2.667 (±1.33)	47.00 (±25.0)	152.3 (±24.0)	0	1.000 (±0.577)	0	0	0	0.667 (±0.333)	0	1.333 (±0.882)	4.333 (±0.882)	15.67 (±4.91)	0.667 (±0.333)	27.00 (±6.51)
28/10/84	177	78.00 (±38.8)	51.30 (±30.4)	0	0.333 (±0.333)	70.67 (±36.8)	46.00 (±29.5)	0	0.667 (±0.667)	0	0	0.333 (±0.333)	0.333 (±0.333)	0	0	3.333 (±1.33)	3.333 (±0.333)	3.667 (±2.33)	0.667 (±0.667)
MAY 1984 (UPPER SITE) INITIATED: 30/4/84																			
1/5/84	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3/5/84	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17/5/84	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31/5/84	31	52.33 (±2.96)	0	0	0	0	0	44.67 (±3.48)	0	0	0	6.333 (±1.20)	0	1.333 (±0.882)	0	0	0	0	0
14/6/84	45	60.30 (±19.9)	4.333 (±1.33)	0	0	1.000 (±0.577)	0	50.33 (±18.7)	2.667 (±1.20)	0	0	6.000 (±1.15)	0.667 (±0.333)	3.000 (±1.53)	1.000 (±0.577)	0	0	0	0
27/6/84	58	19.00 (±3.51)	15.67 (±2.60)	0	0	2.667 (±0.333)	0.333 (±0.333)	1.333 (±0.667)	2.333 (±0.882)	0	0	11.33 (±2.73)	10.33 (±1.20)	2.000 (±1.53)	2.667 (±1.20)	0	0	1.667 (±1.20)	0
31/7/84	92	123.0 (±3.51)	39.67 (±1.45)	6.333 (±2.03)	0	82.67 (±2.03)	17.67 (±2.91)	1.000 (±0)	3.667 (±0.882)	0	0	2.667 (±0.333)	12.33 (±3.71)	0.667 (±0.333)	2.667 (±1.76)	14.67 (±4.91)	1.667 (±0.882)	14.67 (±2.73)	1.667 (±1.20)
14/8/84	106	30.67 (±4.98)	70.67 (±18.8)	7.667 (±2.19)	4.000 (±1.00)	6.000 (±1.53)	24.67 (±6.33)	3.000 (±1.15)	25.67 (±13.3)	0	0	1.000 (±0.577)	1.000 (±0.577)	0	0.667 (±0.333)	4.333 (±2.03)	3.333 (±1.76)	8.667 (±3.38)	11.33 (±2.33)
23/9/84	146	30.00 (±4.58)	137.7 (±4.41)	0.333 (±0.333)	9.333 (±2.85)	19.33 (±7.13)	44.67 (±5.36)	0	61.33 (±7.36)	0	0	0	2.667 (±1.76)	0	0	7.333 (±2.03)	8.667 (±4.81)	3.000 (±1.00)	10.67 (±3.38)

TABLE A2.3. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in June 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
JUNE 1984 (LOWER SITE) INITIATED: 29/5/84																			
30/5/84	1	0.333 (±0.333)	0	0	0	0	0	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0
1/6/84	3	0.667 (±0.333)	0	0	0	0	0	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	0	0	0	0
14/6/84	16	28.67 (±2.33)	0.333 (±0.333)	0	0	14.33 (±3.18)	0	1.000 (±0.577)	0.333 (±0.333)	0	0	10.67 (±1.33)	0	2.333 (±0.667)	0	0.333 (±0.333)	0	0	0
3/7/84	35	26.67 (±6.12)	15.67 (±1.86)	0	0	6.667 (±0.882)	6.333 (±0.333)	0.667 (±0.333)	0	0	0	6.333 (±0.333)	6.333 (±1.67)	4.667 (±1.76)	2.000 (±0.577)	4.333 (±2.33)	1.000 (±0.577)	4.000 (±2.08)	0
30/7/84	62	229.3 (±41.4)	56.00 (±7.64)	0.333 (±0.333)	0	148.7 (±34.5)	30.00 (±1.00)	0	0.667 (±0.333)	0	0	0.667 (±0.333)	9.000 (±0.577)	2.667 (±1.76)	5.000 (±1.53)	33.00 (±4.73)	7.000 (±2.65)	44.00 (±4.04)	4.333 (±2.19)
15/8/84	78	41.00 (±3.21)	74.67 (±10.5)	3.667 (±0.667)	0.333 (±0.333)	7.667 (±1.76)	12.00 (±3.21)	0	0	0	0	0.333 (±0.333)	2.000 (±0.577)	0	2.333 (±1.45)	6.333 (±2.03)	15.33 (±3.38)	22.67 (±0.333)	42.67 (±3.84)
29/9/84	123	29.33 (±7.17)	177.7 (±30.2)	0	3.667 (±0.667)	27.00 (±7.09)	129.0 (±29.2)	0	0	0	0	0.667 (±0.333)	1.000 (±0.577)	0	0.333 (±0.333)	1.000 (±0.577)	19.67 (±3.38)	0.667 (±0.667)	23.67 (±1.20)
9/10/84	133	10.00 (±2.65)	8.667 (±2.60)	0	0	8.667 (±3.38)	7.000 (±1.53)	0	0	0.333 (±0.333)	0	0	0.333 (±0.333)	0	0	0.667 (±0.667)	1.000 (±0.577)	0.333 (±0.333)	0.333 (±0.333)
26/11/84	181	44.33 (±3.48)	53.00 (±4.16)	0.333 (±0.333)	0	37.00 (±3.61)	52.00 (±4.16)	0	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0.667 (±0.667)	0	4.333 (±0.882)	0	2.000 (±2.00)	0.333 (±0.333)
JUNE 1984 (UPPER SITE) INITIATED: 2/6/84																			
14/6/84	12	15.33 (±2.96)	0.333 (±0.333)	0	0	0.333 (±0.333)	0	8.667 (±3.28)	0.333 (±0.333)	0	0	2.333 (±0.667)	0	4.000 (±0.577)	0	0	0	0	0
28/6/84	26	6.000 (±2.31)	9.667 (±0.882)	0	0	0.667 (±0.667)	0	0.333 (±0.333)	3.333 (±0.667)	0	0	4.000 (±1.53)	2.333 (±0.667)	0	4.000 (±0.577)	0	0	1.000 (±0.577)	0
27/7/84	55	89.00 (±13.6)	40.33 (±11.9)	0	0	78.33 (±14.6)	34.67 (±13.9)	0	1.000 (±0.577)	0	0	0	3.667 (±1.33)	0	0	0.667 (±0.667)	0	10.00 (±2.00)	1.000 (±0.577)
15/8/84	74	19.00 (±2.65)	50.00 (±10.8)	0.333 (±0.333)	0	4.333 (±1.20)	38.00 (±12.1)	2.667 (±1.33)	0.333 (±0.333)	0	0	0.333 (±0.333)	0.333 (±0.333)	0	0	1.333 (±0.333)	1.000 (±0)	10.00 (±2.08)	10.33 (±1.67)
29/9/84	119	23.33 (±9.84)	25.00 (±3.79)	0.667 (±0.333)	0.333 (±0.333)	19.00 (±10.0)	13.33 (±2.03)	0	1.000 (±0)	0	0	0.667 (±0.333)	0	0	0	2.000 (±0.577)	0.333 (±0.333)	1.000 (±0)	10.00 (±2.08)
29/10/84	149	21.33 (±8.65)	17.00 (±4.51)	0.333 (±0.333)	0.667 (±0.333)	18.00 (±8.02)	13.00 (±4.04)	0	1.000 (±0)	0	0	0	1.000 (±0.577)	0	0	1.333 (±0.667)	0.667 (±0.667)	1.667 (±0.882)	0.667 (±0.333)

TABLE A2.4. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in July 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
JULY 1984 (LOWER SITE) INITIATED: 3/7/84																			
4/7/84	1	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0
13/7/84	10	108.7 (±32.2)	7.333 (±4.48)	0	0	91.00 (±33.3)	7.000 (±4.73)	0	0	0	0	0	0	0	0	0.333 (±0.333)	0	17.33 (±1.33)	0.333 (±0.333)
29/7/84	26	117.0 (±18.4)	35.33 (±1.86)	7.333 (±3.18)	0	48.00 (±6.03)	24.33 (±1.76)	0	0	0	0	1.000 (±0)	0	0.333 (±0.333)	0	15.00 (±2.00)	1.000 (±0)	45.33 (±11.8)	10.00 (±3.51)
16/8/84	44	49.67 (±1.20)	97.67 (±14.5)	3.667 (±0.882)	7.667 (±2.91)	14.67 (±2.73)	23.00 (±3.06)	0	0	0	0	0.667 (±0.333)	0.667 (±0.333)	0	0.333 (±0.333)	6.000 (±1.53)	11.00 (±2.08)	24.67 (±3.84)	55.00 (±13.2)
28/9/84	87	25.33 (±3.71)	128.3 (±28.6)	0	3.333 (±0.882)	21.33 (±3.18)	95.67 (±25.7)	0	0	0	0	0.667 (±0.333)	0.667 (±0.333)	0	0	2.333 (±0.333)	7.333 (±1.76)	1.000 (±0.577)	21.33 (±3.18)
27/10/84	116	34.00 (±4.16)	15.33 (±2.60)	0.333 (±0.333)	0	31.00 (±4.00)	10.67 (±2.73)	0	0	0	0	0	1.000 (±0.577)	0	0	1.000 (±0)	1.667 (±0.333)	1.667 (±0.882)	2.000 (±1.53)
22/12/84	172	23.67 (±2.85)	53.33 (±6.49)	0	0.333 (±0.333)	14.67 (±0.333)	47.67 (±4.63)	0	0	0	0	0	0	5.667 (±2.40)	0.333 (±0.333)	2.667 (±0.882)	3.000 (±1.00)	0.667 (±0.333)	2.000 (±1.15)
JULY 1984 (UPPER SITE) INITIATED: 3/7/84																			
4/7/84	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13/7/84	10	11.00 (±4.62)	3.667 (±1.20)	0	0	8.667 (±3.76)	3.667 (±1.20)	0	0	0	0	0	0	0	0	0	0	2.333 (±0.882)	0
27/7/84	24	13.33 (±0.882)	8.000 (±4.16)	0	0	5.667 (±2.03)	6.000 (±3.21)	0	0	0	0	0.333 (±0.333)	0	0	0	0	0	7.333 (±1.86)	2.000 (±1.00)
16/8/84	44	13.67 (±4.26)	11.33 (±0.333)	3.000 (±1.53)	0	1.333 (±0.882)	2.000 (±1.15)	1.667 (±1.20)	0	0	0	0.667 (±0.667)	0.333 (±0.333)	0.333 (±0.333)	0	1.333 (±0.333)	0	5.333 (±2.96)	9.000 (±1.53)
29/9/84	88	21.00 (±7.64)	18.00 (±5.69)	0.667 (±0.667)	3.000 (±1.53)	16.00 (±5.13)	7.333 (±2.96)	0	1.000 (±0.577)	0	0	0.667 (±0.333)	0.667 (±0.667)	0	0.333 (±0.333)	3.333 (±2.85)	1.667 (±0.333)	0.333 (±0.333)	4.000 (±2.31)
28/10/84	117	29.33 (±17.3)	5.000 (±1.00)	0.333 (±0.333)	0.667 (±0.667)	25.33 (±14.0)	3.000 (±1.00)	0	0.333 (±0.333)	0	0	0.667 (±0.667)	0.667 (±0.333)	0	0	1.667 (±1.67)	0	1.333 (±1.33)	0.333 (±0.333)
26/11/84	146	10.00 (±0.577)	29.67 (±15.5)	0	0.333 (±0.333)	3.667 (±0.667)	27.67 (±14.0)	0	0	0	0	0.333 (±0.333)	0.667 (±0.667)	0	0	3.667 (±1.20)	0.333 (±0.333)	2.333 (±1.45)	0.667 (±0.667)

