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THE POPULATION ECOLOGY OF THE INTERTIDAL BIVALVE *LASAEA AUSTRALIS*

LILY K. Y. TONG

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy in The University of Sydney, August 1990.

DECLARATION

The work contained in this thesis, except where otherwise acknowledged, is the result of my own investigations.

Signed: Lily

Date: 1st August, 1990.

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I would like to thank my supervisor, Dr. A.J. Underwood for his endless guidance, encouragement and patience throughout this study. Thank you, Tony. This research has also benefitted from discussions with Drs. Joseph Connell and Clive Halnan.

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The past and present Ross Streeters have provided me with a friendly working atmosphere. They shared my joy, failure and boredom. I have especially enjoyed the company of Annadel, Barbara, Francisco, Graham, Karen, Laura, Libby, Pauline and Ricardo.

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My family have provided their support by not disclosing the problems at home in their letters. Alternatively, there haven't been any. In either case, I still thank them.

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ABSTRACT

Populations of the intertidal bivalve *Lasaea australis* were monitored in natural substrata on a shore in New South Wales. Recruitment of newly-metamorphosed individuals into beds of the alga *Corallina officinalis* and the tubeworm *Galeolaria caespitosa* were mainly in summer between November and March. The mean sizes of *Lasaea* were not significantly different between the two substrata nor between two heights on the shore.

The density of *Lasaea* in *Corallina* was greater in the high than in the low-shore at two study sites. A transplant experiment was, however, unable to show conclusively that survival of *Lasaea* in *Corallina* was adversely affected in the low zone. At the two *Galeolaria* sites, the numbers of *Lasaea* were linearly correlated with the volume of tubeworms and the trend for *Lasaea* to be more abundant in the high-shore was also found.

Experimental populations of *Lasaea* could be established in squares of artificial turf (Supergrasse). Juvenile and adult *Lasaea* and sediment particles accumulated in such squares. Their abundance increased continuously with time, even after one year. This was not an artifact, because regenerated *Corallina* was shown to trap *Lasaea* of comparable sizes.

More *Lasaea* and sediment were collected in high than low-shore squares. Bivalves would stay in the Supergrasse; marked animals seeded into the squares remained there for at least three months. During the initial two weeks, *Lasaea* of comparable mean sizes were collected at the three study sites. After a period of one or two years, the mean sizes of the bivalves

differed among sites. The largest *Lasaea* were retrieved from the site with the smallest number of bivalves.

The numbers of *Lasaea* were linearly correlated with the weight of sediment present in two-week-old squares. In order to test whether the bivalve *Lasaea* behaves like a passive sediment particle, the Supergrasse squares were shortened, thinned or seeded with artificial sediment to reduce the amounts of sediment they could retain. These experiments demonstrated that *Lasaea* tended to respond differently from sediment. Despite this, the spatial patterns of accumulation of *Lasaea* and the sediment in the Supergrasse were consistent over time, suggesting that hydrodynamic factors may be governing the patterns of arrival of the bivalves. Physical processes may therefore play a role in the distribution of *Lasaea* in their natural substrata.

TABLE OF CONTENTS

Page

CHAPTER TWO GENERAL MATERIALS AND METHODS

CHAPTER THREE DYNAMICS OF THE *LASAEA* POPULATIONS IN NATURAL SUBSTRATA

CHAPTER FOUR POPULATION STRUCTURE OF *LASAEA* IN ARTIFICIAL SUBSTRATA

CHAPTER FIVE *LASAEA* IN ARTIFICIAL SUBSTRATA

CHAPTER ONE GENERAL INTRODUCTION

Intertidal habitats on temperate rocky shores are often inhabited by sessile filter-feeders such as barnacles or mussels (Ricketts & Calvin, 1952; Lewis, 1964; Stephenson & Stephenson, 1972; Morton & Miller, 1973; Dakin, 1980). Since they are the dominant space-occupants, numerous studies have focussed on the factors influencing their distribution and abundance (Connell, 1961a & b, 1970, 1972; Seed, 1969a & b, 1976; Suchanek, 1978, 1985; Underwood, 1985). Small animals that do not advertise their presence have received far less attention.

Previous studies have emphasized the importance of predation and competition as the structuring forces of rocky shore communities (Paine, 1966; Dayton, 1971; Connell, 1975; Menge, 1976; Menge & Sutherland, 1976). Recently, the role of larval recruitment in determining the distribution and abundance of intertidal organisms has been highlighted by various workers (Underwood & Denley, 1984; Underwood & Fairweather, 1989). The process of recruitment can, in turn, be influenced by physical transport processes (Butman, 1987; Roughgarden *et al.*, 1987, 1988) and by active selection by the larvae (Meadows & Campbell, 1972; Gray, 1974). Hence, the study of intertidal bivalves with a planktonic larval phase should enable an assessment of the importance of biological interactions and recruitment processes on their distribution patterns.

Members of the bivalve genus *Lasaea* are small (less than 6 mm in length) and nearly cosmopolitan (Ponder, 1971; Ó Foighil, 1989). They live in cryptic habitats on rocky shores, for example, crevices, empty barnacle shells, lichen tufts and mussel beds (Glynne-Williams & Hobart, 1952;

Reimer, 1976; Seed & O'Connor, 1980; McGrath & Ó Foighil, 1986; Beauchamp, 1986). All are brooders and release their young either as planktotrophic veligers or crawl-away juveniles (Ó Foighil, 1989). *Lasaea australis* has the former mode of "mixed" development (Pechenik, 1979) and hence possesses a larval dispersive stage in its life-cycle (Polz, 1986; Ó Foighil, 1988). It is worthwhile to evaluate whether current theories regarding the distribution of intertidal space-dominants are still applicable to a tiny, cryptic bivalve. The study of small animals such as *Lasaea* has the advantage that manipulative experiments of a small-scale are a realistic approach for investigating the process in question (Dayton & Tegner, 1984).

Lasaea australis may be the most abundant bivalve on Australian intertidal shores (Dakin, 1980). The only two demographic studies in Australia have been from samples collected from underneath rocks and amongst mussels in Western Australia (Roberts, 1984) and from tubeworm colonies and mussel beds in Victoria (Polz, 1986). There has been no similar work on the coast of New South Wales.

My initial aim was, therefore, to investigate the distribution and abundance of *L. australis* to determine whether the patterns might be explained by the existing models. The association of *Lasaea* with natural substrata suggested that active habitat choice or passive dispersal mechanisms might be operating at the larval or adult stages. By using artificial substrata as experimental units, the bivalve and the sediment turned out to share the same pattern of distribution. This warranted an investigation of whether *Lasaea* behaves exactly as a sediment particle. This allowed assessment of the role of passive transport in determining the pattern of distribution and abundance of *Lasaea* on natural substrata.

CHAPTER TWO GENERAL MATERIALS AND METHODS

2.1 Description of study site

The research was conducted at the Cape Banks Scientific Marine Research Area in Botany Bay (New South Wales, Australia) (Fig. 2.1). The shore is composed of sandstone platforms subjected to a semi-diurnal tide with a maximal range of 2 m. These rock platforms are also influenced by the waves generated by the southerly or easterly winds as well as from the ocean swell.

2.2 Description of *Lasaea australis*

Lasaea australis (Lamarck, 1818) is a small erycinid bivalve with a length generally less than 5 mm. The shell is a triangular oval bearing a prominent umbo (Plate 1). There are distinct concentric ridges on the valves, though they can be less conspicuous in some animals. The shell colour may vary from cream to pink.

Besides New South Wales, *L. australis* also occurs in Victoria, Tasmania, South Australia and Western Australia (Macpherson & Gabriel, 1962). Large numbers can be found among the red coralline algae, calcareous worm tubes, mussel beds and underneath rocks (Dakin, 1980; Roberts, 1984). At Cape Banks, *L. australis* is mainly associated with the red alga *Corallina officinalis* and the tubicolous polychaete *Galeolaria caespitosa*. Some also live in empty tests of the barnacle *Tesseropora rosea*, among the holdfast of the brown alga *Hormosira banksii* and underneath the red encrusting alga *Hildenbrandia* *prototypus.* Like their congeneric members, they are free-living and are only attached to their substrata by a fine byssal thread.

During this study, I have also encountered an unidentified *Lasaea* sp. (described in Polz, 1986; Ponder, pers. comm.) living sympatrically with *L. australis.* They are characterised by a smoother shell with a rounded umbo and have a more limited size range. Since they were not very abundant, they were not included in my study.

Figure 2.1. A map of Australia showing the location of Cape Banks.

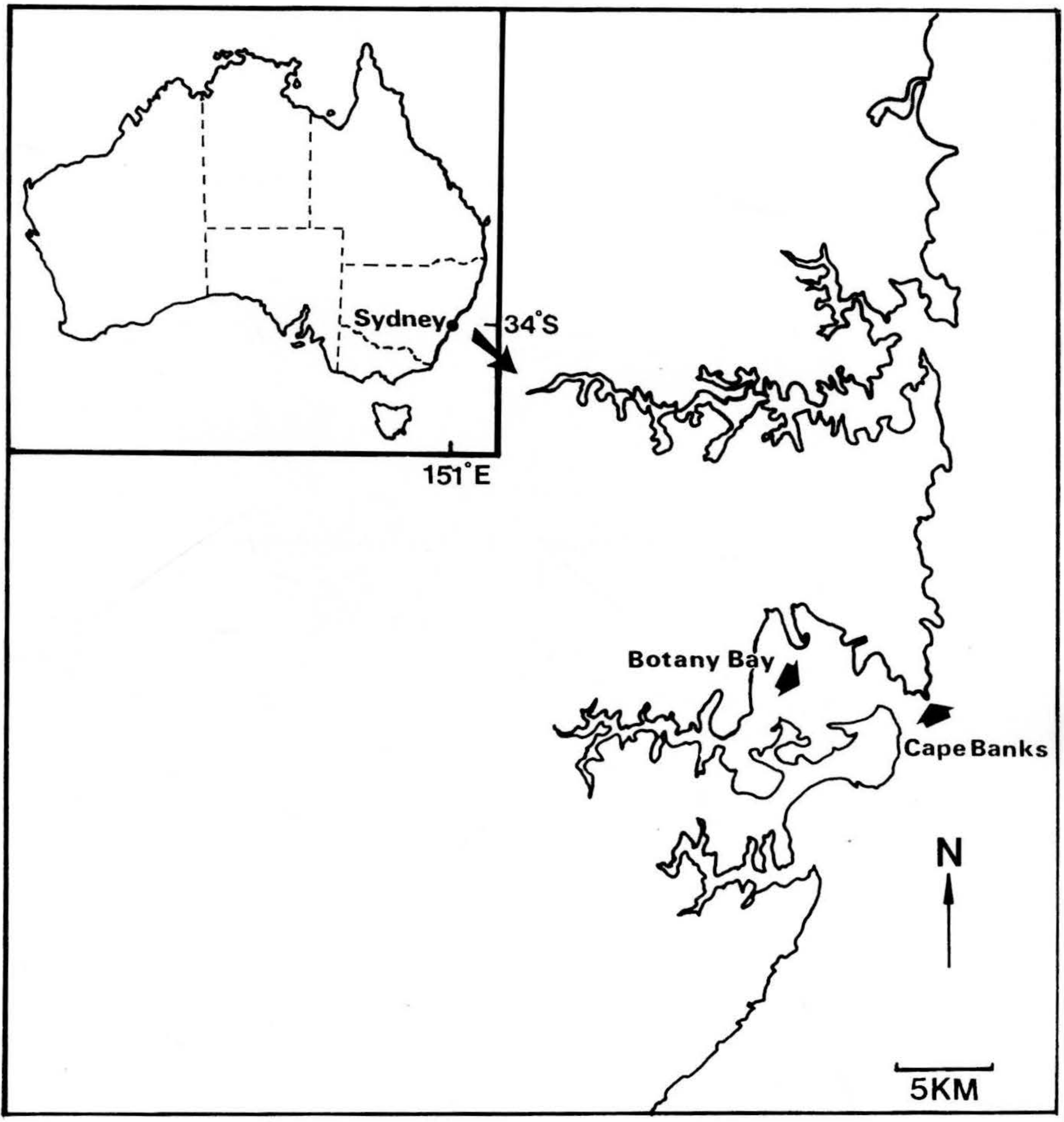

Sydney
34°S
151°E
Botany Bay
Cape Banks
N
5KM

Plate 1. *Lasaea australis* (each square is 1 mm X 1 mm).

CHAPTER THREE DYNAMICS OF THE *LASAEA* POPULATIONS IN NATURAL SUBSTRATA

3.1 Introduction

In a population study, one is interested in the density, distribution and abundance of the species concerned (Krebs, 1972). By sampling a population over different spatial and temporal scales, information on the above variables will be obtained.

At Cape Banks, *Lasaea australis* mainly occurred amongst *Corallina* and the worms, *Galeolaria*. The red coralline alga formed carpets in lower littoral areas or existed as patches among the ascidian *Pyura stolonifera*. They could also be found in pools higher up (pers. obs.). *Galeolaria* formed calcareous encrustations between the barnacle and the algal zones (O'Donnell, 1986). A stratified sampling programme (suggested by Green, 1979; Andrew & Mapstone, 1987) was therefore employed to determine if the population characteristics of *Lasaea* were substratum-dependent and/or height-dependent. Natural experiments of this type (Diamond, 1986) would provide the necessary background information before field experiments can be designed to test for the factors responsible for structuring the *Lasaea* populations.

3.2 Materials and methods

Between March 1987 and January 1989, *Lasaea* were sampled bimonthly from two *Corallina* (CC, CB) and two *Galeolaria* (GP, GC) sites (Fig. 3.1) within four consecutive days, except during bad weather. At each site, a high and a low area were chosen to represent, respectively, the upper and lower region of the *Corallina* or *Galeolaria* bed. Their differences in tidal height can vary between 0.01-0.23 m depending on the site (Table 3.1). At each area, there were four permanent 1 X 1 m^2 plots. Every two months, one sample was taken randomly from each of the plots by hammering a stainless steel corer (internal diameter: 4.12 cm) into the *Corallina* or *Galeolaria* substratum. The underlying sediment was also collected by scraping with a scalpel. Corers of this size would prevent the complete destruction of the plot before the end of the study. Moreover, the samples would contain a reasonable number of *Lasaea* as shown in my pilot study (*Corallina* core: 1<= n =<162; *Galeolaria* core: 14<= n =<97).

The cores were preserved in 0.1% Rose Bengal/alcohol. In order to facilitate sorting, each sample was first divided into two fractions by a 1 mm and a 75 μm sieve. After examination for *Lasaea*, the *Corallina* fronds were cleaned of detritus and epiphytes and oven-dried before weighing to the nearest 0.01 g. This laborious procedure was aborted after three sampling periods when it was shown that the biomass of *Corallina* was not a useful variable for predicting the number of *Lasaea* present (see Section 3.3.2). The volume of the *Galeolaria* core was also estimated to the nearest 0.1 ml by the method of liquid displacement before the worm tubes were broken apart whilst sorting.

The shell length of *Lasaea* was later determined by an Image Analyzer (Tracor Northern-8502) using "maximal projection" as the sizing parameter. Only animals with at least one intact shell valve were measured.