TABLE A2.5. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in August 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
AUGUST 1984 (LOWER SITE) INITIATED: 30/7/84																			
31/7/84	1	3.667 (±1.76)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.667 (±1.76)	0
13/8/84	14	30.67 (±4.67)	3.000 (±1.53)	1.000 (±0.577)	0	3.667 (±0.333)	0.667 (±0.333)	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	1.667 (±0.333)	0	23.67 (±2.96)	2.333 (±1.45)
29/8/84	30	33.33 (±6.94)	32.00 (±12.2)	0.333 (±0.333)	1.000 (±0.577)	8.333 (±0.333)	1.333 (±0.667)	0	0.333 (±0.333)	0	0	0.667 (±0.667)	0	0	0	5.000 (±2.08)	1.667 (±0.333)	19.00 (±6.24)	27.67 (±10.5)
10/9/84	42	16.00 (±1.00)	25.00 (±1.53)	0	0.333 (±0.333)	10.00 (±1.53)	3.667 (±0.882)	0	0	0	0	0	1.000 (±0.577)	0	0	1.333 (±0.333)	4.333 (±2.03)	4.000 (±0.577)	15.67 (±4.26)
9/10/84	71	20.67 (±2.60)	14.00 (±0)	0	0	20.00 (±2.65)	8.000 (±1.53)	0	0	0	0	0	0	0	0	0	0.667 (±0.667)	0.667 (±0.667)	4.667 (±0.882)
27/10/84	89	18.67 (±2.91)	10.33 (±0.882)	0	0	16.67 (±2.33)	9.333 (±0.667)	0	0	0	0	0	0	0	0	0.667 (±0.333)	0.333 (±0.333)	1.333 (±0.333)	0.667 (±0.667)
22/12/84	145	15.33 (±4.48)	36.33 (±2.96)	0	0	12.00 (±2.65)	33.67 (±3.28)	0	0	0	0	0	0	1.333 (±1.33)	0	0.333 (±0.333)	1.333 (±0.333)	1.667 (±0.882)	1.333 (±0.333)
10/2/85	195	22.33 (±3.28)	10.00 (±3.79)	0	0	1.000 (±1.00)	8.000 (±4.00)	0	0	0	0	0.333 (±0.333)	0	11.33 (±2.33)	1.667 (±1.20)	9.667 (±2.67)	0	0	0.333 (±0.333)
AUGUST 1984 (UPPER SITE) INITIATED: 30/7/84																			
31/7/84	1	0.333 (±0.33)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0
13/8/84	14	4.667 (±0.882)	0.667 (±0.667)	0.667 (±0.667)	0	0.333 (±0.333)	0	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	0	0	3.000 (±0.577)	0.667 (±0.667)
29/8/84	30	4.667 (±3.18)	4.333 (±1.45)	0.667 (±0.667)	0.667 (±0.667)	1.000 (±0.577)	0.333 (±0.333)	0.333 (±0.333)	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0.333 (±0.333)	0	2.333 (±1.33)	2.667 (±0.667)
9/9/84	41	7.667 (±1.76)	3.667 (±2.19)	0.333 (±0.333)	0.667 (±0.667)	5.333 (±1.86)	0.333 (±0.333)	0	0.333 (±0.333)	0	0	0	0	0	0	0.333 (±0.333)	0	1.667 (±0.882)	2.333 (±1.33)
7/10/84	69	22.67 (±10.2)	3.333 (±0.667)	0.333 (±0.333)	0.333 (±0.333)	17.33 (±7.33)	1.000 (±0.577)	0.333 (±0.333)	0	0	0	0	0	0	0	4.333 (±3.33)	0.333 (±0.333)	0.333 (±0.333)	1.667 (±0.882)
28/10/84	90	22.00 (±8.50)	5.000 (±1.00)	0.333 (±0.333)	0.333 (±0.333)	20.00 (±8.02)	3.667 (±0.667)	0	0	0	0	0	0	0	0	1.333 (±0.333)	0.667 (±0.333)	0.333 (±0.333)	0.333 (±0.333)
8/11/84	101	4.333 (±1.20)	2.333 (±0.667)	0	0.333 (±0.333)	2.333 (±0.667)	1.667 (±0.667)	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	1.000 (±0.577)	0.333 (±0.333)	0.333 (±0.333)	0
23/12/84	146	12.67 (±1.20)	25.67 (±7.75)	0	0	4.333 (±2.40)	22.33 (±7.36)	0	0	0	0	0	0.333 (±0.333)	3.333 (±1.86)	0	5.000 (±1.15)	2.333 (±0.667)	0	0.667 (±0.333)

TABLE A2.6. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in September 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
SEPTEMBER 1984 (LOWER SITE) INITIATED: 30/8/84																			
9/9/84	10	5.333 (±0.333)	0.333 (±0.333)	0	0	2.000 (±0.577)	0	0	0	0	0	0	0	0	0	0.667 (±0.333)	0.333 (±0.333)	2.667 (±0.333)	0
28/9/84	29	19.00 (±2.31)	8.667 (±1.20)	0	0	16.33 (±3.18)	5.667 (±1.20)	0	0	0	0	0	0	0	0	1.333 (±0.882)	0.333 (±0.333)	1.333 (±1.333)	2.667 (±0.333)
10/10/84	41	17.33 (±6.23)	3.000 (±1.15)	0	0	16.00 (±6.00)	1.667 (±0.667)	0	0	0	0	0	0	0	0	1.000 (±0.577)	0.667 (±0.667)	0.333 (±0.333)	0.667 (±0.667)
21/12/84	113	32.67 (±6.67)	47.33 (±10.7)	0	0	23.33 (±5.04)	44.33 (±10.7)	0	0	0	0	0	0	6.000 (±2.08)	0.667 (±0.333)	2.667 (±0.333)	1.333 (±0.667)	0.667 (±0.667)	1.000 (±1.00)
11/3/85	193	16.67 (±6.12)	12.00 (±3.61)	0	0	1.000 (±0.577)	5.667 (±2.40)	0	0	0	0	0	0	5.667 (±2.19)	4.333 (±1.45)	10.00 (±4.04)	1.667 (±0.333)	0	0.333 (±0.333)
SEPTEMBER 1984 (UPPER SITE) INITIATED: 30/8/84																			
9/9/84	10	2.333 (±0.882)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.667 (±0.333)	0	1.667 (±0.882)	0
28/9/84	29	8.333 (±0.882)	2.667 (±1.20)	0	0	5.667 (±0.667)	0.333 (±0.333)	0	0	0	0	0.333 (±0.333)	0	0	0	1.000 (±0.577)	0.667 (±0.333)	1.333 (±0.882)	1.667 (±0.882)
7/10/84	38	6.667 (±2.40)	2.667 (±0.667)	0.333 (±0.333)	0	4.000 (±1.15)	1.000 (±0)	0.333 (±0.333)	0	0	0	0	0.333 (±0.333)	0	0	2.000 (±1.15)	0.333 (±0.333)	0	1.000 (±0.577)
6/11/84	68	27.33 (±11.3)	3.000 (±0.577)	0	0.333 (±0.333)	19.67 (±8.09)	1.667 (±0.667)	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	5.333 (±2.96)	0.667 (±0.667)	1.667 (±0.333)	0.333 (±0.333)
9/12/84	101	24.00 (±7.77)	20.67 (±6.96)	0	0	8.667 (±4.33)	13.33 (±4.81)	0	0.333 (±0.333)	1.333 (±1.33)	0	0	0.333 (±0.333)	9.000 (±2.00)	0	3.667 (±1.20)	5.000 (±2.08)	1.333 (±0.882)	1.667 (±0.333)
21/1/85	144	9.000 (±1.73)	15.67 (±3.48)	0	0	1.333 (±0.333)	6.333 (±2.19)	0	0	0	1.333 (±1.33)	0	0	3.000 (±1.00)	4.667 (±1.86)	4.667 (±1.33)	2.000 (±0.577)	0	1.333 (±0.882)
4/2/85	158	5.333 (±2.40)	1.667 (±0.333)	0	0	0	0	0	0	0	0	0	0	4.000 (±2.31)	0.667 (±0.333)	1.333 (±0.667)	1.000 (±0.577)	0	0