A pilot experiment was run to test if the difference in density of *Lasaea* at the two levels of a *Corallina* bed was caused by the differential survival of the bivalve. Cores of *Corallina* with the underlying sandstone (about 2 cm thick) were made by a diamond-rimmed corer (internal diameter: 5.96 cm). These cores could later be glued back to the hollowed bedrock by a quick-setting cement (Quickcrete). At the start of the experiment in May 1987, three 1 X 1 m^2 plots were designated in each of the high (+0.84 m C.D.) and low (+0.53 m C.D.) area of a *Corallina* bed near Site PB (Fig. 3.1). Four random cores were drilled from each of the plots and were then treated as followed:

(1) the Control (T_0, Time zero) core was removed;
(2) the Transplanted core was taken to a plot at a different level;
(3) the Disturbed core was replaced on the same spot;
(4) the Translocated core was moved to another plot at the same level.

The latter two cores were controls for manipulation (Chapman, 1986; Underwood, 1988). After four weeks (T_1, Time 1), another Control sample was cored from each plot and all the experimental cores were removed. The numbers of *Lasaea* in the cores were counted.

3.3 Results

3.3.1 Size structure of *Lasaea* in *Corallina* and *Galeolaria*

Frequency histograms of each population were constructed by pooling the animals across the four replicates (Fig. 3.2). They showed a polymodal distribution with overlapping size groups. No attempt was therefore made to separate them into individual size classes.

The *Lasaea* collected throughout the sampling period had a size range of 0.13-5.65 mm. At Site CB, about 90% of the high and low *Corallina* populations were smaller than 1.5 mm. The populations at the other three sites were, however, dominated by animals less than 2 mm in length.

Recruitment was mainly in summer (between November and March) in both years when individuals less than 0.5 mm formed a distinct peak. This event was more obvious in January 1989 when juveniles comprised more than 40% of the population, notably at the *Galeolaria* sites GP and GC.

The size distribution of the *Lasaea* populations was mostly positively skewed. There was, however, a shift towards normality in November 1987 at CC High and in November 1988 at CB High, CC High, GC High and GC Low (g_1= 0.045-0.528). Populations from the *Corallina* low sites were not considered in this analysis because of the limited sample size.

The shell lengths of *Lasaea* (in micrometres) were normalised by logarithmic transformation (base 10) as recommended in Underwood (1981). The temporal variation of the mean value of the log length was similar for the various populations at each of the heights (Fig. 3.3). In general, there was a slight increase from March till November followed by a drop in January and then a rise again from the March low. The trough was created by the summer recruitment which was more intense in January 1989, as was evident from the sharper decrease in the mean value.

The mean size was not different for *Lasaea* collected from the high and low areas at each site as well as between the *Corallina* and the *Galeolaria* substrata (Fig. 3.4; Table 3.2). *Lasaea* at Site CB were, however, significantly smaller than those at the other *Corallina* site CC.

3.3.2 Density of *Lasaea* in *Corallina*

At Sites CB and CC, the numbers of *Lasaea* were not linearly related to the biomass of the associated *Corallina* ($P > 0.9$) from samples collected between March and July 1987 (Fig. 3.5). Hence, the determination of biomass of *Corallina* was terminated.

The density of *Lasaea* was quite variable over the sampling period at each site (Fig. 3.6) ($P < 0.01$ for effect of Month; Table 3.3). The large value recorded in January 1989 compared with the other months again reflected the intense recruitment during that period. At each site, the density of *Lasaea* was greater in the high than in the low areas. Between sites, *Lasaea* was more numerous in CC High than in CB High, but the reverse was true for the low zones (Fig. 3.7).

The results of the pilot transplant experiment are summarised in Fig. 3.8. There were significant effects of Height and Treatment on the density of *Lasaea* (ANOVA; Table 3.4), but the Student-Newman-Keuls test was incapable of separating the treatment means into distinct groups. No conclusion could be drawn, except that the mean number of *Lasaea* from the high-shore cores was more than that from the low-shore ones.

3.3.3 Density of *Lasaea* in *Galeolaria*

At each of the Sites GP and GC, the number of *Lasaea* was found to be linearly related to the volume of the *Galeolaria* core ($P < 0.01$) after pooling the samples across the whole study period. For the two sites, the slopes of the regression lines for cores from each height were homogeneous ($P > 0.05$) but they had different elevations ($P < 0.05$; ANCOVA) (Fig. 3.9). Therefore, at either site, more *Lasaea* were found in the high than in the low areas for the same volume of *Galeolaria* examined.

3.4 Discussion

Brooding individuals were found in the September to March samples (one brooder in the May sample) which preceded the main recruitment period recorded between November and March. *Lasaea* less than 0.5 mm in length were, however, always present in the samples. They were either slow-growing juveniles or there was always some proportion of the population brooding throughout the year as reported by Roberts (1984).

Since there is no well-defined peak in the population histograms, the usual graphical procedure of separating them into cohorts (described in Cassie, 1954; Underwood, 1975; Cerrato, 1980) will be inaccurate (Grant, 1989). As an alternative, the mean size of the whole population was analysed. Although this may have masked the change in size of the individual age groups, recruitment in summer was clearly highlighted by the reduction of mean size of the population. The slight increase in the means between the recruitment seasons would probably represent growth of the individuals. This cumulative effect of growth would have contributed to the shift of the histograms from a positively skewed distribution toward a more normal one observed in November 1988.

The average size of a *Lasaea* population was not dependent on the source of the substratum. There was no significant difference between the mean size of the bivalves from the *Galeolaria* sites and the *Corallina* sites.

Growth-rate of bivalves has often been documented to decrease upshore because the time available for filter-feeding is inversely related to the period of emersion (Seed, 1976; Griffiths, 1981; Butler, 1987; but see Green & Hobson, 1970). There was no observed size gradient for *Lasaea* down the shore. If the average size is a good reflection of the magnitude of growth, this would imply no difference in growth-rate between the high and low-shore populations. First, a tidal height difference of 0.01-0.23 m between the two levels (Table 3.1) might not be drastic enough to cause a detectable disparity in growth. Second, *L. australis* from the high level might compensate physiologically by increasing their filtration rate as has been demonstrated in *L. rubra* (Morton *et al.*, 1957). Lastly, differences in rate of mortality of *Lasaea* at the the two levels could have masked the response of growth to tidal height. All this remains a speculation until the growth of marked animals at contrasting heights can be monitored.

Lasaea attach by a fine byssus to the articulated fronds of *Corallina*, especially around the basal region of the algae. Sometimes, the bivalve was trapped by *Corallina* because the newly-grown tips of the fronds were attached to the shell valve. Besides *Lasaea*, there was a suite of invertebrates depending on *Corallina* for shelter, food, as an attachment site or as a sediment trap (Hayward, 1980).

The biomass of the *Corallina* fronds, representing the amount of algal material, did not affect the density of *Lasaea* in a linear fashion. The bivalve might be responding to some other properties of the algal substratum, such as the sediment content (Wigham, 1975) which was not monitored in this study.

There was a trend for *Lasaea* to be more numerous in the high zone of the *Corallina* bed across the two sites. The pilot transplant experiment failed to show conclusively that the survival of *Lasaea* was adversely affected in the low zone. The experiment, if repeated, should be run with more replicates to reduce the standard error and for a longer time span for the adverse effect, if any, to operate fully.

In *Galeolaria*, most of the *Lasaea* were among the interstices of the worm tubes and a few inside the empty tubes. They were paler in coloration than their counterparts in the coralline algae. A reduction in pigmentation with depth of the crevice has also been observed in *L. rubra* (Morton, 1954). In addition to the live animals, the shells of dead *Lasaea* were often trapped because they could not be readily washed off.

The number of *Lasaea* showed a linear relationship with the volume of *Galeolaria*. The *Galeolaria* volume gives an estimate of the amount of worm tubes in the core and, indirectly, the space available for colonization by *Lasaea*. Hence, the above two variables are related. Again, there were relatively more *Lasaea* in the high than in the low zone of the *Galeolaria* bed, but a transplant experiment has not been attempted to test for the differential survival of *Lasaea* at the two zones.

The distribution pattern of *Lasaea* at various levels of the *Corallina* and *Galeolaria* belt could be influenced by factors such as larval recruitment and adult survival (Underwood & Denley, 1984). *Lasaea* might have less success in recruitment or higher post-recruitment mortality or both in the low zones. The role played by these factors in shaping the observed pattern of *Lasaea* in the natural substrata is waiting to be tested by field manipulative experiments.

Figure 3.1. A map of Cape Banks showing the study sites.