TABLE A2.7. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in October 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
OCTOBER 1984 (LOWER SITE) INITIATED: 23/9/84																			
27/9/84	4	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0	0	0
10/10/84	17	67.00 (±10.5)	4.667 (±1.76)	0	0	64.00 (±11.6)	4.667 (±1.76)	0	0	0	0	0	0	0	0	1.000 (±0.577)	0	2.000 (±1.53)	0
27/10/84	34	11.33 (±2.73)	3.333 (±0.667)	0	0	10.67 (±2.85)	1.667 (±0.882)	0	0	0	0	0	0	0	0	0.333 (±0.333)	0	0.333 (±0.333)	1.667 (±1.20)
25/11/84	63	9.333 (±1.20)	61.67 (±9.82)	0	0	5.333 (±1.33)	60.33 (±10.5)	0	0	0	0	0	0	0.333 (±0.333)	0	3.333 (±0.333)	1.000 (±0.577)	0.333 (±0.333)	0.333 (±0.333)
21/12/84	89	7.333 (±0.882)	8.667 (±3.38)	0	0	2.000 (±1.15)	6.667 (±3.76)	0	0	0	0	0	0	3.667 (±1.76)	0	1.333 (±0.882)	1.333 (±0.882)	0.333 (±0.333)	0.667 (±0.333)
8/4/85	197	16.00 (±2.08)	23.33 (±1.45)	0	0	1.333 (±1.33)	9.333 (±1.45)	0	0	0	0	0	0	0.667 (±0.333)	4.000 (±2.08)	14.00 (±1.53)	9.667 (±0.882)	0	0.333 (±0.333)
OCTOBER 1984 (UPPER SITE) INITIATED: 23/9/84																			
27/9/84	4	0.667 (±0.333)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0
7/10/84	14	5.333 (±0.667)	1.000 (±0)	0.333 (±0.333)	0	3.000 (±0.577)	0.333 (±0.333)	0	0	0	0	0.333 (±0.333)	0	0	0	0.667 (±0.333)	0	1.000 (±0.577)	0.333 (±0.333)
28/10/84	35	15.67 (±2.73)	3.667 (±1.76)	1.000 (±1.00)	0	10.67 (±1.76)	2.333 (±0.882)	0.333 (±0.333)	0	0.333 (±0.333)	0	0	0.333 (±0.333)	0	0	1.333 (±0.333)	0.333 (±0.333)	2.000 (±1.00)	0.667 (±0.667)
7/11/84	45	2.000 (±0.577)	3.667 (±1.33)	0	0.667 (±0.667)	1.000 (±0.577)	1.333 (±0.667)	0	0.333 (±0.333)	0	0	0	0	0	0	0	0.667 (±0.333)	1.000 (±0.577)	0.667 (±0.667)
9/12/84	77	8.333 (±1.45)	9.000 (±2.31)	0	0.667 (±0.667)	0.333 (±0.333)	5.667 (±1.33)	0	0	0.333 (±0.333)	0	0	0	5.333 (±0.667)	0	0.667 (±0.667)	1.000 (±1.00)	1.667 (±0.333)	1.667 (±0.333)
21/1/85	120	9.333 (±3.33)	6.333 (±2.60)	0	0	0.333 (±0.333)	2.000 (±0.577)	0	0	0	0.333 (±0.333)	0	0	4.667 (±1.76)	1.333 (±1.33)	4.333 (±2.03)	1.000 (±1.00)	0	1.667 (±0.667)
5/3/85	163	8.333 (±0.882)	11.33 (±4.48)	0	0	0	1.667 (±1.20)	0	0	0	0.333 (±0.333)	0	0	2.000 (±0.577)	5.333 (±1.86)	6.333 (±0.667)	3.333 (±1.86)	0	0.667 (±0.667)

TABLE A2.8. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in November 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
NOVEMBER 1984 (LOWER SITE) INITIATED: 28/10/84																			
25/11/84	28	15.67 (±1.20)	5.000 (±1.15)	0	0	11.00 (±2.52)	5.000 (±1.15)	0	0	0	0	0.333 (±0.333)	0	0.667 (±0.333)	0	1.333 (±0.667)	0	2.333 (±0.667)	0
21/12/84	54	6.667 (±1.67)	5.333 (±1.45)	0	0	2.000 (±1.15)	3.333 (±1.45)	0	0	0	0	0	0.333 (±0.333	3.000 (±1.53)	0.333 (±0.333)	1.667 (±0.882)	0.667 (±0.667)	0	0.667 (±0.333)
6/3/85	129	20.67 (±10.2)	9.333 (±2.60)	0	0	1.333 (±1.33)	4.333 (±2.03)	0	0	0	0	0	0	9.333 (±3.93)	1.667 (±0.882)	10.00 (±5.13)	2.333 (±0.667)	0	1.000 (±0.577)
8/4/85	162	6.333 (±1.20)	21.67 (±10.7)	0	0	0	1.000 (±0)	0	0	0	0	0	0	0.667 (±0.333)	10.33 (±4.84)	5.667 (±1.33)	9.667 (±5.70)	0	0.667 (±0.333)
7/5/85	191	5.333 (±0.882)	7.000 (±1.00)	0	0	0	0.333 (±0.333)	0	0	0	0	2.667 (±0.882)	0	0	1.000 (±0.577)	2.667 (±0.882)	5.667 (±0.333)	0	0
NOVEMBER 1984 (UPPER SITE) INITIATED: 29/10/84																			
6/11/84	8	4.000 (±1.15)	0.333 (±0.333)	0	0	0	0	0	0	0	0	0.667 (±0.333)	0.333 (±0.333)	0	0	0.333 (±0.333)	0	3.000 (±0.577)	0
25/11/84	27	13.00 (±2.08)	1.667 (±0.882)	0	0	8.333 (±2.91)	0.333 (±0.333)	0	0	0	0	0.333 (±0.333)	0.333 (±0.333)	0.333 (±0.333)	0	3.333 (±1.76)	0.333 (±0.333)	0.667 (±0.333)	0.667 (±0.333)
8/12/84	40	3.667 (±1.67)	3.667 (±0.882)	0	0	0.667 (±0.333)	1.000 (±1.00)	0	0	0	0	0	0.333 (±0.333)	0.667 (±0.667)	0	1.667 (±0.667)	1.333 (±0.882)	0.667 (±0.667)	1.000 (±0)
7/1/85	70	1.667 (±0.882)	5.000 (±1.15)	0	0	0	1.333 (±0.882)	0.333 (±0.333)	0	0	0	0	0	0.333 (±0.333)	0	0.667 (±0.667)	1.333 (±0.667)	0.333 (±0.333)	2.333 (±0.333)
22/1/85	85	0.667 (±0.333)	1.333 (±0.882)	0	0	0	0.667 (±0.333)	0	0	0	0	0	0	0.333 (±0.333)	0	0.333 (±0.333)	0.333 (±0.333)	0	0.333 (±0.333)
23/2/85	117	8.000 (±1.15)	2.667 (±0.882)	0	0	0	1.333 (±0.333)	0	0.333 (±0.333)	0	0	0	0	2.667 (±0.882)	0.333 (±0.333)	5.333 (±0.333)	0.667 (±0.667)	0	0
7/4/85	160	6.333 (±2.60)	14.00 (±1.53)	0	0	0.333 (±0.333)	4.000 (±1.73)	1.333 (±0.667)	0	0	0	0	0	0.667 (±0.667)	2.333 (±0.333)	4.000 (±1.53)	7.333 (±0.667)	0	0.333 (±0.333)

TABLE A2.9. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in December 1984.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
DECEMBER 1984 (LOWER SITE) INITIATED: 25/11/84																			
22/12/84	27	8.000 (±2.00)	2.000 (±1.00)	0	0	4.667 (±1.33)	2.000 (±1.00)	0	0	0	0	0	0	1.000 (±0.577)	0	0.667 (±0.333)	0	1.667 (±0.333)	0
6/3/85	101	14.67 (±2.91)	5.333 (±1.45)	0.667 (±0.667)	0	2.667 (±1.33)	3.333 (±1.20)	0	0	0	0	0	0	3.333 (±1.20)	0.667 (±0.667)	8.000 (±1.53)	0.667 (±0.333)	0	0.667 (±0.667)
7/4/85	133	7.333 (±3.38)	7.000 (±2.08)	0	0.667 (±0.667)	0	1.667 (±1.20)	0	0	0	0	0	0	0.333 (±0.333)	1.667 (±0.882)	7.000 (±3.51)	2.333 (±0.882)	0	0.667 (±0.667)
2/5/85	158	15.00 (±6.35)	7.000 (±1.15)	0.333 (±0.333)	0	0	0.333 (±0.333)	1.333 (±0.333)	0.667 (±0.333)	0	0	1.000 (±0.577)	0	9.000 (±3.79)	1.000 (±0)	3.000 (±1.53)	5.000 (±1.15)	0.333 (±0.333)	0
5/6/85	192	71.33 (±19.5)	60.67 (±20.3)	0	0.333 (±0.333)	48.67 (±16.2)	38.33 (±12.3)	4.667 (±0.882)	2.333 (±0.882)	0	0	9.000 (±2.08)	6.000 (±1.53)	6.000 (±1.00)	7.333 (±2.33)	2.333 (±0.667)	5.667 (±3.18)	0.667 (±0.667)	0.667 (±0.667)
DECEMBER 1984 (UPPER SITE) INITIATED: 25/11/84																			
8/12/84	13	2.000 (±0)	0	0	0	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0.667 (±0.333)	0	1.000 (±0.577)	0
7/1/85	43	2.333 (±1.33)	1.333 (±0.333)	0	0	0.667 (±0.333)	0.333 (±0.333)	0	0	0	0	0	0	1.000 (±0.577)	0	0.667 (±0.667)	0	0	1.000 (±0.577)
20/1/85	56	0	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0	0	0	0
23/2/85	90	7.333 (±1.20)	1.333 (±0.333)	0	0	0	0.667 (±0.333)	0	0	0	0	0	0	4.000 (±0.577)	0	3.333 (±1.20)	0.667 (±0.333)	0	0
23/3/85	118	2.667 (±0.882)	4.000 (±1.53)	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0.667 (±0.333)	2.333 (±0.882)	3.333 (±1.33)	0	0
7/5/85	163	269.0 (±71.8)	35.67 (±1.76)	0	0	0.667 (±0.333)	0	245.0 (±72.2)	26.00 (±2.00)	0	0	5.000 (±1.00)	0	11.67 (±1.45)	3.667 (±0.882)	6.667 (±0.882)	6.000 (±0.577)	0	0