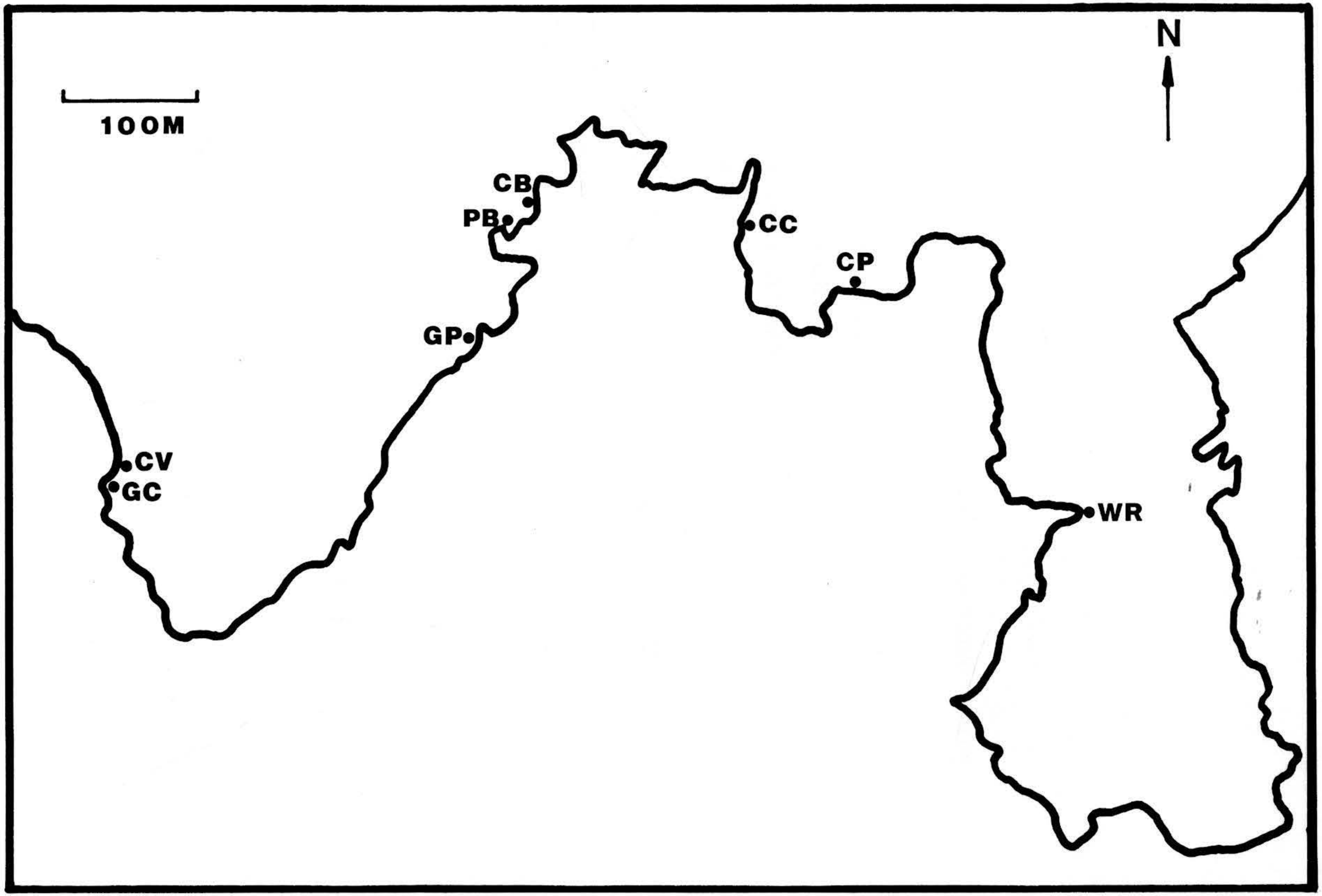
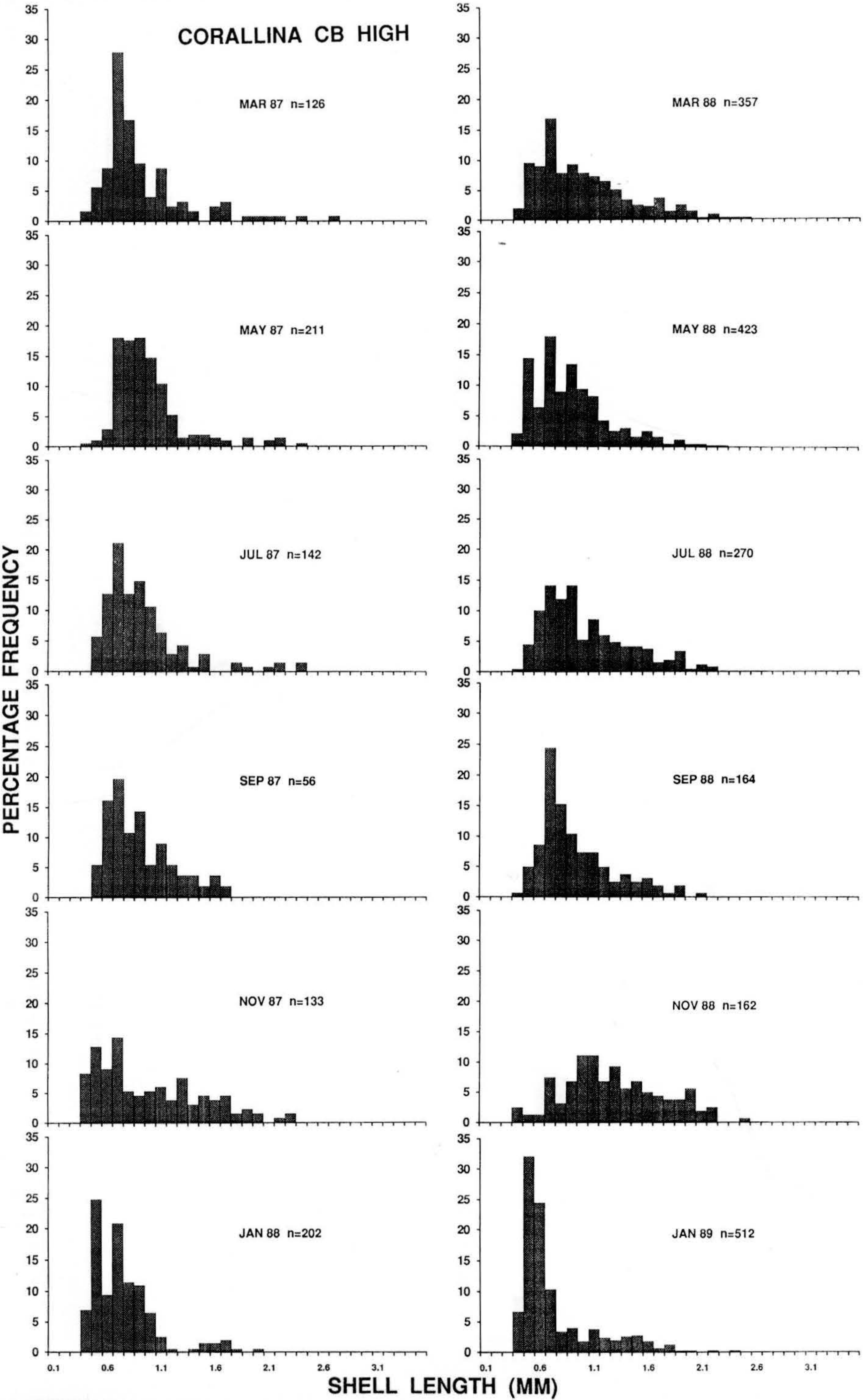
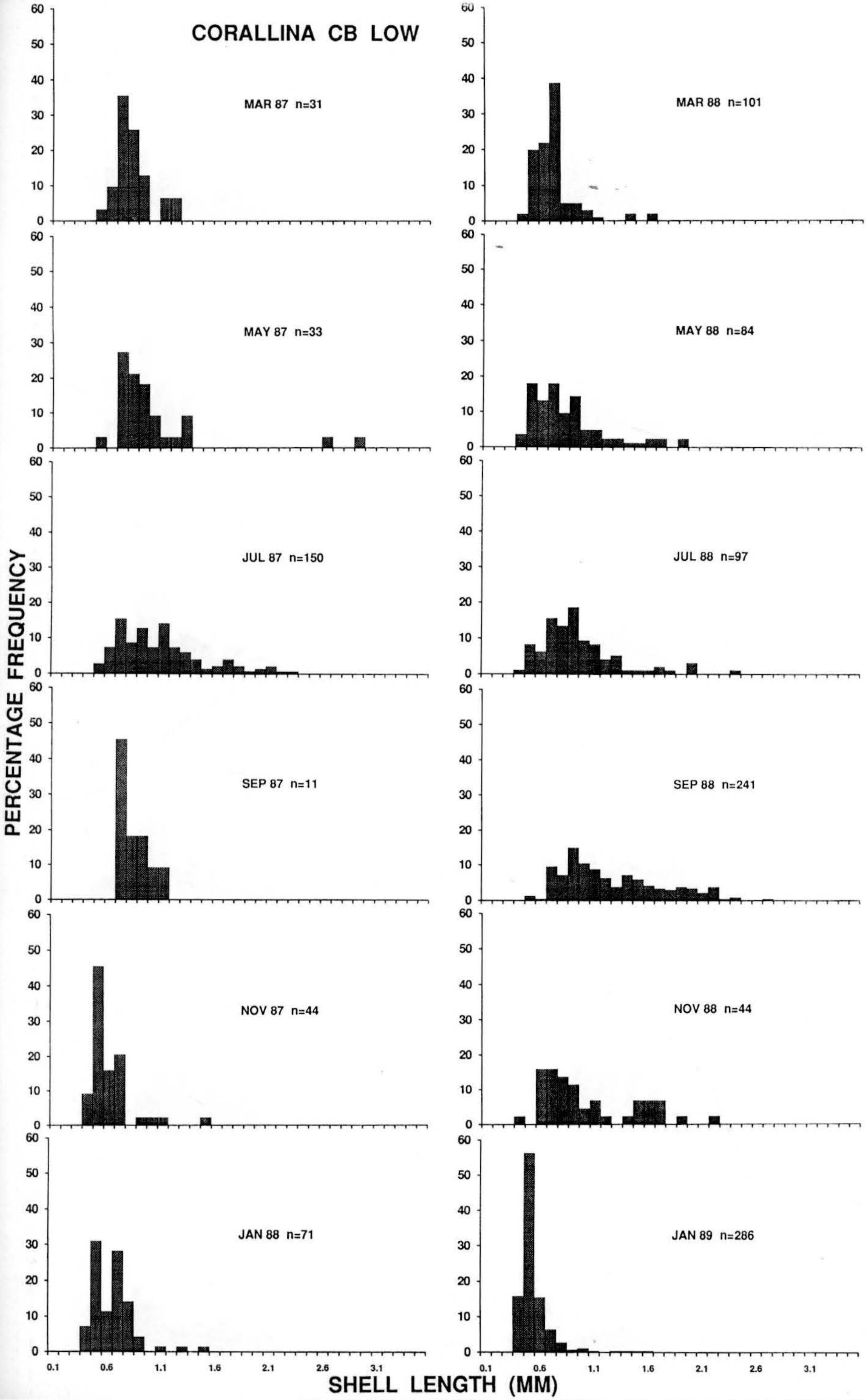
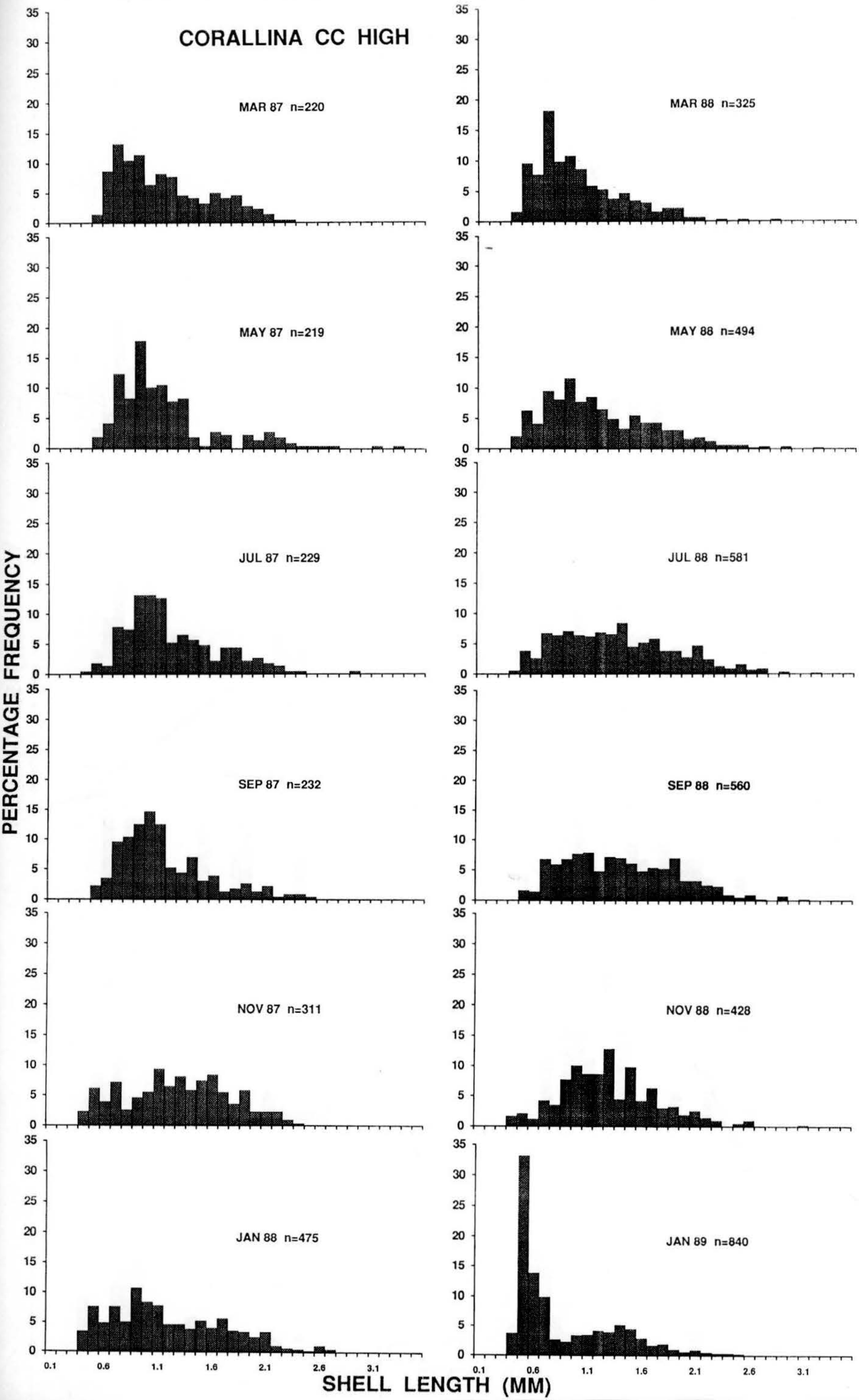

100M
N
CB
PB
CC
CP
GP
CV
GC
WR

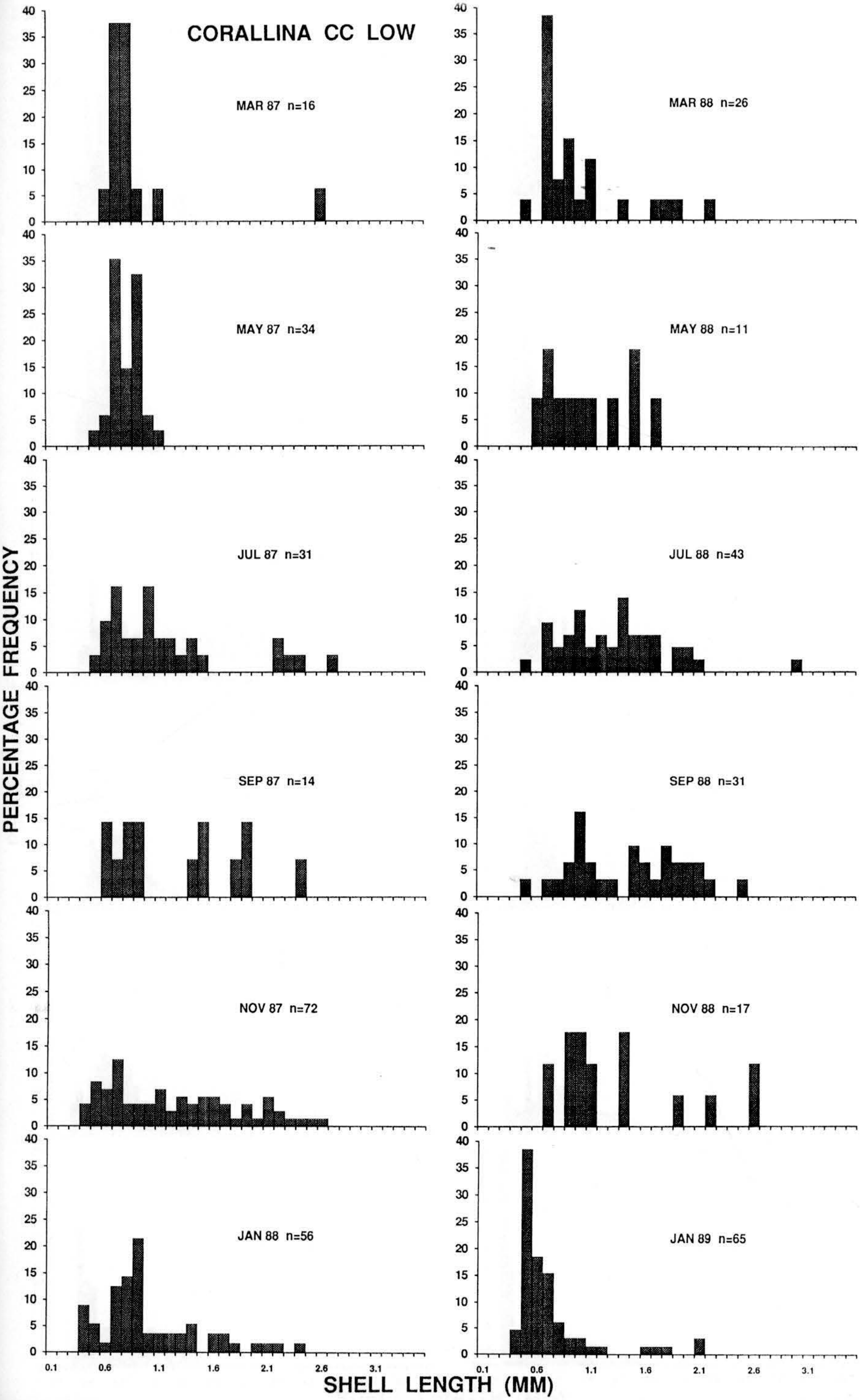
Figure 3.2. Size-frequency histograms of *Lasaea*. Data were pooled from four replicates.

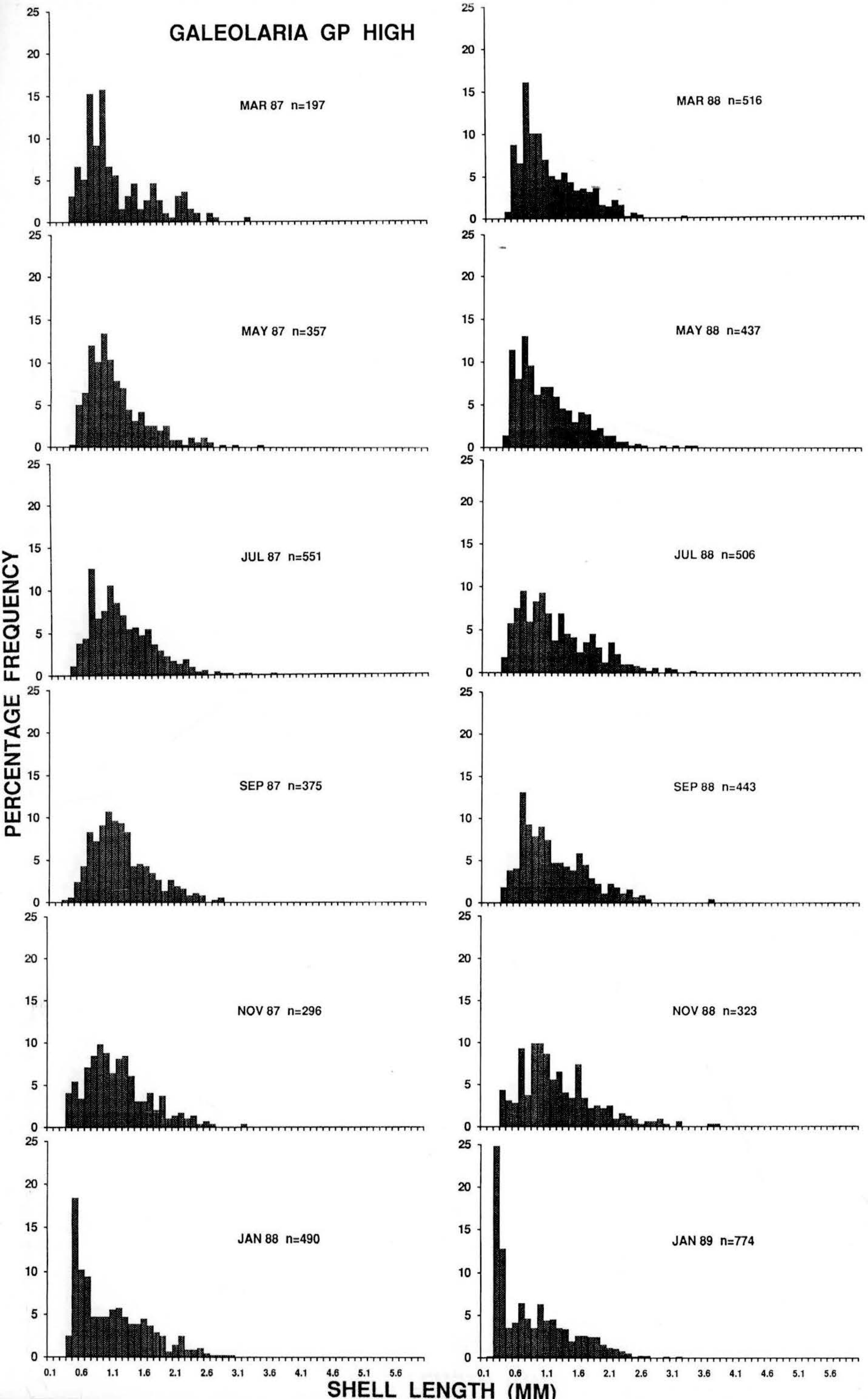
a. *Corallina* Site CB High
b. *Corallina* Site CB Low
c. *Corallina* Site CC High
d. *Corallina* Site CC Low
e. *Galeolaria* Site GP High
f. *Galeolaria* Site GP Low
g. *Galeolaria* Site GC High
h. *Galeolaria* Site GC Low

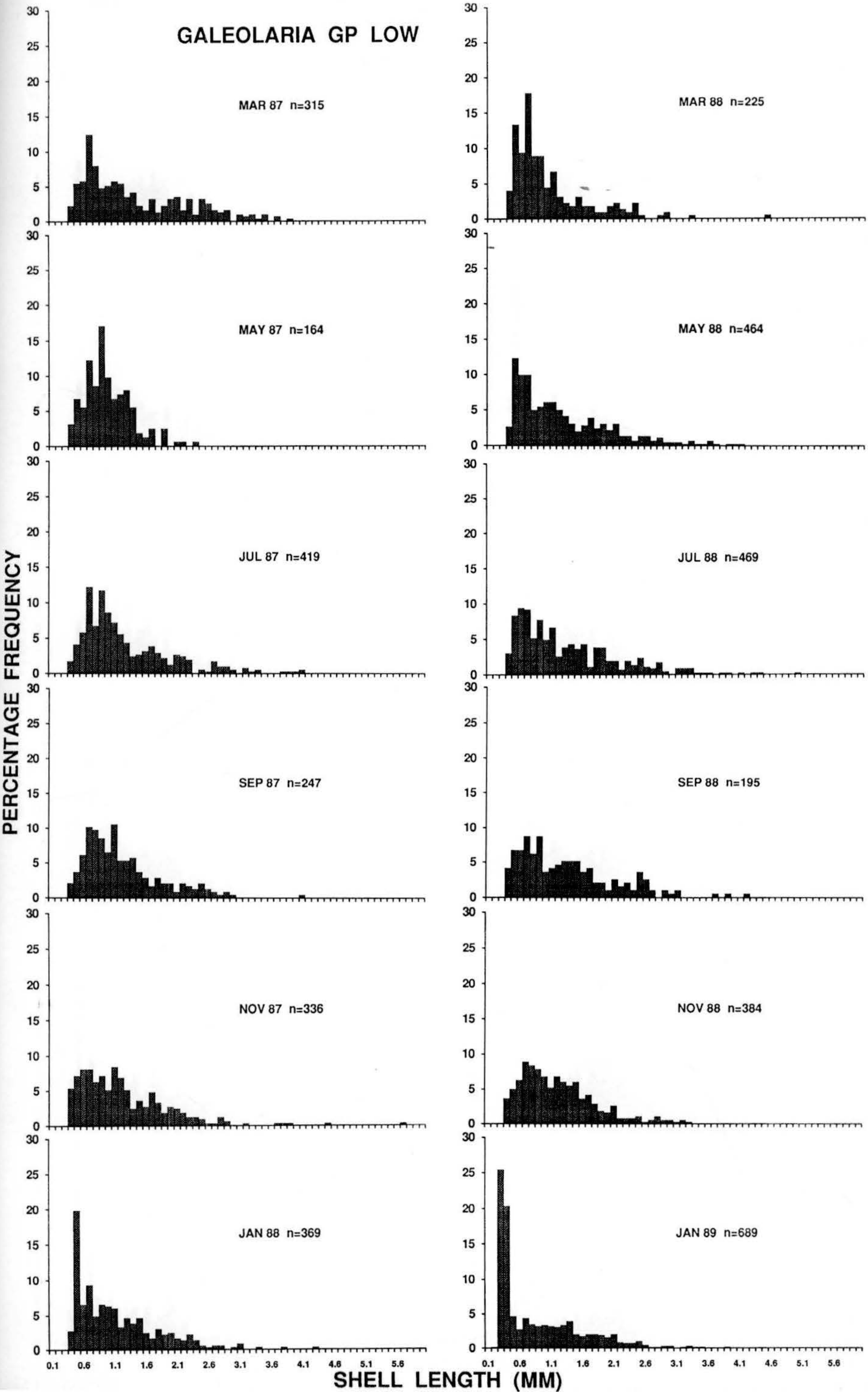

CORALLINA CB HIGH
MAR 87 n=126
MAY 87 n=211
JUL 87 n=142
SEP 87 n=56
NOV 87 n=133
JAN 88 n=202
MAR 88 n=357
MAY 88 n=423
JUL 88 n=270
SEP 88 n=164
NOV 88 n=162
JAN 89 n=512
PERCENTAGE FREQUENCY
0
5
10
15
20
25
30
35
0.1
0.6
1.1
1.6
2.1
2.6
3.1
SHELL LENGTH (MM)

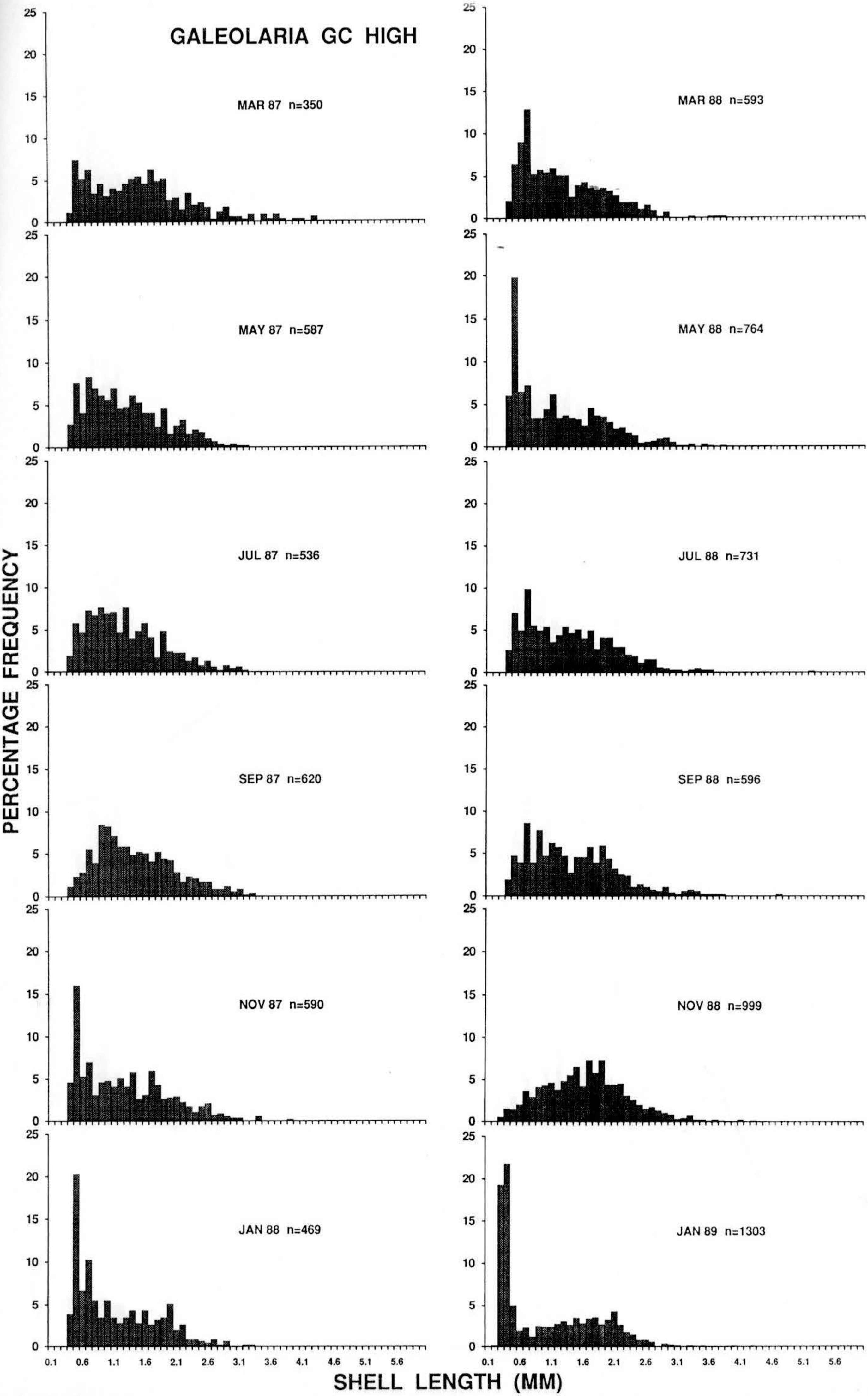

CORALLINA CB LOW
MAR 87 n=31
MAR 88 n=101
MAY 87 n=33
MAY 88 n=84
JUL 87 n=150
JUL 88 n=97
SEP 87 n=11
SEP 88 n=241
NOV 87 n=44
NOV 88 n=44
JAN 88 n=71
JAN 89 n=286
0
10
20
30
40
50
60
PERCENTAGE FREQUENCY
0.1
0.6
1.1
1.6
2.1
2.6
3.1
SHELL LENGTH (MM)


CORALLINA CC HIGH
MAR 87 n=220
MAR 88 n=325
MAY 87 n=219
MAY 88 n=494
JUL 87 n=229
JUL 88 n=581
SEP 87 n=232
SEP 88 n=560
NOV 87 n=311
NOV 88 n=428
JAN 88 n=475
JAN 89 n=840
PERCENTAGE FREQUENCY
0
5
10
15
20
25
30
35
0.1
0.6
1.1
1.6
2.1
2.6
3.1
SHELL LENGTH (MM)


CORALLINA CC LOW
MAR 87 n=16
MAR 88 n=26
MAY 87 n=34
MAY 88 n=11
JUL 87 n=31
JUL 88 n=43
SEP 87 n=14
SEP 88 n=31
NOV 87 n=72
NOV 88 n=17
JAN 88 n=56
JAN 89 n=65
PERCENTAGE FREQUENCY
0
5
10
15
20
25
30
35
40
0.1
0.6
1.1
1.6
2.1
2.6
3.1
SHELL LENGTH (MM)


GALEOLARIA GP HIGH
MAR 87 n=197
MAY 87 n=357
JUL 87 n=551
SEP 87 n=375
NOV 87 n=296
JAN 88 n=490
MAR 88 n=516
MAY 88 n=437
JUL 88 n=506
SEP 88 n=443
NOV 88 n=323
JAN 89 n=774
PERCENTAGE FREQUENCY
0
5
10
15
20
25
SHELL LENGTH (MM)
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
4.6
5.1
5.6


GALEOLARIA GP LOW
MAR 87 n=315
MAR 88 n=225
MAY 87 n=164
MAY 88 n=464
JUL 87 n=419
JUL 88 n=469
SEP 87 n=247
SEP 88 n=195
NOV 87 n=336
NOV 88 n=384
JAN 88 n=369
JAN 89 n=689
PERCENTAGE FREQUENCY
0
5
10
15
20
25
30
SHELL LENGTH (MM)
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
4.6
5.1
5.6


GALEOLARIA GC HIGH
MAR 87 n=350
MAY 87 n=587
JUL 87 n=536
SEP 87 n=620
NOV 87 n=590
JAN 88 n=469
MAR 88 n=593
MAY 88 n=764
JUL 88 n=731
SEP 88 n=596
NOV 88 n=999
JAN 89 n=1303
PERCENTAGE FREQUENCY
0
5
10
15
20
25
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
4.6
5.1
5.6
SHELL LENGTH (MM)

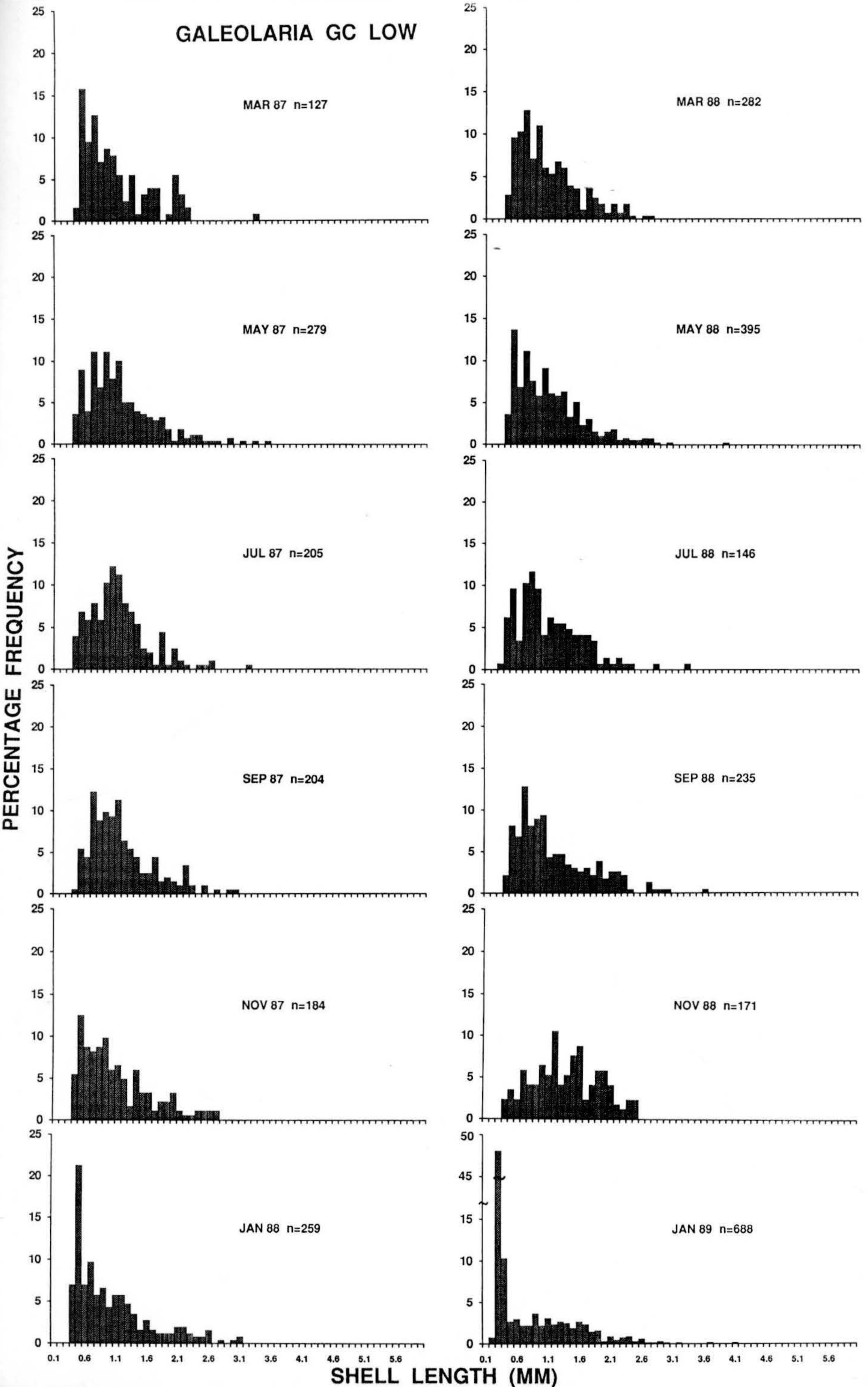

GALEOLARIA GC LOW
MAR 87 n=127
MAR 88 n=282
MAY 87 n=279
MAY 88 n=395
JUL 87 n=205
JUL 88 n=146
SEP 87 n=204
SEP 88 n=235
NOV 87 n=184
NOV 88 n=171
JAN 88 n=259
JAN 89 n=688
PERCENTAGE FREQUENCY
0
5
10
15
20
25
45
50
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
4.6
5.1
5.6
SHELL LENGTH (MM)