TABLE A2.10. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in January 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
JANUARY 1985 (LOWER SITE) INITIATED: 22/12/84																			
6/3/85	74	12.67 (±1.67)	0.667 (±0.667)	0	0	1.000 (±0.577)	0.333 (±0.333)	0	0	0	0	0	0	5.000 (±1.53)	0	6.667 (±1.45)	0.333 (±0.333)	0	0
7/4/85	106	4.000 (±1.00)	7.000 (±1.00)	0	0	0	0.667 (±0.333)	0	0	0	0	0	0	0.333 (±0.333)	3.000 (±1.00)	3.667 (±0.667)	3.333 (±0.333)	0	0
7/5/85	136	15.00 (±3.21)	6.000 (±3.06)	0	0	0	0	1.000 (±0.577)	0	0	0	6.333 (±1.76)	0	4.667 (±2.73)	3.000 (±2.52)	3.000 (±1.53)	3.000 (±0.577)	0	0
4/6/85	164	41.00 (±3.00)	33.00 (±4.00)	0	0	28.00 (±4.58)	17.33 (±2.33)	3.667 (±0.882)	1.333 (±0.333)	0	0	4.000 (±2.31)	6.333 (±1.76)	3.000 (±0.577)	3.667 (±1.76)	2.000 (±0.577)	4.333 (±0.882)	0.333 (±0.333)	0
5/7/85	195	69.00 (±15.8)	37.00 (±6.81)	3.333 (±1.45)	0	44.67 (±7.75)	26.67 (±6.49)	0.667 (±0.333)	1.333 (±0.882)	0	0	1.667 (±1.20)	3.000 (±1.15)	4.667 (±1.67)	2.000 (±0)	5.333 (±2.60)	2.333 (±0.882)	8.667 (±4.18)	1.667 (±1.20)
JANUARY 1985 (UPPER SITE) INITIATED: 23/12/84																			
7/1/85	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20/1/85	28	1.000 (±0.577)	0	0	0	0	0	0	0	0	0	0	0	0	0	1.000 (±0.577)	0	0	0
24/2/85	63	4.000 (±1.00)	0.667 (±0.333)	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0	3.667 (±0.882)	0.667 (±0.333)	0	0
23/3/85	90	2.333 (±0.667)	3.000 (±1.53)	0	0	0	0	0	0	0	0	0	0	0.667 (±0.667)	0.333 (±0.333)	1.667 (±0.667)	2.667 (±1.45)	0	0
21/4/85	119	32.00 (±2.65)	5.667 (±0.667)	0	0	0	0	13.33 (±1.45)	1.000 (±1.00)	0	0	0	0	13.33 (±2.91)	2.000 (±0.577)	5.333 (±1.45)	2.667 (±0.667)	0	0
5/6/85	164	361.3 (±60.2)	188.0 (±17.5)	0	0	44.00 (±8.19)	29.67 (±1.45)	301.0 (±59.1)	140.0 (±19.0)	0	0	12.33 (±4.10)	0	3.000 (±3.00)	12.00 (±2.65)	1.000 (±0.577)	6.333 (±1.45)	0	0

TABLE A2.11. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in February 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
FEBRUARY 1985 (LOWER SITE) INITIATED: 10/2/85																			
24/3/85	42	1.667 (±0.667)	0	0	0	0	0	0	0	0	0	0	0	0	0	1.667 (±0.667)	0	0	0
22/4/85	71	13.00 (±0.577)	2.000 (±1.00)	0	0	0	0	2.333 (±0.667)	0.667 (±0.333)	0	0	1.000 (±0)	0.333 (±0.333)	4.667 (±0.882)	0.333 (±0.333)	5.000 (±0.577)	0.667 (±0.667)	0	0
20/5/85	99	23.33 (±4.10)	13.00 (±3.00)	0	0	3.000 (±1.00)	1.333 (±0.667)	8.000 (±2.08)	3.333 (±1.33)	0	0	8.333 (±0.882)	1.333 (±0.333)	1.333 (±0.882)	3.667 (±0.882)	2.667 (±0.333)	3.333 (±1.86)	0	0
20/6/85	130	171.0 (±33.3)	79.33 (±27.8)	30.33 (±6.69)	0	107.7 (±34.4)	63.67 (±27.4)	2.333 (±1.20)	2.667 (±1.20)	0	0	7.000 (±2.00)	8.000 (±1.15)	9.667 (±3.18)	2.000 (±1.15)	7.000 (±0.577)	3.000 (±1.00)	6.333 (±1.33)	0
5/8/85	176	402.0 (±80.3)	168.0 (±25.5)	9.333 (±3.84)	28.67 (±5.90)	236.7 (±55.1)	102.7 (±17.5)	0.333 (±0.333)	0.333 (±0.333)	0.667 (±0.333)	0	1.667 (±0.882)	4.667 (±0.882)	5.000 (±3.61)	5.000 (±2.52)	35.00 (±4.36)	9.667 (±0.667)	112.7 (±69.0)	16.33 (±8.33)
FEBRUARY 1985 (UPPER SITE) INITIATED: 4/2/85																			
24/2/85	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5/3/85	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21/3/85	45	0.667 (±0.333)	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0	0	0.667 (±0.333)	0.333 (±0.333)	0	0
22/4/85	77	14.00 (±3.21)	2.000 (±0.577)	0	0	0	0	6.667 (±3.84)	1.000 (±1.00)	0	0	0	0	3.000 (±1.15)	0.667 (±0.667)	4.333 (±0.667)	0.333 (±0.333)	0	0
19/5/85	104	73.33 (±15.6)	20.67 (±5.24)	0	0	1.333 (±0.882)	0.333 (±0.333)	70.00 (±16.1)	13.33 (±5.36)	0	0	1.333 (±0.882)	0.333 (±0.333)	0.667 (±0.333)	2.333 (±0.667)	0	4.333 (±0.667)	0	0
30/6/85	146	33.00 (±5.29)	18.67 (±2.60)	1.667 (±0.333)	0	9.000 (±1.53)	5.667 (±2.40)	10.00 (±2.31)	9.667 (±0.882)	0	0	3.333 (±1.67)	1.333 (±0.667)	1.667 (±1.20)	0.667 (±0.333)	4.667 (±2.40)	1.000 (±1.00)	2.333 (±0.882)	0.333 (±0.333)

TABLE A2.12. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in March 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
MARCH 1985 (LOWER SITE) INITIATED: 11/3/85																			
24/3/85	13	0.333 (±0.333)	0	0	0	0	0	0	0	0	0	0	0	0	0	0.333 (±0.333)	0	0	0
20/4/85	40	5.333 (±0.882)	1.000 (±0.577)	0	0	0	0	1.667 (±0.882)	0.667 (±0.667)	0	0	0	0	0	0	3.333 (±1.20)	0.333 (±0.333)	0	0
20/5/85	70	14.00 (±4.36)	6.000 (±1.73)	0	0	0.333 (±0.333)	0	7.667 (±3.48)	0.667 (±0.667)	0	0	2.000 (±1.00)	0	0.667 (±0.333)	0	3.333 (±0.882)	5.000 (±1.15)	0	0
21/6/85	102	36.00 (±1.15)	9.667 (±0.882)	8.000 (±2.08)	0	7.667 (±0.333)	2.667 (±0.882)	2.000 (±0.577)	2.000 (±0.577)	0	0	4.333 (±1.86)	2.000 (±1.15)	4.667 (±2.19)	0.333 (±0.333)	5.000 (±0.577)	2.667 (±1.20)	4.333 (±1.33)	0
16/8/85	158	135.0 (±9.29)	112.0 (±8.62)	0.333 (±0.333)	8.000 (±2.08)	103.3 (±7.31)	74.00 (±7.64)	1.000 (±1.00)	4.333 (±1.20)	0.333 (±0.333)	0	0.333 (±0.333)	4.000 (±1.15)	1.333 (±0.882)	3.000 (±1.00)	21.00 (±2.89)	14.33 (±2.67)	6.667 (±2.96)	4.333 (±1.33)
2/9/85	175	25.00 (±1.15)	49.00 (±3.51)	0	0.333 (±0.333)	16.33 (±2.33)	31.33 (±0.333)	0.333 (±0.333)	0.333 (±0.333)	0.667 (±0.667)	0.333 (±0.333)	0	0	0.333 (±0.333)	1.667 (±0.882)	2.000 (±0.577)	9.333 (±1.76)	5.333 (±1.33)	5.000 (±2.65)
MARCH 1985 (UPPER SITE) INITIATED: 5/3/85																			
21/3/85	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8/4/85	34	1.667 (±0.882)	0	0	0	0	0	0	0	0	0	0	0	0	0	1.667 (±0.882)	0	0	0
23/4/85	49	6.000 (±0.577)	0.667 (±0.333)	0	0	0	0	3.000 (±0.577)	0	0	0	0	0	0.667 (±0.667)	0	2.333 (±0.333)	0.667 (±0.333)	0	0
19/5/85	75	46.33 (±3.38)	9.000 (±2.08)	0	0	4.333 (±0.667)	0.333 (±0.333)	39.00 (±4.16)	5.000 (±3.61)	0	0	2.333 (±1.20)	0.333 (±0.333)	0	0	0.667 (±0.667)	3.333 (±1.20)	0	0
17/6/85	104	39.67 (±7.67)	30.33 (±5.93)	0	0	23.67 (±7.17)	21.33 (±7.97)	8.333 (±2.19)	6.000 (±4.04)	0	0	5.000 (±1.53)	2.000 (±1.00)	0.667 (±0.333)	0.333 (±0.333)	1.333 (±0.882)	0.667 (±0.667)	0.667 (±0.333)	0
5/8/85	153	122.3 (±4.10)	45.67 (±2.96)	17.67 (±4.63)	0	31.67 (±4.57)	23.67 (±5.24)	1.333 (±0.667)	2.333 (±0.882)	1.000 (±0)	0	3.667 (±2.03)	2.333 (±0.882)	3.333 (±0.882)	0.333 (±0.333)	43.00 (±1.53)	15.67 (±2.33)	20.00 (±8.00)	1.333 (±0.667)