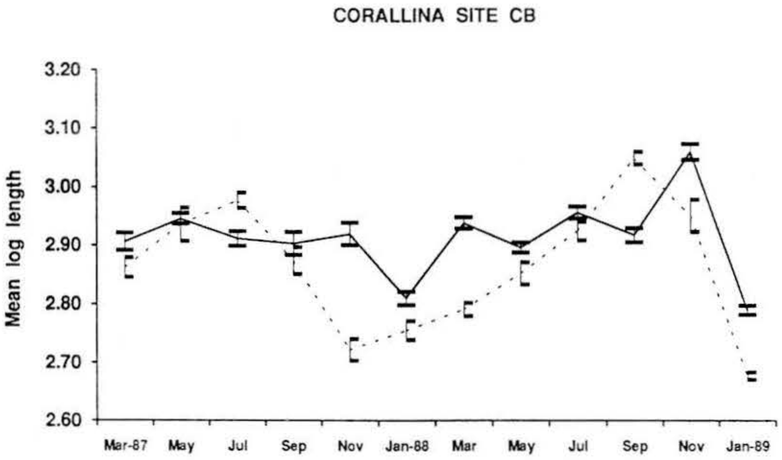
Figure 3.3. Bimonthly variation of mean (± S.E.) of the log shell length of *Lasaea* in the high (____) and low (_ _ _) areas.

a. *Corallina* Site CB

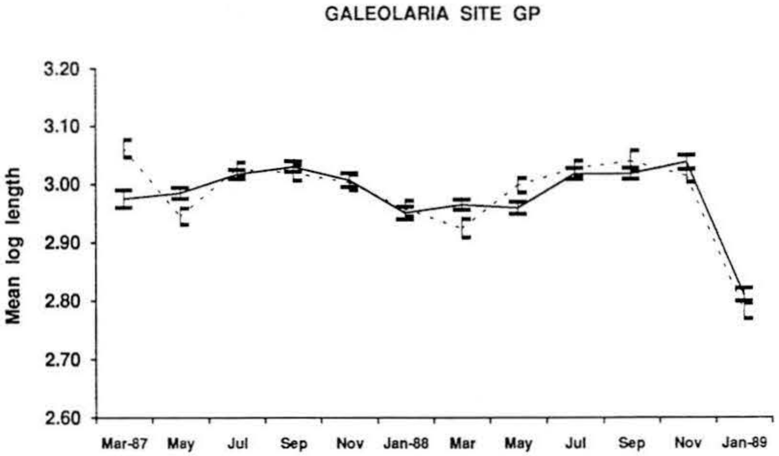
b. *Corallina* Site CC

c. *Galeolaria* Site GP

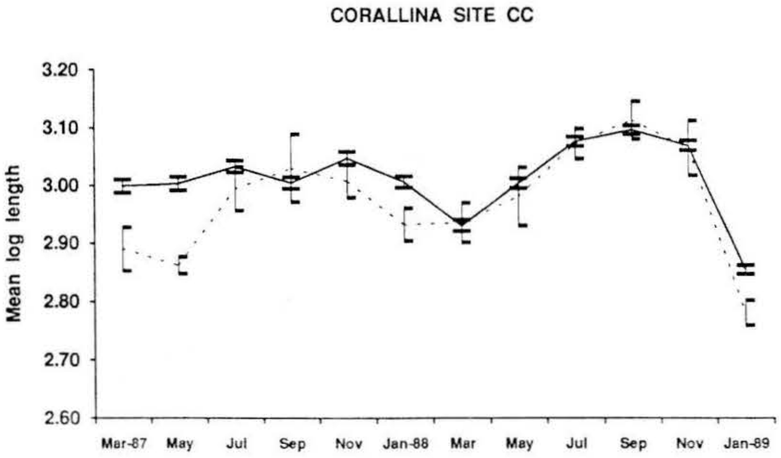
d. *Galeolaria* Site GC



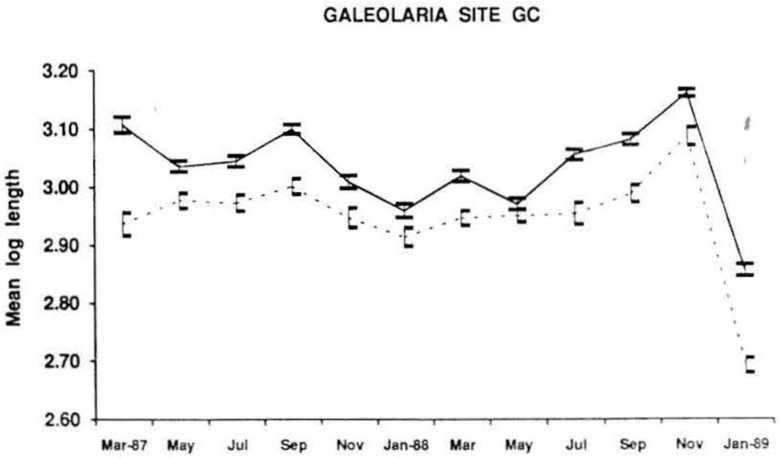
CORALLINA SITE CB



GALEOLARIA SITE GP



CORALLINA SITE CC



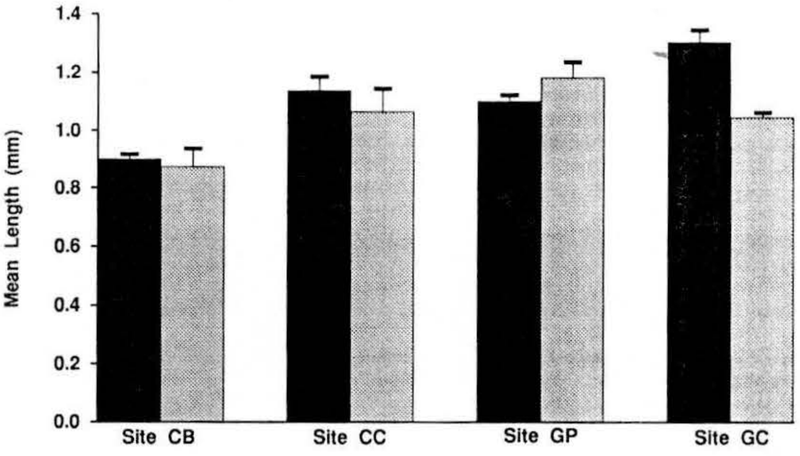
GALEOLARIA SITE GC

Figure 3.4. Mean (+ S.E.) shell length of *Lasaea* (from months excluding November and January) in the high (black) and low (stippled) areas.

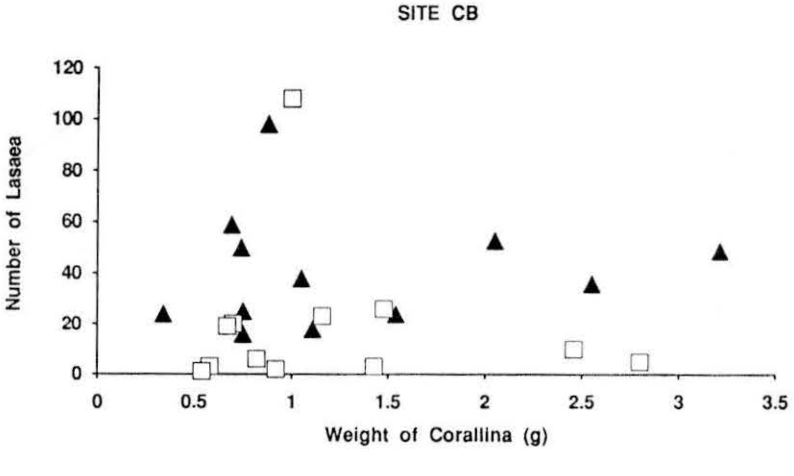
Figure 3.5. Relationship between biomass of *Corallina* and the number of associated *Lasaea* from the high (▲) and low (❐) areas.

a. Site CB

b. Site CC



SITE CB



SITE CC

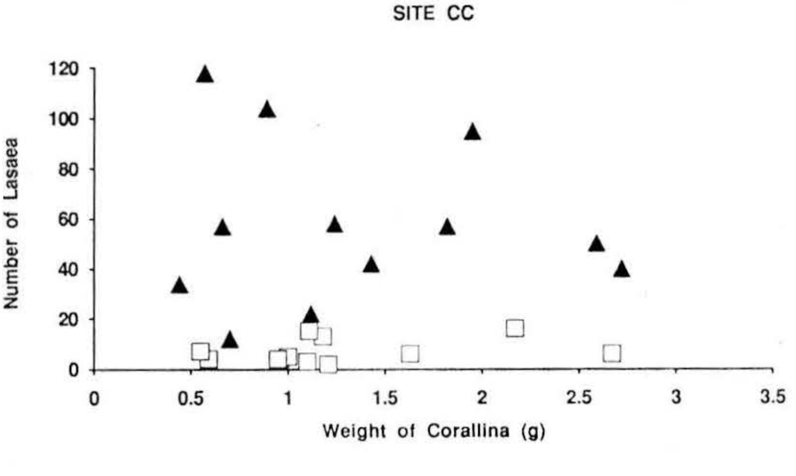
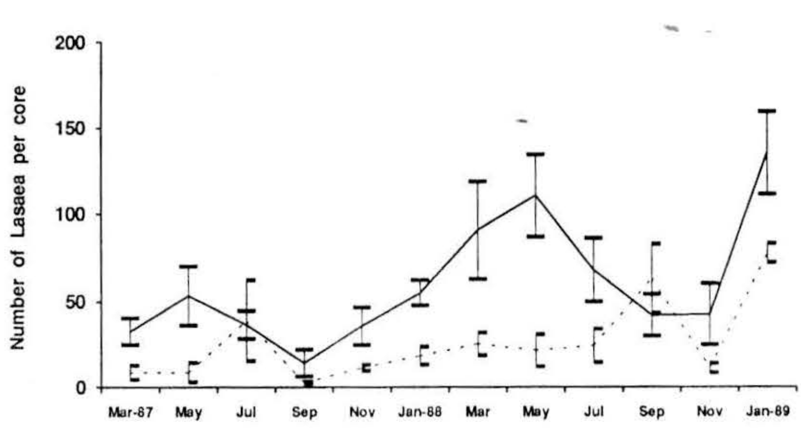


Figure 3.6. Bimonthly variation of mean (± S.E.) density of *Lasaea* from *Corallina* in the high (_____) and low (_ _ _) areas.

a. Site CB

b. Site CC

Figure 3.7. Mean (+ S.E.) density of *Lasaea* from *Corallina* in the high (black) and low (stippled) areas. Data were pooled from twelve sampling periods.


SITE CB

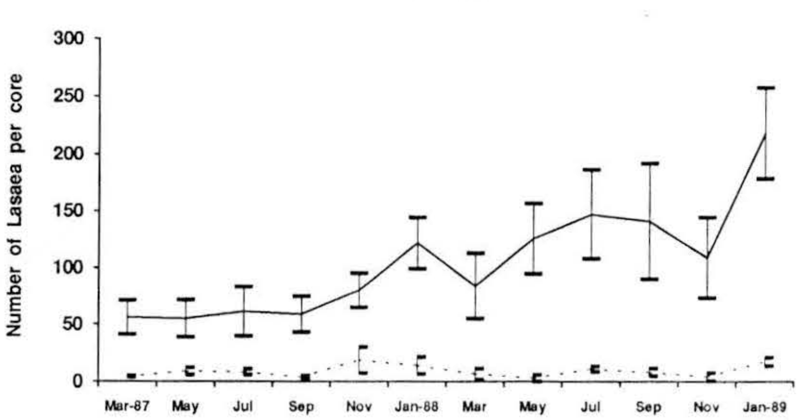
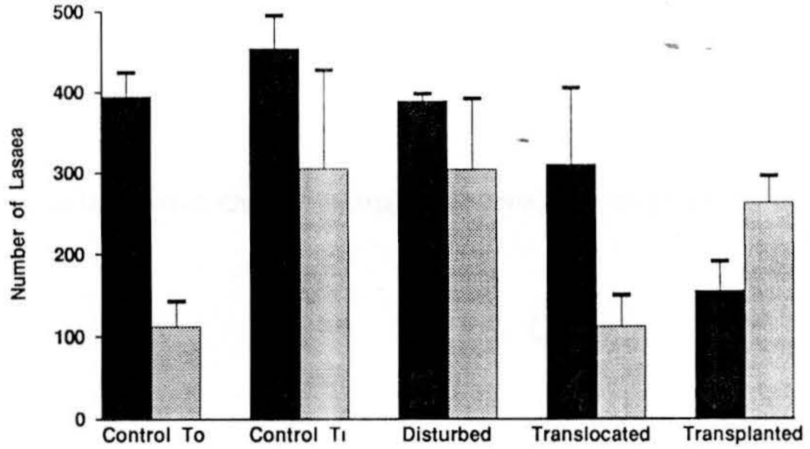

SITE CC

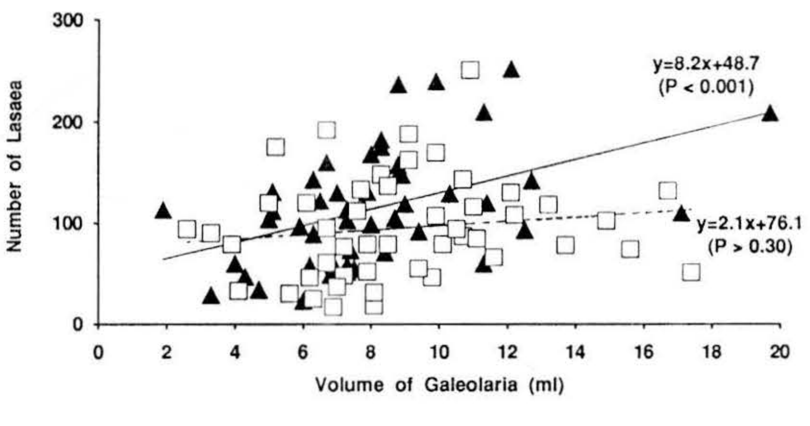
Figure 3.8. Mean (+ S.E.) density of *Lasaea* from high-shore (black) and low-shore (stippled) *Corallina* cores treated in the following manner:

Control T_0 : drilled at the start
Control T_1 : drilled at the end
Disturbed : replaced on the same spot
Translocated : intrashore-level transplant
Transplanted : intershore-level transplant

Figure 3.9. Relationship between volume of *Galeolaria* and the number of associated *Lasaea* from the high (▲) and low (❐) areas.

a. Site GP
b. Site GC




SITE GP

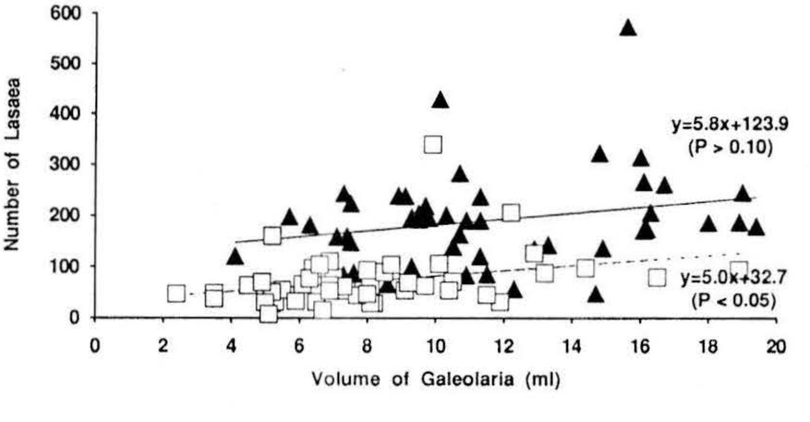

SITE GC

Table 3.1.

The mean height (m above chart datum) (S.D., *n*=2) of the 8 sampling areas.