TABLE A2.13. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in April 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
APRIL 1985 (LOWER SITE) INITIATED: 8/4/85																			
20/4/85	12	1.333 (±0.882)	0.333 (±0.333)	0	0	0	0	0.333 (±0.333)	0	0	0	0	0	0.333 (±0.333)	0.333 (±0.333)	0.667 (±0.333)	0	0	0
7/5/85	29	5.333 (±1.33)	1.333 (±0.667)	0	0	0	0	1.000 (±0)	0.333 (±0.333)	0	0	2.667 (±1.45)	0.667 (±0.667)	0.333 (±0.333)	0	1.333 (±0.667)	0.333 (±0.333)	0	0
4/6/85	57	12.00 (±2.00)	7.000 (±1.53)	0	0	2.667 (±0.333)	1.000 (±0.577)	4.667 (±1.45)	0.333 (±0.333)	0	0	2.000 (±1.00)	2.667 (±1.20)	0.667 (±0.667)	0.333 (±0.333)	2.000 (±0)	2.667 (±0.333)	0	0
22/6/85	75	22.00 (±4.04)	4.000 (±0.577)	2.667 (±0.882)	0	4.333 (±0.882)	2.000 (±0.577)	0.667 (±0.333)	0	0	0	4.000 (±1.00)	1.333 (±0.667)	3.000 (±1.15)	0	4.333 (±1.33)	0.667 (±0.333)	2.667 (±1.76)	0
16/8/85	130	110.0 (±21.0)	95.0 (±21.7)	8.667 (±6.33)	2.667 (±0.882)	77.00 (±9.54)	66.33 (±12.3)	1.000 (±0.577)	1.333 (±0.333)	0	0	0	3.667 (±1.45)	1.000 (±0)	2.333 (±1.20)	16.67 (±6.17)	15.67 (±6.69)	5.333 (±0.882)	2.667 (±1.76)
29/9/85	174	62.67 (±2.33)	70.00 (±10.0)	1.000 (±0.577)	8.000 (±6.11)	53.00 (±2.52)	44.67 (±0.667)	0	1.000 (±1.00)	0	0	0	0.333 (±0.333)	0	1.333 (±0.882)	7.667 (±1.67)	9.333 (±2.60)	0.333 (±0.333)	4.667 (±0.333)
APRIL 1985 (UPPER SITE) INITIATED: 7/4/85																			
21/4/85	14	2.333 (±0.882)	0.333 (±0.333)	0	0	0	0	1.000 (±0.577)	0	0	0	0	0	1.000 (±0)	0	0.333 (±0.333)	0.333 (±0.333)	0	0
1/5/85	24	4.333 (±2.33)	1.333 (±0.333)	0	0	0	0	2.667 (±1.33)	0.333 (±0.333)	0	0	0.667 (±0.667)	0	0	1.000 (±0)	1.000 (±0.577)	0	0	0
21/5/85	44	37.00 (±8.14)	6.333 (±2.73)	0	0	0.667 (±0.333)	0.333 (±0.333)	35.00 (±8.14)	3.667 (±1.86)	0	0	0.667 (±0.333)	1.000 (±0.577)	0	0	0.667 (±0.333)	1.333 (±0.882)	0	0
18/6/85	72	23.33 (±4.91)	18.33 (±2.91)	0	0	10.67 (±3.18)	9.333 (±2.91)	7.000 (±3.06)	8.333 (±2.60)	0	0	3.667 (±1.20)	0.333 (±0.333)	0	0	1.000 (±0)	0.333 (±0.333)	1.000 (±0.577)	0
18/8/85	133	34.00 (±2.65)	24.00 (±3.46)	2.667 (±0.333)	0	18.00 (±2.00)	12.67 (±1.45)	1.667 (±0.667)	2.667 (±1.20)	0.333 (±0.333)	0	0	3.333 (±1.45)	0	0	7.333 (±0.882)	4.333 (±0.882)	3.667 (±0.333)	1.000 (±0.577)
2/9/85	148	16.33 (±3.28)	22.67 (±6.23)	1.667 (±0.333)	2.667 (±0.333)	5.000 (±1.53)	5.000 (±0.577)	0.667 (±0.667)	6.333 (±5.33)	5.000 (±2.08)	0.333 (±0.333)	0	0	0	0	2.333 (±0.882)	4.000 (±0.577)	1.667 (±0.667)	4.000 (±0)

TABLE A2.14. – The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in May 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
MAY 1985 (LOWER SITE) INITIATED: 7/5/85																			
21/5/85	14	8.667 (±1.20)	0.667 (±0.667)	0	0	0	0	4.667 (±1.76)	0.333 (±0.333)	0	0	3.333 (±0.333)	0	0	0	0.667 (±0.333)	0.333 (±0.333)	0	0
18/6/85	42	31.67 (±10.3)	7.667 (±0.667)	2.000 (±1.00)	0	5.667 (±2.03)	3.333 (±1.20)	1.000 (±1.00)	0	0	0	2.000 (±1.53)	3.333 (±0.333)	3.667 (±1.76)	0	4.000 (±1.00)	1.000 (±0.577)	13.33 (±6.74)	0
17/8/85	102	156.7 (±25.9)	151.0 (±36.5)	1.667 (±1.20)	2.000 (±1.00)	102.0 (±21.0)	91.00 (±25.1)	0.667 (±0.333)	4.000 (±2.00)	0	0	1.333 (±0.333)	1.667 (±1.20)	1.667 (±0.667)	2.333 (±1.20)	41.00 (±4.36)	36.67 (±6.06)	8.000 (±1.73)	13.33 (±6.74)
14/9/85	130	44.67 (±4.41)	43.67 (±4.33)	0.333 (±0.333)	1.667 (±1.20)	36.00 (±2.65)	26.67 (±5.78)	0.333 (±0.333)	0	0.667 (±0.333)	0	0	1.333 (±0.333)	0	0.667 (±0.667)	6.333 (±1.45)	7.000 (±1.53)	1.000 (±0)	6.333 (±2.33)
29/10/85	175	124.7 (±41.6)	55.33 (±11.1)	0.667 (±0.333)	0.333 (±0.333)	110.7 (±39.0)	47.67 (±10.3)	0	0.667 (±0.333)	0.333 (±0.333)	0.667 (±0.333)	0.333 (±0.333)	0	0.333 (±0.333)	0.333 (±0.333)	9.667 (±0.667)	4.333 (±0.667)	2.667 (±1.76)	1.333 (±0.333)
MAY 1985 (UPPER SITE) INITIATED: 7/5/85																			
22/5/85	15	138.0 (±60.9)	2.333 (±0.882)	0	0	0.333 (±0.333)	0	137.0 (±60.9)	2.333 (±0.882)	0	0	0.667 (±0.333)	0	0	0	0	0	0	0
5/6/85	29	15.67 (±7.22)	5.333 (±1.67)	0	0	1.000 (±0)	0.333 (±0.333)	3.333 (±1.45)	3.667 (±1.33)	0	0	10.00 (±6.51)	1.000 (±0.577)	1.000 (±1.00)	0.333 (±0.333)	0.333 (±0.333)	0	0	0
19/6/85	43	22.00 (±8.50)	8.000 (±5.00)	0	0	0.333 (±0.333)	0.667 (±0.333)	6.000 (±2.89)	1.667 (±0.882)	0	0	12.33 (±6.64)	5.333 (±4.33)	1.000 (±1.00)	0	1.667 (±0.882)	0.333 (±0.333)	0.667 (±0.667)	0
15/8/85	100	70.00 (±7.81)	33.33 (±8.19)	8.667 (±2.67)	0	31.33 (±4.18)	11.00 (±2.31)	4.333 (±1.86)	3.000 (±2.08)	0.333 (±0.333)	0	2.667 (±0.333)	12.00 (±6.08)	1.333 (±0.333)	0.333 (±0.333)	15.33 (±2.03)	6.000 (±0.577)	3.667 (±1.86)	0.667 (±0.667)
30/9/85	146	47.33 (±6.69)	106.3 (±47.3)	0.667 (±0.333)	8.667 (±2.67)	21.67 (±1.86)	21.33 (±0.667)	3.000 (±1.15)	54.33 (±44.5)	4.667 (±1.86)	0.333 (±0.333)	2.667 (±2.67)	4.667 (±1.76)	0.333 (±0.333)	0.667 (±0.667)	10.00 (±1.53)	12.33 (±0.667)	1.667 (±0.882)	3.000 (±1.53)

TABLE A2.15. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in June 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
JUNE 1985 (LOWER SITE) INITIATED: 5/6/85																			
20/6/85	15	34.67 (±4.10)	1.000 (±0.577)	23.67 (±3.33)	0	3.667 (±0.333)	1.000 (±0.577)	0	0	0	0	1.667 (±0.333)	0	1.667 (±1.67)	0	0.667 (±0.667)	0	3.333 (±0.333)	0
19/8/85	75	217.3 (±22.5)	85.00 (±9.87)	6.333 (±1.76)	24.00 (±3.51)	150.3 (±16.0)	49.33 (±11.3)	0	0	0.333 (±0.333)	0	1.333 (±0.667)	1.333 (±0.333)	2.667 (±1.76)	0.667 (±0.667)	26.00 (±3.51)	5.667 (±2.33)	28.67 (±4.67)	4.000 (±0.577)
15/9/85	102	147.3 (±44.1)	49.67 (±0.882)	2.333 (±0.333)	5.333 (±2.03)	97.33 (±28.6)	29.67 (±3.18)	0.667 (±0.333)	0	11.33 (±4.70)	0.333 (±0.333)	0.667 (±0.667)	0.333 (±0.333)	0	0	22.00 (±7.94)	6.000 (±1.15)	12.67 (±4.70)	6.667 (±0.882)
17/10/85	134	276.0 (±87.0)	102.0 (±7.77)	1.667 (±0.882)	1.000 (±0)	216.7 (±71.2)	78.33 (±4.33)	0.667 (±0.333)	0.333 (±0.333)	12.67 (±4.37)	2.667 (±1.33)	0	0.667 (±0.667)	1.333 (±0.333)	0.667 (±0.333)	34.33 (±11.8)	9.667 (±0.882)	8.000 (±1.53)	8.667 (±4.06)
13/12/85	191	189.3 (±77.2)	163.3 (±59.9)	1.000 (±0.577)	2.667 (±1.45)	110.0 (±52.4)	125.7 (±54.7)	0	0.667 (±0.333)	0.667 (±0.667)	6.333 (±2.33)	0.333 (±0.333)	0.333 (±0.333)	41.33 (±17.0)	1.333 (±0.333)	33.00 (±7.64)	19.33 (±6.44)	3.000 (±1.15)	6.000 (±1.15)
JUNE 1985 (UPPER SITE) INITIATED: 5/6/85																			
17/6/85	12	6.333 (±2.03)	0.333 (±0.333)	0	0	0.333 (±0.333)	0.333 (±0.333)	0.667 (±0.333)	0	0	0	1.000 (±0)	0	0	0	0	0	4.333 (±2.03)	0
30/6/85	25	8.000 (±2.52)	5.333 (±2.03)	1.667 (±0.667)	0	1.667 (±0.882)	0.333 (±0.333)	0	0	0	0	1.667 (±0.667)	0	1.000 (±1.00)	0	1.333 (±0.333)	0.667 (±0.333)	0.667 (±0.667)	4.333 (±2.03)
20/8/85	76	43.67 (±2.96)	24.67 (±1.33)	2.333 (±0.882)	1.667 (±0.667)	28.00 (±1.53)	14.33 (±2.96)	1.333 (±0.882)	0	0.333 (±0.333)	0	0	2.667 (±0.667)	0.667 (±0.667)	0.667 (±0.667)	9.000 (±2.65)	4.333 (±1.33)	0.667 (±0.333)	1.000 (±0.577)
12/9/85	99	18.33 (±4.70)	25.67 (±6.44)	1.333 (±0.882)	2.333 (±0.882)	10.67 (±2.96)	12.67 (±2.91)	0.667 (±0.333)	1.000 (±0.577)	0.333 (±0.333)	0.333 (±0.333)	0.333 (±0.333)	0	0	0.333 (±0.333)	3.667 (±1.45)	7.333 (±2.73)	1.000 (±0.577)	0.333 (±0.333)
30/10/85	147	66.00 (±19.7)	27.67 (±5.04)	1.000 (±0.577)	1.333 (±0.882)	43.67 (±13.9)	20.33 (±3.48)	0	0	3.333 (±1.33)	0.333 (±0.333)	0.333 (±0.333)	0.667 (±0.333)	0	0.667 (±0.667)	15.00 (±3.51)	3.000 (±1.00)	2.000 (±0.577)	1.000 (±0.577)