	CC	CB	GP	GC
High	0.60(0.1)	0.56(0.09)	0.97(0.05)	1.35(0)
Low	0.59(0.08)	0.37(0.04)	0.89(0.05)	1.12(0.18)

Table 3.2.

Analysis of mean log shell length of the eight *Lasaea* populations (Sites were nested within Substrata). The eight replicates were the values from months excluding the major recruitment season, *i.e.*, November and January. Cochran's test was significant (0.05 > P > 0.01). Therefore, the F-ratio is considered to be significant only when $P < 0.01$. In this and subsequent tables, * denotes $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

SOURCE	DF	MS	*F*
Substratum	1	0.0344	1.14
Site (Sub)	2	0.0303	10.82 ***
Height	1	0.0153	1.61
Sub X Ht	1	0.0008	0.08
Site (Sub) X Ht	2	0.0095	3.39 *
Residual	56	0.0028	
Total	63		

SNK-test on the means for significant effect of Site (Sub):

Corallina substratum:	CB	<	CC
	2.915		3.002
Galeolaria substratum:	GP		GC
	$\underline{3.000}$		$\underline{3.009}$

(values underlined are not significantly different at $P = 0.05$ in this and subsequent tables)

Table 3.3.

Analysis of number of *Lasaea* per core from the four *Corallina* populations. All data were transformed as square-root(x+1) to homogenize the variance (Cochran's test).

SOURCE	DF	MS	*F*
Site	1	6.33	1.12
Month	11	37.86	6.72 **
Height	1	1096.76	5.25
Si X Mth	11	5.63	1.25
Si X Ht	1	208.97	31.90 ***
Mth X Ht	11	8.83	1.35
Si X Mth X Ht	11	6.55	1.46
Residual	144	4.50	
Total	191		

SNK-test on the means for significant effect of Si X Ht:

	high		low
at CB:	7.27	>	4.57
at CC:	9.72	>	2.85
at high:	CB	<	CC
at low:	CB	>	CC

SNK-test on the means for significant effect of Month:

Jan89	>	Sep88	Jul88	May88	Jan88	Mar88	Nov87
9.80		6.97	6.95	6.85	6.51	6.32	5.56
		Jul87	Nov88	May87	Mar87	Sep87	
		5.51	5.37	5.03	4.56	3.78	

Table 3.4.

Analysis of numbers of *Lasaea* in the *Corallina* cores from a transplant experiment. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Height	1	110170.8	9.41 **
Treatment	4	37385.5	3.19 *
Ht X T	4	32269.7	2.76
Residual	20	11711.4	
Total	29		

SNK-test on the means for significant effect of Treatment:

Transplanted	Moved	Control T_0	Disturbed	Control T_1
207	210	253	346	379

SNK-test on the means for significant effect of Height:

low	<	high
218		339

CHAPTER FOUR POPULATION STRUCTURE OF *LASAEA* IN ARTIFICIAL SUBSTRATA

4.1 Introduction

The study of algal associates often involves destructive sampling of the algae because of the small size of the cryptofauna (Colman, 1939; Wieser, 1952; Fretter & Manly, 1977; Dean & Connell, 1987a). There have been few reports on the successful manipulation of live algae for field experiments (but see Dean & Connell, 1987b). Instead, most workers have approached the problem by the use of plastic algal mimics (Myers & Southgate, 1980; Dean & Connell, 1987b; Gibbons, 1988). These artificial substrata housed a similar suite of organisms as their natural counterparts. In addition to algal studies, artificial units have been used quite commonly in seagrass research (Bell *et al.*, 1985; Virnstein & Curran, 1986; Sogard, 1989).

In this study, the *Corallina* were badly damaged after the complete defaunation of *Lasaea* because the fronds were so tightly packed. Hence, an algal mimic was used as an experimental unit. Besides its relative ease of manipulation, artificial substrata can serve as a standard unit for investigating the effect of the different spatial and temporal factors on *Lasaea*.

4.2 Materials and methods

The artificial turf with the tradename "Supergrasse" was used as an artificial substratum. It is composed of tufts of polypropylene strips arranged in regular rows on a latex back. Each experimental unit was 12 X 12 cm^2 with the edges reinforced by a contact adhesive "Kwik Grip". The square was then secured to the rock platform at the four corners by lead washers and stainless steel screws fitted to line plugs embedded within predrilled holes.

At the end of the experiment, the organisms attached to the surface of the Supergrasse were first removed. The material trapped among the tufts was then brushed off and preserved in 0.1% Rose Bengal/alcohol. To facilitate sorting, each sample was first divided into three fractions by passing through a series of 1 mm, 265 μm and 75 μm sieves. The 75 μm sieve could retain the *Lasaea* recruits (length: 225-270 μm, height: 205-225 μm) while the 1 mm sieve would eliminate the amphipods and the isopods from the main fraction (*i.e.* >265 μm-1 mm) of the sample. After removing the *Lasaea* from each fraction, the sediment component consisting of sand grains and shell grit was oven-dried before weighing to the nearest 0.01 g.

Supergrasse squares were initially set up at Sites CV, CP and WR (see Fig. 3.1) in December 1987 and January 1988 to investigate the *Lasaea* populations in the artificial substratum after a long exposure period. Four plots (2-19 m apart) were assigned to each of the mid and low intertidal levels at each site (see Table 4.1 for their absolute heights). Within each of these 1-2.5 m^2 plots were five squares each secured to a flat, bare area. In November 1988 (*i.e.* after 11 months), two squares were removed from each of the two plots at each height at Site CV to free the space for another experiment. At Sites CP and WR, the squares were not retrieved until January 1989 (after 12-13 months). In December 1989 (after 23-24 months), another two squares were recovered from each of the remaining two plots at each level of all three sites. Squares with a lot of *Lasaea* were subsampled by randomly choosing four 3 X 3 cm^2 areas. The results were then expressed as per square basis after correction for the area occupied by the washers. In order to save time, the <= 265 µm fraction consisting mainly of detritus was discarded. The shell lengths of *Lasaea* were only determined for one sample from each plot using an Image Analyzer.

In order to monitor the arrival of *Lasaea* over a shorter time scale, three 1 m^2 plots were set up at the mid and low areas at Site PB (see Table 4.1 & Fig. 3.1) in April 1988. The plots at each height were 2-4 m apart and within each plot were four randomly distributed Supergrasse squares. At Week 1, 2, 4 and 11 respectively, one square was removed from each plot for analysis. Two *Lasaea* samples at each height were measured from squares exposed for two and eleven weeks respectively.

In order to test the retention property of Supergrasse for *Lasaea*, fifty animals (shell length: 1.5-2.2 mm) were seeded into the central 7 X 7 cm^2 zone of each square. Animals were marked with an Indian ink dot, protected by a transparent "Supa Glue" coating. Three 1 m^2 plots (2-4 m apart) each with four of these squares were set up near Site CB (Fig. 3.1) in April 1988. At Week 1, 2, 4 and 12 respectively, the numbers of marked *Lasaea* remaining in a square from each plot was determined.

A short-term arrival experiment was also set up at Sites CV, CP and WR in February 1989. At the mid and low areas, two 1-2.5 m^2 plots each with three Supergrasse squares were left on the rock platform for two weeks. One *Lasaea* sample from each plot was also measured.

To show that the arrival of *Lasaea* into the Supergrasse squares was not an artificial phenomenon, the *Corallina* fronds were scraped off from two 1 X 1 m^2 plots at both Site A (near Site CP) and Site B (near Site CB) in May 1989. The basal crust of *Corallina* was brushed to clean off any attached *Lasaea*. After allowing the fronds to regenerate for six months, two *Corallina* cores (diameter: 4.12 cm) were taken from each plot to check for the presence of *Lasaea*. The shell lengths of the animals in each sample were also determined.

4.3 Results

4.3.1 Structure of *Lasaea* populations in Supergrasse over a three-month period

The numbers of *Lasaea* collected in the artificial substrata were found to increase with time (Fig. 4.1). At each height, there were significantly more animals in Week 4 and Week 11 than in Week 1 and Week 2 (Table 4.2). During the first two weeks of exposure, there was no significant difference in the numbers of *Lasaea* between the two heights, but, by Week 4, more bivalves were present in the higher area and this trend continued until Week 11.

Similar to the condition in *Lasaea*, the amount of sediment accumulated in the Supergrasse increased with period of exposure (Fig. 4.2). There was a drastic increase in sediment from Week 4 to Week 11 but this was not observed in the numbers of *Lasaea* (Table 4.3). Moreover, there was no increased with time and there was a significant rise from Week 2 onwards (Fig. 4.8; Table 4.7).

4.3.3 Structure of *Lasaea* populations in Supergrasse during a two-week period

About 90% of all six *Lasaea* populations collected in February 1989 were less than 1 mm in length (Fig. 4.9) with a mean value of 0.5-0.7 mm (Fig. 4.10). These six populations did not differ significantly in size from one another (Table 4.8). There was, however, a marked difference in density at the three sites (Fig. 4.11; Table 4.9). Irrespective of height on the shore, *Lasaea* was least abundant at Site CV. At Sites CP and WR, more *Lasaea* were present at the higher level, while at Site CV, they were equally scarce at the two heights.

The amount of sediment collected in the squares followed a similar pattern except that no significant difference was detected across the three sites in the low shore (Fig. 4.12; Table 4.10). When the samples from the two heights were pooled, the numbers of *Lasaea* were again significantly correlated with the biomass of the sediment at each of the study sites (Fig. 4.13).

4.3.4 Structure of *Lasaea* populations in Supergrasse over a two-year period

All the *Lasaea* populations from long-term Supergrasse squares displayed a large size range (Fig. 4.14). Unlike the situation at Sites CP and WR, *Lasaea* 0.2-0.5 mm in length did not form a distinct peak in the CV populations because these one-year-old squares were removed two months earlier. Therefore, they failed to trap the recruits that arrived in January 1989. The two-year-old squares also failed to collect any recruits and hence lacked a peak of young bivalves. Subsequent population analyses were therefore carried out on animals more than 0.5 mm in size.

The mean shell-length of the twelve populations varied between 1.1-2.1 mm (Fig. 4.15). *Lasaea* from Year 2 squares were larger than those from Year 1 (Table 4.11). Besides, members of the CV population were consistently larger than those from the other two populations. Interestingly, similar to the situation in natural substrata, there was no significant difference in size between the animals collected at the two heights.

The numbers of *Lasaea* collected in the squares showed a more variable pattern because the Year X Site X Height interaction was found to be significant (Fig. 4.16; Table 4.12). To summarise, *Lasaea* were either more abundant in Year 2 than in Year 1 squares or there was no significant difference between them. With respect to tidal height, the mid shore squares either contained more *Lasaea* than low shore ones or no significant difference was detected. Except in one situation, the CV squares always supported the least number of *Lasaea*.

As with the abundance of bivalves, squares from Site CV contained the least quantity of sediment regardless of their position on the shore and period of exposure (Fig. 4.17; Table 4.13). The effect of height was most obvious at Site WR whereby a greater biomass of sediment was accumulated at the higher level.

Unlike the pattern in the short-term study, the total numbers of *Lasaea* in the Supergrasse squares were not significantly correlated with the biomass of the co-occurring sediment at the three sites in the two years ($P > 0.05$; Fig. 4.18).

4.3.5 Structure of *Lasaea* populations in regenerated *Corallina*

Lasaea was able to colonize the regenerated fronds of *Corallina* during the six months. The population from each plot at each of the sites was polymodal (Fig. 4.19). Their mean shell-lengths varied between 1.1-1.5 mm which were not significantly different from each other (Fig. 4.20; Table 4.14).

4.4 Discussion

During the first week of deployment, Supergrasse squares were already colonized by *Lasaea*. These bivalves presumably arrived via the water column because postlarval *Lasaea* could be found in some preliminary plankton samples. Migration into the squares by crawling seemed unlikely because the closest source population could be tens of metres away. Various workers have reported the active entry of postlarval bivalves into the water column (Bayne, 1964; Sigurdsson *et al.*, 1976; Prezant & Chalermwat, 1984; Lane *et al.*, 1985; Beukema & de Vlas, 1989) by secreting mucous threads to increase the viscous drag of the animals. Highsmith (1985) suggested that this mechanism of byssal drifting was useful for dispersal, especially for brooding invertebrates. *Lasaea australis* broods its embryos, but it produces free-swimming larvae and therefore does not have to rely solely on this method for dispersal. Active entry of *Lasaea* into the water column was hence doubtful. Instead, passive transport was more likely because *Lasaea* was often associated with substrata such as *Corallina*, *Hormosira* holdfasts and underneath encrusting *Hildenbrandia* which were quite susceptible to dislodgement by waves.

Suspended particles in the water column would be deposited at places where there was a reduction in water flow or an abrupt change in shore profile (Sanders, 1958; Matthiessen, 1960). A decrease in water flow has been recorded amongst algae (Fretter & Manly, 1977; Dean & Connell, 1987c) and presumably within the artificial tufts used in this study. The Supergrasse squares therefore functioned as sediment traps. The trapped material was, however, free to leave because the squares are not closed traps. The 30% reduction of marked *Lasaea* throughout the three-month period possibly indicates this initial loss of bivalves before they have settled down properly in the squares.

In general, the amounts of *Lasaea* and sediment collected in the Supergrasse squares increased with the period of exposure on the rock platform presumably because of the increase in volume of water flow over the squares with time. This rise was still apparent from the first to the second year. Where height was shown to be important at a study site, there was always a trend for more material to be collected in the mid than in the low shore. A similar pattern of accumulation of sediment was reported in plastic algal mats by Gibbons (1988). This was probably due to the greater force of waves at the low shore thus lowering the chance of sediment accumulating there.

In some experiments, the pattern of accumulation of *Lasaea* and sediment in Supergrasse squares over time and space were similar. During short periods (two weeks and three months), there was a significant linear correlation between the numbers of *Lasaea* and the amount of sediment collected. This relationship was, however, not observed in the one-year and two-year study. This aspect of *Lasaea*-sediment interaction will be dealt with in more detail in Chapter 5.

Since there was a continuous influx of *Lasaea* into Supergrasse squares, the time scale for short-term experiments was chosen to be two weeks during which about 50-200 animals could possibly be sampled. The size of the bivalves then collected would reflect the size range of the animals being washed off. The mean shell-length of *Lasaea* populations from two-week-old squares were respectively 0.4-0.6 mm and 0.5-0.7 mm for the April 1988 and the February 1989 samples. This suggested that smaller animals were more vulnerable to dislodgement than larger ones. Similar results have been documented for the bivalve *Corbicula fluminea* in streams (Payne *et al.*, 1989). With an increase in period of exposure, the *Lasaea* populations in the squares would comprise a mixture of recent and early settlers. During that period, there would be growth of the early settlers and the source populations from which the recent settlers originated. Hence, this might explain the increase in mean size of *Lasaea* detected from Week 2 to Week 11.

The short-term and long-term Supergrasse experiments were set up in the same area at the three study sites. No statistical comparison was run because of their different starting time. The two-week study revealed no size difference between the *Lasaea* populations at the three sites. If this pattern of arrival was consistent over time, the disparity in size between the *Lasaea* populations from long-term squares at the three study sites would be caused by a post-settlement process. At Site CV, the squares were always sparsely colonized by *Lasaea* and sediment over both time scales. First, the south-east ocean swell would probably have unloaded most of its suspended particles by the time it traversed into the cove to Site CV. Second, intense wave action (pers. obs.) would reduce sedimentation there. Therefore, assuming that the numbers of *Lasaea* were influenced by the amount of sediment, after a period of one to two years, the density of *Lasaea* at Site CV was recorded to be 2-4 times less than at the other two sites.

The bivalves were, however, significantly larger at Site CV. If the mean size of the population reflects growth, this would imply a density-dependent effect on the growth of *Lasaea*. By seeding marked *Lasaea* at different densities into the Supergrasse squares, the response of rate of growth to density could be monitored. Excessive numbers of animals would have to be added to compensate for the loss during the initial stage of the experiment.

A reduction in growth has been observed by increasing the density of burrowing bivalves in experimental plots (Peterson & Black, 1987; Peterson & Beal, 1989). This phenomenon of nutrient depletion at the benthic boundary layer by suspension-feeders has only been demonstrated in laboratory flume study (Wildish & Kristmanson, 1984), in sheltered estuarine environment (Fréchette & Bourget, 1985; Fréchette *et al.*, 1989) and using submerged panels (Buss & Jackson, 1981). Whether a similar process occurs in the more dynamic, well-mixed rocky intertidal environment remains to be tested.

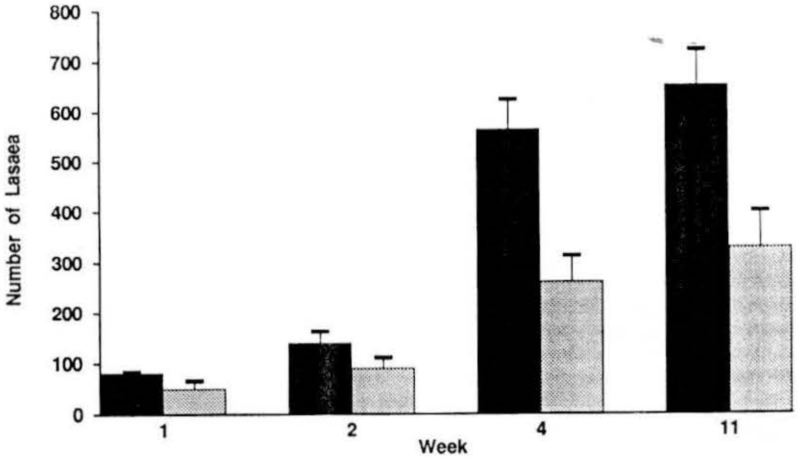
Corallina officinalis produced encrusting and erect thalli. This heterotrichous character of the algae enabled their quick recovery after any physical or biological disturbance (Littler & Kauker, 1984). The power of regeneration of *Corallina* was also observed in this study because newly-grown fronds had already appeared four months after the areas were scraped. This offered a virgin substratum for colonization by *Lasaea* via the water column and by a few crawling migrants from the neighbouring *Corallina* bed. This reinforced the notion that the trapping of *Lasaea* by Supergrasse squares was not an artificial phenomenon.

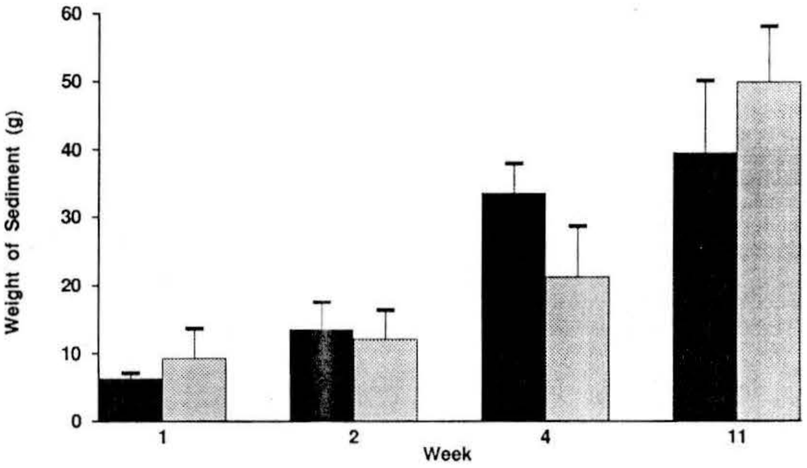
The Supergrasse squares used in this study were not an exact replica of *Corallina* due to the regular arrangement of the artificial tufts. Despite their nature, they did not seem to show any deleterious effect on the survival of *Lasaea* and bivalve populations could establish there for at least two years. *Lasaea* as small as 0.2 mm from the recruitment peak in January 1989 (see Chapter 3) were picked up by the Year 1 squares at Sites CP and WR. Therefore, Supergrasse squares could function as traps for young recruits and adults and a suite of other marine organisms. Unlike *Corallina,* Supergrasse is more uniform in physical structure and thereby minimises the variation due to inherent characteristics of the substratum. This renders it a suitable experimental unit in manipulative experiments for testing the effect of other main factors on *Lasaea* and other algal associates.

Figure 4.1. Mean (+ S.E.) number of *Lasaea* collected in Supergrasse squares over a three-month period in the mid (black) and low (stippled) areas.

Figure 4.2. Mean (+ S.E.) weight of sediment collected in Supergrasse squares over a three-month period in the mid (black) and low (stippled) areas.

Figure 4.3. Relationship between biomass of sediment and the number of *Lasaea* collected in Supergrasse squares over a three-month period from the mid (▲) and low (❐) areas.


800
700
600
500
400
300
200
100
0
Number of Lasaea
1
2
4
11
Week


60
50
40
30
20
10
0
Weight of Sediment (g)
1
2
4
11
Week

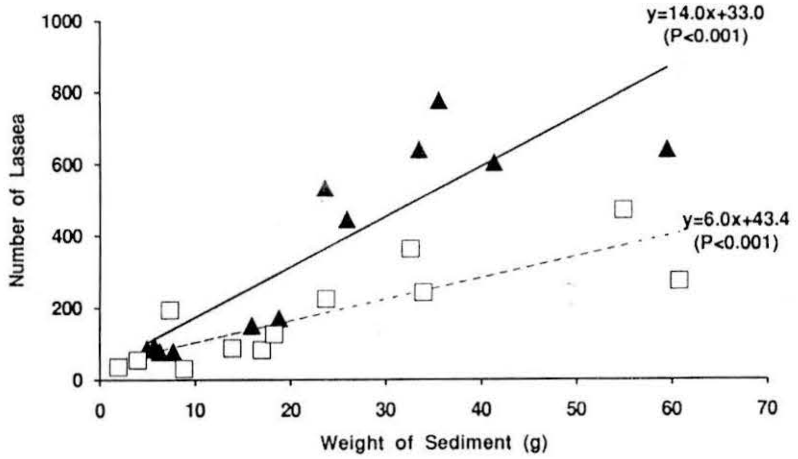
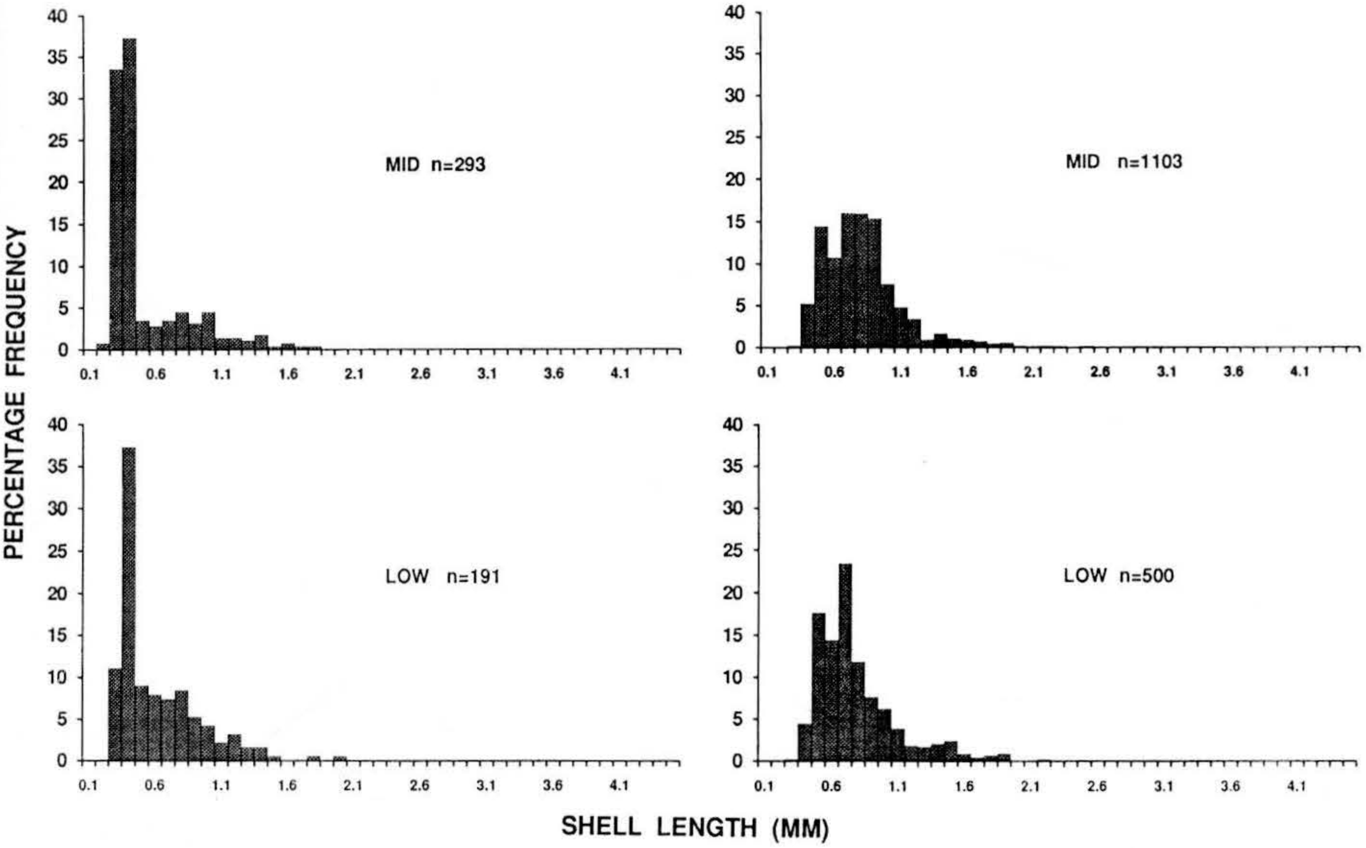

1000
800
600
400
200
0
Number of Lasaea
0
10
20
30
40
50
60
70
Weight of Sediment (g)
y=14.0x+33.0
(P<0.001)
y=6.0x+43.4
(P<0.001)

Figure 4.4. Size-frequency histograms of *Lasaea* from two-week (left) and eleven-week (right) Supergrasse squares at the two heights. Data were pooled from two replicates.

Figure 4.5. Mean (+ S.E.) shell length of *Lasaea* from two-week and eleven-week Supergrasse squares in the mid (black) and low (stippled) areas.


PERCENTAGE FREQUENCY
MID n=293
MID n=1103
LOW n=191
LOW n=500
0
5
10
15
20
25
30
35
40
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
SHELL LENGTH (MM)

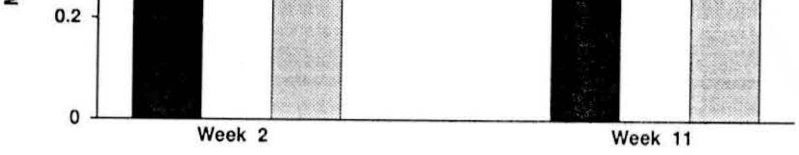
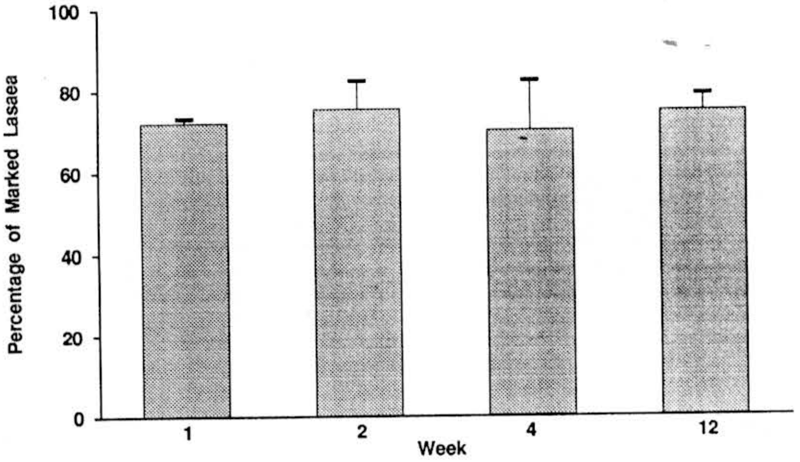
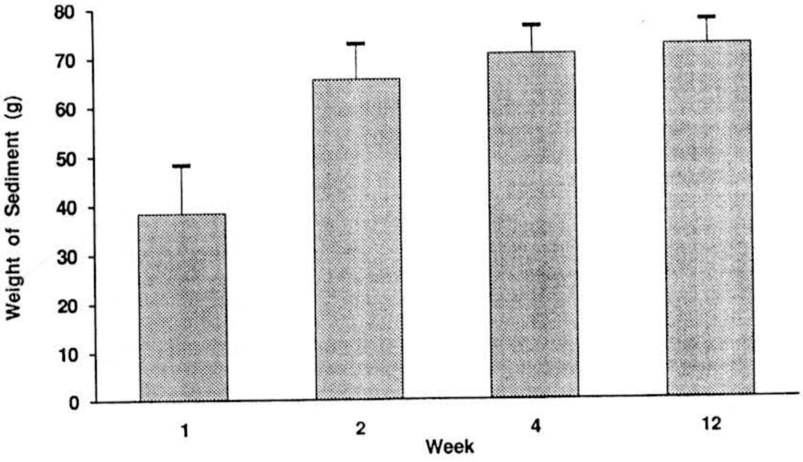

Mean Length (mm)
0
0.2
0.4
0.6
0.8
Week 2
Week 11

Figure 4.6. Mean (+ S.E.) percentage of marked *Lasaea* remaining in Supergrasse squares over a three-month period.

Figure 4.7. Mean (+ S.E.) weight of sediment collected in Supergrasse squares over a three-month period.

Figure 4.8. Mean (+ S.E.) number of *Lasaea* collected in Supergrasse squares over a three-month period.