TABLE A2.16. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in July 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
JULY 1985 (LOWER SITE) INITIATED: 5/7/85																			
17/8/85	43	88.00 (±9.67)	21.67 (±4.91)	8.667 (±5.24)	0	56.00 (±9.50)	20.00 (±5.29)	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	0	4.667 (±1.20)	1.667 (±0.882)	18.00 (±6.24)	0
16/9/85	73	86.67 (±36.2)	42.67 (±10.0)	1.000 (±0.577)	8.333 (±5.36)	43.33 (±22.9)	16.67 (±4.84)	1.000 (±0.577)	0.333 (±0.333)	7.333 (±5.84)	0.333 (±0.333)	0	0.333 (±0.333)	0	0	9.000 (±5.03)	4.333 (±2.19)	5.000 (±2.65)	12.33 (±2.40)
28/10/85	115	120.0 (±33.3)	54.67 (±21.1)	0	0.333 (±0.333)	99.33 (±26.4)	42.33 (±14.9)	0	0	2.333 (±0.667)	4.333 (±3.33)	0	0	0.667 (±0.333)	0	15.00 (±6.08)	3.667 (±1.45)	2.667 (±1.76)	4.000 (±2.08)
12/1/86	191	96.67 (±25.2)	77.67 (±25.1)	0.333 (±0.333)	1.000 (±0)	15.67 (±6.23)	65.33 (±22.7)	0	0	1.333 (±1.33)	0.667 (±0.333)	0	0	34.33 (±11.9)	0.333 (±0.333)	43.00 (±8.89)	9.000 (±2.31)	2.000 (±0.577)	1.333 (±0.882)
JULY 1985 (UPPER SITE) INITIATED: 30/6/85																			
20/8/85	51	53.67 (±6.98)	24.67 (±2.91)	3.000 (±0.577)	0	28.33 (±2.60)	20.33 (±2.40)	1.000 (±1.00)	0.333 (±0.333)	0	0	0.667 (±0.667)	0	0	0	10.67 (±2.33)	4.000 (±0.577)	9.667 (±1.86)	0
13/9/85	75	50.67 (±20.9)	33.33 (±8.65)	1.000 (±0.577)	2.333 (±0.333)	30.00 (±13.1)	16.00 (±7.09)	1.333 (±0.333)	0	1.000 (±0.577)	0	0	0	0	0	16.33 (±7.17)	7.000 (±1.53)	0.667 (±0.333)	7.667 (±1.45)
18/10/85	110	102.3 (±36.3)	31.33 (±11.5)	1.000 (±1.00)	1.000 (±0.577)	46.33 (±15.7)	16.33 (±6.23)	0.333 (±0.333)	0	13.67 (±9.94)	1.000 (±0.577)	1.000 (±0.577)	0	0	0	33.67 (±14.4)	12.00 (±4.36)	4.667 (±1.86)	1.000 (±0.577)
15/11/85	138	23.33 (±4.06)	22.67 (±9.56)	0	1.000 (±1.00)	7.667 (±2.03)	5.667 (±2.03)	0	0.333 (±0.333)	1.333 (±0.333)	7.667 (±6.23)	0	0.667 (±0.667)	4.667 (±1.86)	0	9.333 (±2.91)	3.333 (±1.33)	0.333 (±0.333)	2.000 (±0.577)
13/12/85	166	48.00 (±15.7)	35.00 (±9.29)	0	0.667 (±0.667)	8.000 (±2.00)	13.33 (±4.26)	0	0.333 (±0.333)	0	4.667 (±1.86)	0	0	20.67 (±6.69)	2.000 (±1.53)	18.67 (±6.94)	13.00 (±4.73)	0.667 (±0.333)	1.000 (±1.00)

TABLE A2.17. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in August 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
AUGUST 1985 (LOWER SITE) INITIATED: 5/8/85																			
19/8/85	14	32.00 (±5.51)	3.000 (±0)	6.667 (±3.53)	0	16.67 (±2.91)	3.000 (±0)	0	0	0	0	0	0	0	0	1.000 (±0.577)	0	7.667 (±0.882)	0
28/8/85	23	29.33 (±6.36)	16.67 (±3.33)	3.000 (±0)	6.333 (±3.28)	14.67 (±3.18)	7.000 (±0.577)	1.000 (±1.00)	0	0.667 (±0.333)	0	0	0	0	0	4.000 (±1.53)	1.000 (±0)	6.000 (±0.577)	2.333 (±0.333)
14/9/85	40	120.7 (±71.7)	22.33 (±1.45)	1.333 (±0.333)	3.333 (±0.333)	86.33 (±56.1)	10.33 (±3.18)	0	0	0	0.667 (±0.333)	0	0	0.333 (±0.333)	0	29.33 (±14.4)	3.000 (±1.15)	3.333 (±1.67)	5.000 (±1.53)
28/9/85	54	153.3 (±91.3)	53.33 (±30.2)	0.667 (±0.333)	1.333 (±0.333)	135.7 (±82.8)	42.00 (±25.3)	0.333 (±0.333)	0	0.333 (±0.333)	0	0	0	0	0	12.33 (±7.36)	8.333 (±4.48)	4.000 (±1.00)	1.667 (±0.882)
27/10/85	83	460.0 (±292.0)	87.67 (±34.5)	0	0.667 (±0.333)	407.0 (±265.0)	70.67 (±31.7)	0.333 (±0.333)	0.333 (±0.333)	1.000 (±1.00)	0.333 (±0.333)	0	0	0.333 (±0.333)	0.333 (±0.333)	46.00 (±24.5)	10.33 (±1.45)	4.667 (±0.882)	5.000 (±1.15)
27/2/86	206	233.0 (±84.5)	375.0 (±206.0)	0	0	21.00 (±7.09)	299.0 (±175.0)	0	0.333 (±0.333)	0	0.333 (±0.333)	0	0	60.67 (±34.2)	1.333 (±0.882)	151.0 (±46.8)	67.67 (±29.7)	0.333 (±0.333)	6.000 (±1.15)
AUGUST 1985 (UPPER SITE) INITIATED: 5/8/85																			
15/8/85	10	11.33 (±3.76)	0.667 (±0.667)	5.667 (±2.91)	0	2.667 (±0.882)	0.667 (±0.667)	0	0	0	0	0	0	0.333 (±0.333)	0	0.333 (±0.333)	0	2.333 (±0.667)	0
28/8/85	23	16.00 (±2.31)	10.00 (±3.79)	3.333 (±1.76)	5.333 (±3.18)	1.667 (±1.67)	2.667 (±0.882)	0	0	3.667 (±1.33)	0	0.333 (±0.333)	0	0.333 (±0.333)	0	4.000 (±0.577)	0.333 (±0.333)	2.667 (±0.882)	1.667 (±0.667)
13/9/85	39	69.00 (±30.1)	15.67 (±2.67)	0.667 (±0.333)	2.667 (±1.45)	40.67 (±25.8)	4.000 (±2.00)	0.333 (±0.333)	0	0.333 (±0.333)	2.333 (±1.45)	0	0	0	0.333 (±0.333)	26.00 (±10.7)	3.667 (±0.882)	0.667 (±0.333)	2.667 (±0.333)
29/9/85	55	75.33 (±24.1)	19.67 (±9.24)	0	1.667 (±1.20)	25.67 (±9.17)	5.333 (±2.85)	0.333 (±0.333)	0.333 (±0.333)	2.333 (±1.45)	1.000 (±1.00)	0	0.333 (±0.333)	0	0	43.00 (±19.4)	10.67 (±6.12)	3.333 (±1.45)	0.333 (±0.333)
26/10/85	82	187.3 (±26.6)	28.00 (±9.29)	1.667 (±0.333)	0	71.67 (±21.9)	15.00 (±8.74)	0.667 (±0.333)	0	36.67 (±2.73)	0.667 (±0.333)	1.333 (±0.667)	0	0.667 (±0.333)	0	62.67 (±12.1)	11.00 (±2.52)	10.67 (±1.45)	1.000 (±0.577)
28/11/85	115	25.33 (±6.44)	70.00 (±19.7)	0	1.000 (±0.577)	4.667 (±0.333)	16.33 (±6.57)	0	0.667 (±0.667)	0.333 (±0.333)	31.67 (±4.26)	0	1.333 (±0.667)	5.667 (±4.18)	0.333 (±0.333)	13.33 (±1.45)	15.00 (±7.00)	1.000 (±0.577)	2.000 (±1.00)
13/1/86	161	176.0 (±7.94)	62.00 (±8.14)	0	0.667 (±0.667)	11.00 (±7.55)	14.67 (±3.76)	0	0	0	4.333 (±1.67)	0	0	86.00 (±3.51)	0.333 (±0.333)	78.00 (±9.87)	35.33 (±7.51)	1.000 (±0)	6.000 (±1.00)

TABLE A2.18. - The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in September 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
SEPTEMBER 1985 (LOWER SITE) INITIATED: 2/9/85																			
16/9/85	14	10.00 (±1.53)	3.000 (±1.53)	0	0	7.333 (±0.882)	3.000 (±1.53)	0	0	0.333 (±0.333)	0	0	0	0	0	2.000 (±1.15)	0	0.333 (±0.333)	0
28/9/85	26	3.667 (±1.33)	5.667 (±1.20)	0	0	2.333 (±1.20)	3.667 (±0.667)	0	0	0	0.333 (±0.333)	0	0	0	0	1.333 (±0.333)	1.333 (±0.667)	0	0.333 (±0.333)
28/10/85	56	27.33 (±5.55)	5.667 (±0.333)	0	0	20.67 (±2.33)	5.333 (±0.882)	0	0	0	0	0.333 (±0.333)	0	0.333 (±0.333)	0	5.333 (±2.73)	1.333 (±0.882)	0.667 (±0.333)	0
27/1/86	147	45.33 (±9.39)	24.00 (±4.51)	0	0	10.00 (±1.00)	18.67 (±1.76)	0	0	0	0	0	0.333 (±0.333)	18.00 (±5.20)	0.333 (±0.333)	17.33 (±8.41)	4.000 (±2.52)	0	0.667 (±0.333)
25/3/86	204	30.00 (±3.06)	29.00 (±7.64)	0.667 (±0.667)	0	0	5.333 (±1.20)	0	0	0	0	0	0	7.667 (±3.28)	14.00 (±4.93)	21.67 (±0.882)	9.667 (±2.60)	0	0
SEPTEMBER 1985 (UPPER SITE) INITIATED: 2/9/85																			
12/9/85	10	3.000 (±1.53)	2.000 (±1.15)	1.000 (±0.577)	0	2.000 (±1.15)	2.000 (±1.15)	0	0	0	0	0	0	0	0	0	0	0	0
29/9/85	27	12.33 (±2.03)	4.333 (±1.76)	0	1.000 (±0.577)	4.667 (±2.03)	1.000 (±1.00)	0.667 (±0.333)	0	1.667 (±1.667)	0	0	0	0	0	3.667 (±0.882)	2.000 (±1.00)	1.333 (±0.667)	0.333 (±0.333)
29/10/85	57	17.33 (±6.49)	5.667 (±1.76)	0	0	6.000 (±2.65)	1.333 (±0.667)	0	0.333 (±0.333)	2.333 (±0.333)	1.333 (±1.33)	0.667 (±0.667)	0	0	0	7.333 (±2.67)	1.667 (±0.667)	1.000 (±0.577)	0.667 (±0.667)
27/11/85	86	8.333 (±2.96)	3.000 (±1.15)	0	0	0.667 (±0.333)	0	0	0.333 (±0.333)	0.333 (±0.333)	1.333 (±0.882)	0	0	2.333 (±0.882)	0	3.667 (±2.19)	0.333 (±0.333)	1.333 (±0.333)	1.000 (±0.577)
12/1/86	132	43.00 (±8.02)	18.00 (±3.46)	0	0	1.667 (±0.882)	3.000 (±0)	0	0	0	0.667 (±0.667)	0	0.667 (±0.667)	24.67 (±5.24)	2.667 (±1.20)	16.67 (±2.33)	9.333 (±2.33)	0	1.667 (±0.667)
27/2/86	178	33.00 (±5.86)	18.67 (±6.77)	0	0	0	0.333 (±0.333)	0	0	0	0.333 (±0.333)	0	0	14.00 (±4.04)	9.667 (±7.67)	19.00 (±2.00)	8.333 (±1.33)	0	0

TABLE A2.19. – The mean number of recruits (=R) and mortalities (=M) (± 1 standard error) for each taxonomic group examined, at each sampling date for the panels initiated, at both sites, in October 1985.

DATE	DAYS IMM.	TOTAL		SPONGES		SERPULIDS		BARNACLES		ANOMIIDS		HYDROIDS		CTENOSTOMES		CHEILOSTOMES		ASCIDIANS	
		R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M	R	M
OCTOBER 1985 (LOWER SITE) INITIATED: 29/9/85																			
12/10/85	13	24.33 (±5.46)	2.000 (±0)	0	0	19.33 (±4.67)	2.000 (±0)	0	0	0.333 (±0.333)	0	2.333 (±0.667)	0	0	0	0.667 (±0.333)	0	1.667 (±0.882)	0
27/10/85	28	27.00 (±6.11)	12.67 (±1.20)	0	0	23.33 (±5.78)	8.667 (±1.76)	0	0	0.333 (±0.333)	0	0	2.000 (±0.577)	0.333 (±0.333)	0	2.333 (±0.333)	1.000 (±0)	0.667 (±0.333)	1.000 (±0.577)
27/11/85	59	10.00 (±3.06)	9.667 (±1.20)	0.333 (±0.333)	0	7.000 (±2.00)	7.000 (±0.577)	0	0	0	0.333 (±0.333)	0	0.333 (±0.333)	2.000 (±1.00)	0.333 (±0.333)	0.667 (±0.667)	0.333 (±0.333)	0	1.333 (±0.667)
9/2/86	133	32.33 (±8.29)	37.33 (±11.3)	0	0.333 (±0.333)	5.667 (±0.333)	28.33 (±10.3)	0	0	0	0	0	0	8.667 (±4.33)	2.000 (±0.577)	18.00 (±4.51)	6.667 (±0.333)	0	0
10/3/86	162	17.33 (±5.04)	22.00 (±7.51)	0	0	0.333 (±0.333)	4.667 (±1.45)	0	0	0	0.333 (±0.333)	0	0	5.667 (±1.33)	8.000 (±3.79)	11.33 (±3.84)	9.000 (±3.21)	0	0
23/4/86	206	15.67 (±2.33)	32.33 (±7.97)	0	0	0	3.333 (±1.45)	0	0	0	0	0	0	0.333 (±0.333)	6.333 (±0.882)	15.33 (±2.40)	22.67 (±5.70)	0	0
OCTOBER 1985 (UPPER SITE) INITIATED: 30/9/85																			
18/10/85	18	7.000 (±2.52)	0.333 (±0.333)	0.333 (±0.333)	0	2.333 (±0.882)	0	0	0	0.667 (±0.667)	0	1.000 (±0.577)	0	0	0	1.667 (±0.667)	0.333 (±0.333)	1.000 (±0.577)	0
26/10/85	26	3.000 (±1.00)	2.000 (±1.15)	0	0.333 (±0.333)	0.667 (±0.667)	0.333 (±0.333)	0	0	0.867 (±0.333)	0	0	0.667 (±0.333)	0.333 (±0.333)	0	1.333 (±0.333)	0	0	0.667 (±0.333)
15/11/85	46	8.333 (±2.91)	2.333 (±0.333)	0	0	1.333 (±1.33)	0.667 (±0.667)	0	0	0	0.667 (±0.333)	0.333 (±0.333)	0.333 (±0.333)	1.000 (±0.577)	0.333 (±0.333)	5.000 (±1.53)	0.333 (±0.333)	0.667 (±0.667)	0
13/12/85	74	36.00 (±9.45)	6.000 (±1.53)	0	0	6.000 (±2.65)	1.000 (±1.00)	0	0	0	0.333 (±0.333)	0.333 (±0.333)	0.333 (±0.333)	13.67 (±4.41)	0.667 (±0.333)	16.00 (±4.58)	3.333 (±0.882)	0	0.333 (±0.333)
12/1/86	104	30.33 (±8.37)	29.33 (±8.41)	0	0	0.333 (±0.333)	2.667 (±1.45)	0	0	0	0.333 (±0.333)	0	0	21.00 (±8.96)	8.667 (±3.84)	9.000 (±0.577)	17.00 (±5.03)	0	0.667 (±0.333)
8/2/86	131	22.33 (±7.36)	17.33 (±4.33)	0	0	0	1.000 (±0.577)	0	0	0	0	0	0	13.00 (±3.00)	7.333 (±4.84)	9.333 (±4.37)	9.000 (±0.577)	0	0
24/3/86	175	39.67 (±8.84)	50.33 (±14.9)	0	0	0.333 (±0.333)	3.333 (±1.45)	0	0	0	0	0	0	12.00 (±1.53)	28.33 (±6.49)	27.33 (±7.54)	18.67 (±9.13)	0	0

APPENDIX 3

BINOMIAL REGRESSION ANALYSIS OF BRYOZOAN COMPETITION

Pr_W (total data set)	= 0.310		
Pr_W (weighted data set)	= 0.310)		
(scaled deviance = 607.76	179 d.f.	*)	
Pr_W vs. *Alcyonidium*	= 0		
Pr_W vs. *C.aurita*	= 0.285		
Pr_W vs. *C.craticula*	= 0.646		
Pr_W vs. *C.lineata*	= 0.668		
Pr_W vs. *C.hyalina*	= 1.000		
Pr_W vs. *C.cryptooecium*	= 0.357		
Pr_W vs. *E.pilosa*	= 1.000		
Pr_W vs. *E.coccinea*	= 0.137		
Pr_W vs. *F.hispida*	= 0		
Pr_W vs. *M.nitida*	= 0.428		
Pr_W vs. *M.ciliata*	= 0.909		
Pr_W vs. *S.unicornis*	= 0.748		
(scaled deviance = 157.06	168 d.f.	ns	change = -450.7 -11 d.f. *)
Pr_W in SECTOR 1	= 0.247		
Pr_W in SECTOR 2	= 0.305		
Pr_W in SECTOR 3	= 0.310		
Pr_W in SECTOR 4	= 0.443		
Pr_W in SECTOR 5	= 0.444		
Pr_W in SECTOR 6	= 0.400		
Pr_W in SECTOR 7	= 0.636		
Pr_W in SECTOR 8	= 0.410		
Pr_W in SECTOR 9	= 0.429		
Pr_W in SECTOR 10	= 0.284		
Pr_W in SECTOR 11	= 0.310		
Pr_W in SECTOR 12	= 0.179		
(scaled deviance = 569.30	168 d.f.	*	change = -38.46 -11 d.f. *)
Pr_W at SITE 1	= 0.280		
Pr_W at SITE 2	= 0.600		
Pr_W at SITE 3	= 0.525		
Pr_W at SITE 4	= 0.476		
(scaled deviance = 585.57	176 d.f.	*	change = -22.19 -3 d.f. *)
Pr_W in SEASON 1	= 0.224		
Pr_W in SEASON 2	= 0.330		
(scaled deviance = 601.33	178 d.f.	*	change = -6.43 -1 d.f. *)

TABLE A3.1. - The probabilities of winning (Pr_W) for the total *Alcyonidium* spp. datum set, and the scaled deviances and the change in scaled deviance between fits of the current and minimal models, with the associated degrees of freedom and significance.

* = $P < 0.05$; ns = Not significant.

Pr_{W+T} (total data set)	=	0.799			
Pr_{W+T} (weighted data set)	=	0.799			
(scaled deviance = 459.95	179 d.f.	*)			
Pr_{W+T} vs. *Alcyonidium*	=	1.000			
Pr_{W+T} vs. *C.aurita*	=	0.428			
Pr_{W+T} vs. *C.craticula*	=	1.000			
Pr_{W+T} vs. *C.lineata*	=	0.852			
Pr_{W+T} vs. *C.hyalina*	=	1.000			
Pr_{W+T} vs. *C.cryptooecium*	=	0.572			
Pr_{W+T} vs. *E.pilosa*	=	1.000			
Pr_{W+T} vs. *E.coccinea*	=	0.332			
Pr_{W+T} vs. *F.hispida*	=	1.000			
Pr_{W+T} vs. *M.nitida*	=	0.632			
Pr_{W+T} vs. *M.ciliata*	=	0.909			
Pr_{W+T} vs. *S.unicornis*	=	0.750			
(scaled deviance = $^{+}$158.58	168 d.f.	ns	change = -301.37	-11 d.f.	*)
Pr_{W+T} in SECTOR 1	=	0.818			
Pr_{W+T} in SECTOR 2	=	0.819			
Pr_{W+T} in SECTOR 3	=	0.724			
Pr_{W+T} in SECTOR 4	=	0.800			
Pr_{W+T} in SECTOR 5	=	0.667			
Pr_{W+T} in SECTOR 6	=	0.943			
Pr_{W+T} in SECTOR 7	=	0.939			
Pr_{W+T} in SECTOR 8	=	0.923			
Pr_{W+T} in SECTOR 9	=	0.857			
Pr_{W+T} in SECTOR 10	=	0.761			
Pr_{W+T} in SECTOR 11	=	0.724			
Pr_{W+T} in SECTOR 12	=	0.687			
(scaled deviance = 432.25	168 d.f.	*	change = -27.7	-11 d.f.	*)
Pr_{W+T} at SITE 1	=	0.801			
Pr_{W+T} at SITE 2	=	0.800			
Pr_{W+T} at SITE 3	=	0.775			
Pr_{W+T} at SITE 4	=	0.810			
(scaled deviance = 459.79	176 d.f.	*	change = -0.16	-3 d.f.	ns)
Pr_{W+T} in SEASON 1	=	0.853			
Pr_{W+T} in SEASON 2	=	0.786			
(scaled deviance = 456.56	178 d.f.	*	change = -3.39	-1 d.f.	ns)

TABLE A3.2. – The probabilities of not losing (i.e. win + tie; Pr_{W+T}) for the total *Alcyonidium* spp. datum set, and the scaled deviances and change in scaled deviance between fits of the current and minimal models, with the associated degrees of freedom and significance.

* = $P < 0.05$; ns = Not significant; $^{+}$ = no convergence in iterative fitting of model (results only approximate).

Pr_W	=	0.669			
(scaled deviance = 38.761	39 d.f.	ns)			
Pr_W in SECTOR 1	=	0.643			
Pr_W in SECTOR 2	=	0.706			
Pr_W in SECTOR 3	=	0.571			
Pr_W in SECTOR 4	=	0.813			
Pr_W in SECTOR 5	=	1.000			
Pr_W in SECTOR 6	=	1.000			
Pr_W in SECTOR 7	=	0.400			
Pr_W in SECTOR 8	=	0.875			
Pr_W in SECTOR 9	=	0.333			
Pr_W in SECTOR 10	=	0.667			
Pr_W in SECTOR 11	=	0.714			
Pr_W in SECTOR 12	=	0.500			
(scaled deviance = 26.928	28 d.f.	ns	change = -11.833	-11 d.f.	ns)
Pr_W at SITE 1	=	0.699			
Pr_W at SITE 2	=	0.750			
Pr_W at SITE 3	=	0.650			
Pr_W at SITE 4	=	0.500			
(scaled deviance = 36.568	36 d.f.	ns	change = -2.193	-3 d.f.	ns)
Pr_W in SEASON 1	=	0.737			
Pr_W in SEASON 2	=	0.657			
(scaled deviance = 38.283	38 d.f.	ns	change = -0.478	-1 d.f.	ns)

TABLE A3.3. - The probabilities of winning (Pr_W) for the *Alcyonidium* spp. vs. *Callopora lineata* interaction, and the scaled deviances and change in scaled deviance between fits of the current and minimal models, with the associated degrees of freedom and significance.

* = $P < 0.05$; ns = Not significant.

Pr_{W+T}	= 0.851		
(scaled deviance = 39.293	39 d.f.	ns)	
Pr_{W+T} in SECTOR 1	= 0.893		
Pr_{W+T} in SECTOR 2	= 0.706		
Pr_{W+T} in SECTOR 3	= 1.000		
Pr_{W+T} in SECTOR 4	= 0.937		
Pr_{W+T} in SECTOR 5	= 1.000		
Pr_{W+T} in SECTOR 6	= 1.000		
Pr_{W+T} in SECTOR 7	= 1.000		
Pr_{W+T} in SECTOR 8	= 1.000		
Pr_{W+T} in SECTOR 9	= 0.667		
Pr_{W+T} in SECTOR 10	= 0.750		
Pr_{W+T} in SECTOR 11	= 0.857		
Pr_{W+T} in SECTOR 12	= 0.714		
(scaled deviance = $^{+}$24.476	28 d.f.	ns	change = -14.817 -11 d.f. ns)
Pr_{W+T} at SITE 1	= 0.843		
Pr_{W+T} at SITE 2	= 0.750		
Pr_{W+T} at SITE 3	= 0.900		
Pr_{W+T} at SITE 4	= 0.857		
(scaled deviance = 38.554	36 d.f.	ns	change = -0.739 -3 d.f. ns)
Pr_{W+T} in SEASON 1	= 0.895		
Pr_{W+T} in SEASON 2	= 0.843		
(scaled deviance = 38.930	38 d.f.	ns	change = -0.363 -1 d.f. ns)

TABLE A3.4. - The probabilities of not losing (i.e. win + tie; Pr_{W+T}) for the *Alcyonidium* spp. vs. *Callopora lineata* interaction, and the scaled deviances and change in scaled deviance between fits of the current and minimal models, with the associated degrees of freedom and significance.

* = $P < 0.05$; ns = Not significant; $^{+}$ = no convergence in iterative fitting of model (results only approximate).

(a)

		ALCYONIDIUM WIN	*ALCYONIDIUM* WIN + TIE
FIT		*	*
FIT SP2	1	ns	ns
	SP2(2)	ns	ns
	SP2(3)	ns	ns
	SP2(4)	ns	ns
	SP2(5)	ns	ns
	SP2(6)	-	-
	SP2(7)	ns	ns
	SP2(8)	ns	ns
	SP2(9)	-	-
	SP2(10)	ns	ns
	SP2(11)	ns	ns
	SP2(12)	-	-
	SP2(13)	ns	ns
	SP2(14)	ns	ns
	SP2(15)	-	-
	SP2(16)	-	-
	SP2(17)	ns	ns
	SP2(18)	-	-
FIT SECTOR	1	*	*
	SECT(2)	ns	ns
	SECT(3)	ns	ns
	SECT(4)	*	ns
	SECT(5)	ns	ns
	SECT(6)	ns	ns
	SECT(7)	*	ns
	SECT(8)	*	ns
	SECT(9)	ns	ns
	SECT(10)	ns	ns
	SECT(11)	ns	ns
	SECT(12)	ns	*
FIT SITE	1	*	*
	SITE(2)	*	ns
	SITE(3)	*	ns
	SITE(4)	ns	ns
FIT SEASON	1	*	*
	SEAS(2)	*	ns

(b)

		Alcyonidium vs. *C.lineata* WIN	*Alcyonidium* vs. *C.lineata* WIN + TIE
FIT		*	*
FIT SECTOR	1	ns	*
	SECT(2)	ns	ns
	SECT(3)	ns	ns
	SECT(4)	ns	ns
	SECT(5)	ns	ns
	SECT(6)	ns	ns
	SECT(7)	ns	ns
	SECT(8)	ns	ns
	SECT(9)	ns	ns
	SECT(10)	ns	ns
	SECT(11)	ns	ns
	SECT(12)	ns	ns
FIT SITE	1	*	*
	SITE(2)	ns	ns
	SITE(3)	ns	ns
	SITE(4)	ns	ns
FIT SEASON	1	ns	*
	SEAS(2)	ns	ns

TABLE A3.5. - The significance of the *t*-tests for each parameter from the win and win+tie analyses for (a) the complete *Alcyonidium* spp. datum set, and (b) the *Alcyonidium* spp. vs. the *Callopora lineata* interaction.

* = $P < 0.05$; ns = Not significant;
- = no observations

INTERACTION	*Alcyonidium* spp. vs. *C.lineata* - WIN		*Alcyonidium* spp. vs. *C.lineata* - WIN + TIE	
	S.D.	CHANGE	S.D.	CHANGE
(a) FIT	ns	-	ns	-
FIT SECTOR	ns	ns	+ns	ns
FIT SITE	ns	ns	ns	ns
FIT SEASON	ns	ns	ns	ns
(b) FIT	ns	-	ns	-
FIT* SECTOR	ns	ns	+ns	ns
FIT* SITE	+ns	ns	+ns	ns
FIT* SEASON	+ns	ns	+ns	ns
(c) FIT	ns	-	ns	-
FIT* SEASON	ns	ns	ns	ns
FIT* SITE	ns	ns	ns	ns
FIT* SECTOR	+ns	ns	+ns	ns

TABLE A3.6. - The significance of the scaled deviances (S.D.) of the models and the change in fit (CHANGE) between the current and minimal or precurrent models for (a) the single parameter models, and (b+c) the multiple interaction models developed for the *Alcyonidium* spp. vs. *Callopora lineata* interaction. In (a) each parameter is added independently to the minimal model; in (b) and (c) the parameters are added sequentially into the models, the order of parameter addition being reversed in (c).

* = $P < 0.05$; ns = Not significant; + = no convergence in iterative fitting of model (results only approximate).