Percentage of Marked Lasaea
100
80
60
40
20
0
1
2
4
12
Week


Weight of Sediment (g)
80
70
60
50
40
30
20
10
0
1
2
4
12
Week

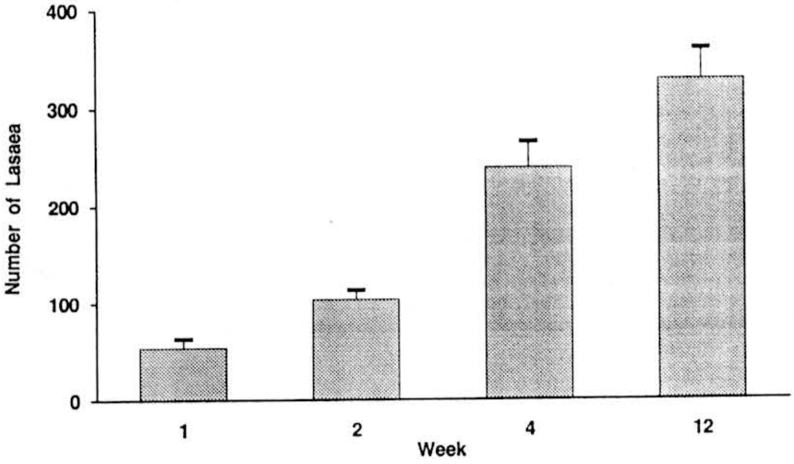
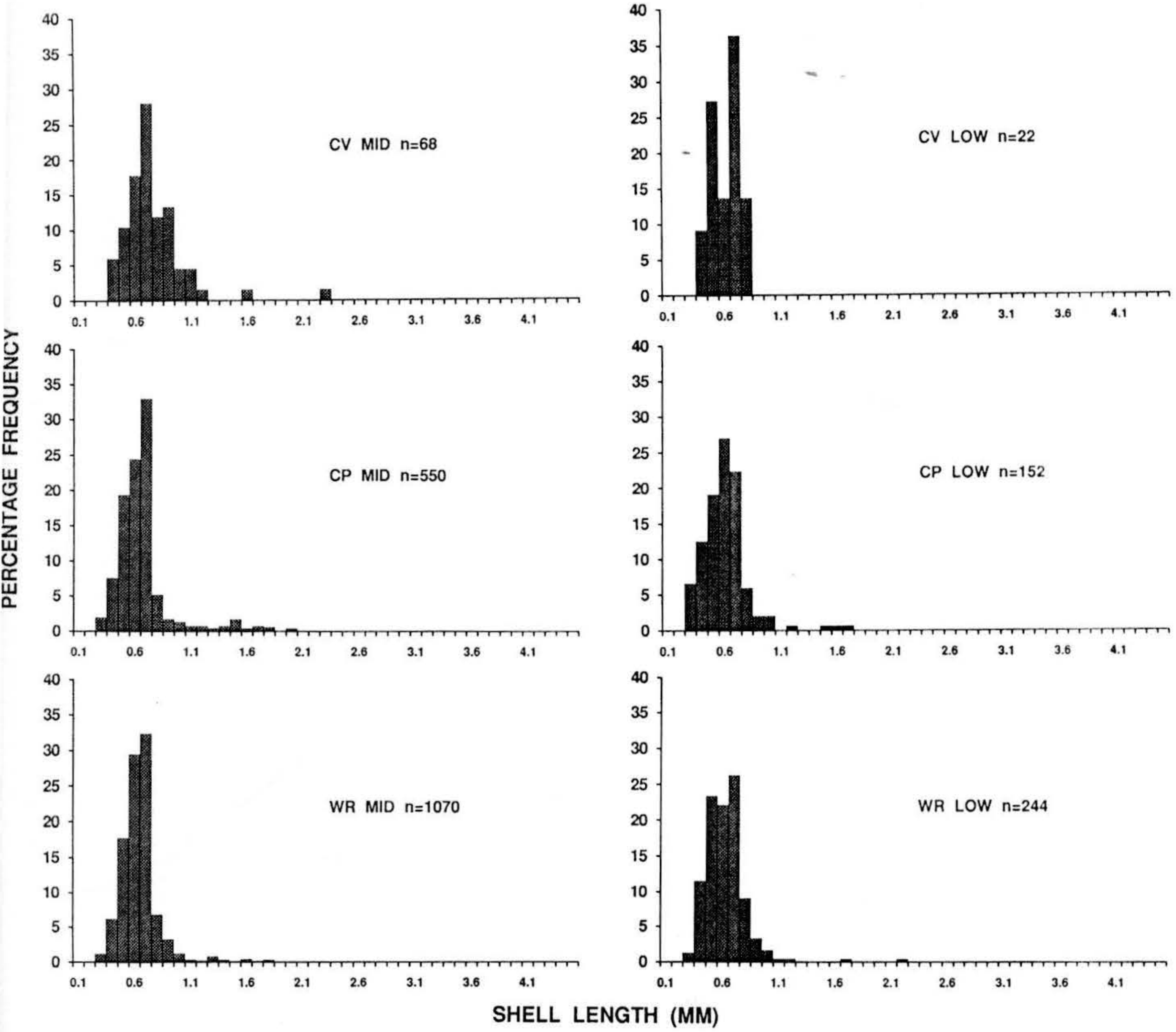

Number of Lasaea
400
300
200
100
0
1
2
4
12
Week

Figure 4.9. Size-frequency histograms of *Lasaea* from two-week Supergrasse squares at the two heights of the three study sites. Data were pooled from two replicates.

Figure 4.10. Mean (+ S.E.) shell length of *Lasaea* from two-week Supergrasse squares in the mid (black) and low (stippled) areas at the three study sites.


PERCENTAGE FREQUENCY
SHELL LENGTH (MM)
CV MID n=68
CV LOW n=22
CP MID n=550
CP LOW n=152
WR MID n=1070
WR LOW n=244
0
5
10
15
20
25
30
35
40
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1

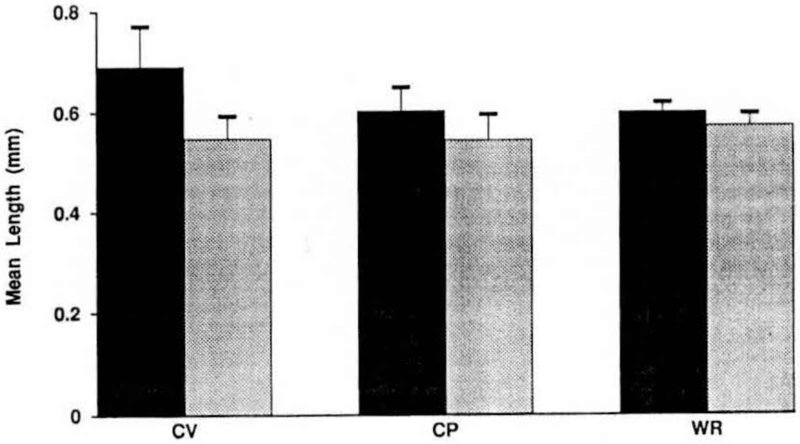
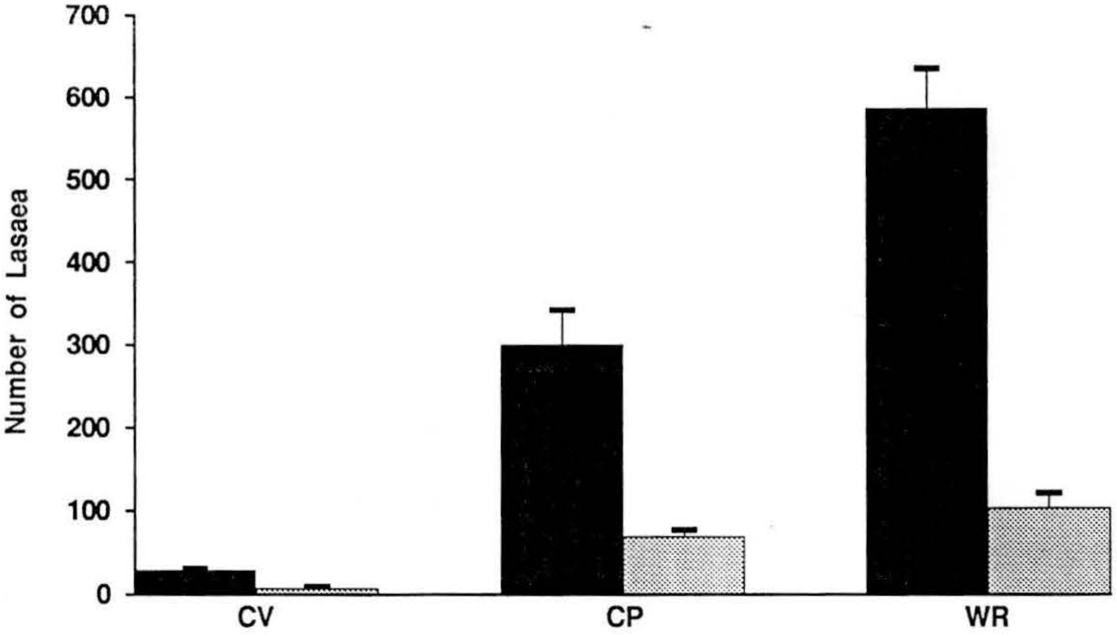

Mean Length (mm)
0
0.2
0.4
0.6
0.8
CV
CP
WR

Figure 4.11. Mean (+ S.E.) number of *Lasaea* collected in two-week Supergrasse squares in the mid (black) and low (stippled) areas at the three study sites. Data were pooled from two plots.

Figure 4.12. Mean (+ S.E.) weight of sediment collected in two-week Supergrasse squares in the mid (black) and low (stippled) areas at the three study sites. Data were pooled from two plots.


Number of Lasaea
700
600
500
400
300
200
100
0
CV
CP
WR

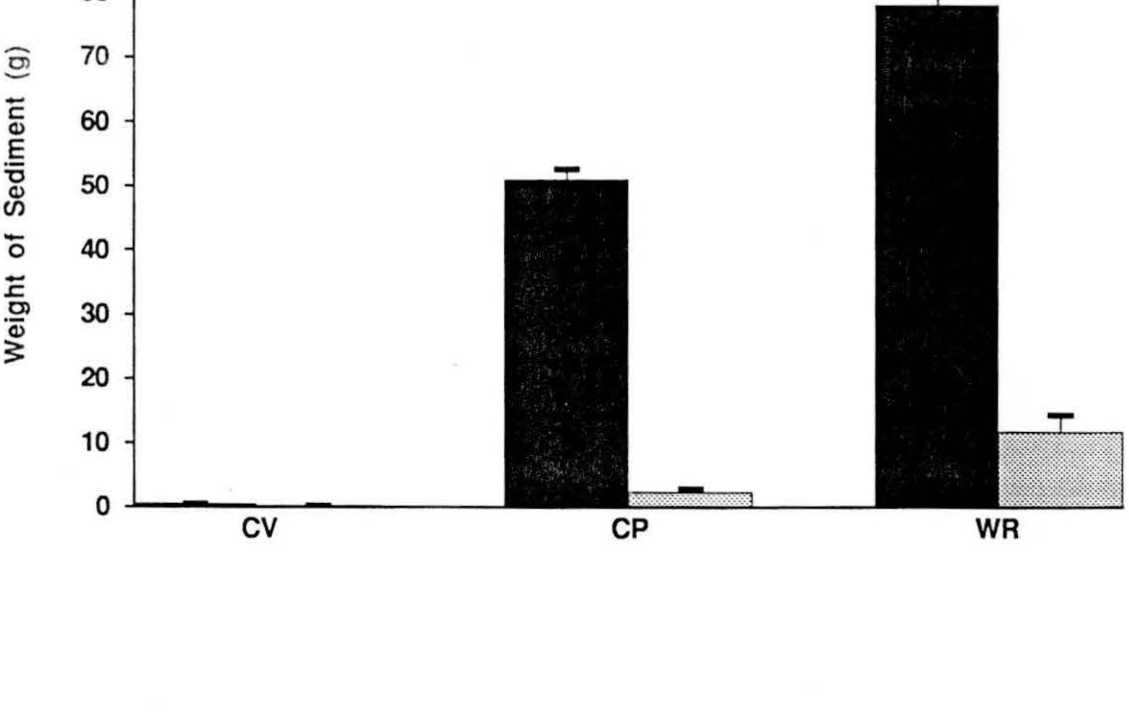
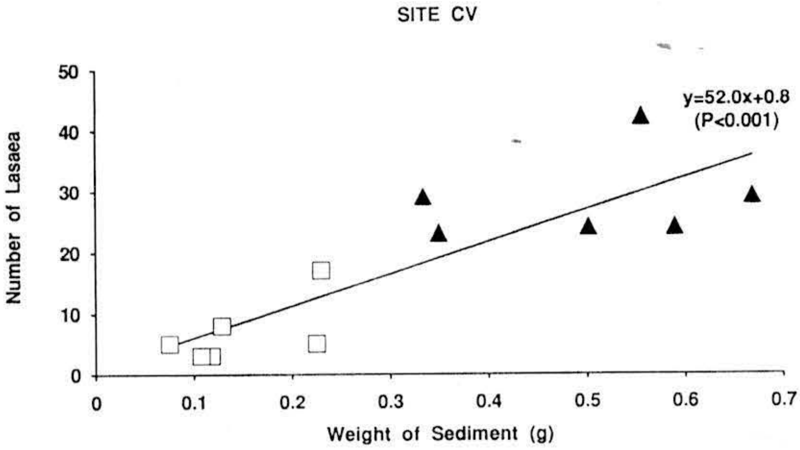

Weight of Sediment (g)
90
80
70
60
50
40
30
20
10
0
CV
CP
WR

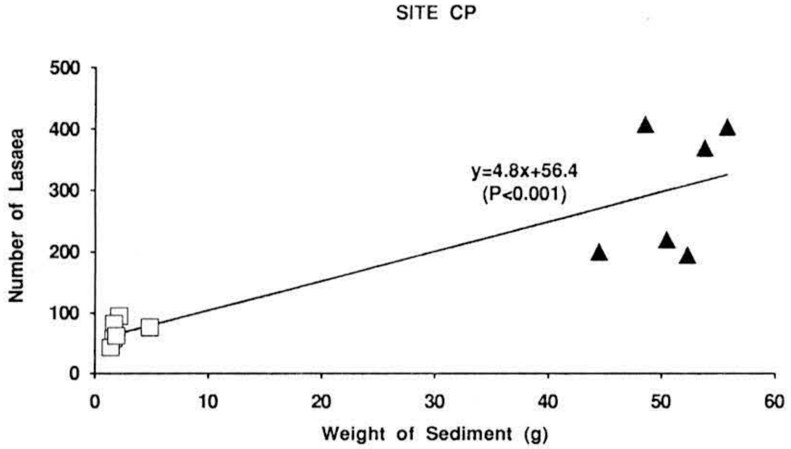
Figure 4.13. Relationship between biomass of sediment and the number of *Lasaea* collected in two-week Supergrasse squares from the mid (▲) and low (❐) areas.

a. Site CV

b. Site CP

c. Site WR


SITE CV
Number of Lasaea
Weight of Sediment (g)
y=52.0x+0.8
(P<0.001)
0
10
20
30
40
50
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7


SITE CP
Number of Lasaea
Weight of Sediment (g)
y=4.8x+56.4
(P<0.001)
0
100
200
300
400
500
0
10
20
30
40
50
60

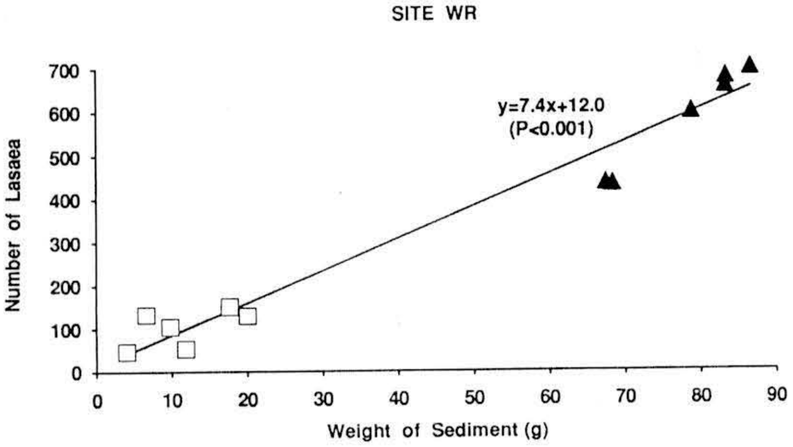

SITE WR
Number of Lasaea
Weight of Sediment (g)
y=7.4x+12.0
(P<0.001)
0
100
200
300
400
500
600
700
0
10
20
30
40
50
60
70
80
90

Figure 4.14. Size-frequency histograms of *Lasaea* from one-year (left) and two-year (right) Supergrasse squares at the two heights of the three study sites. Data were pooled from two replicates.

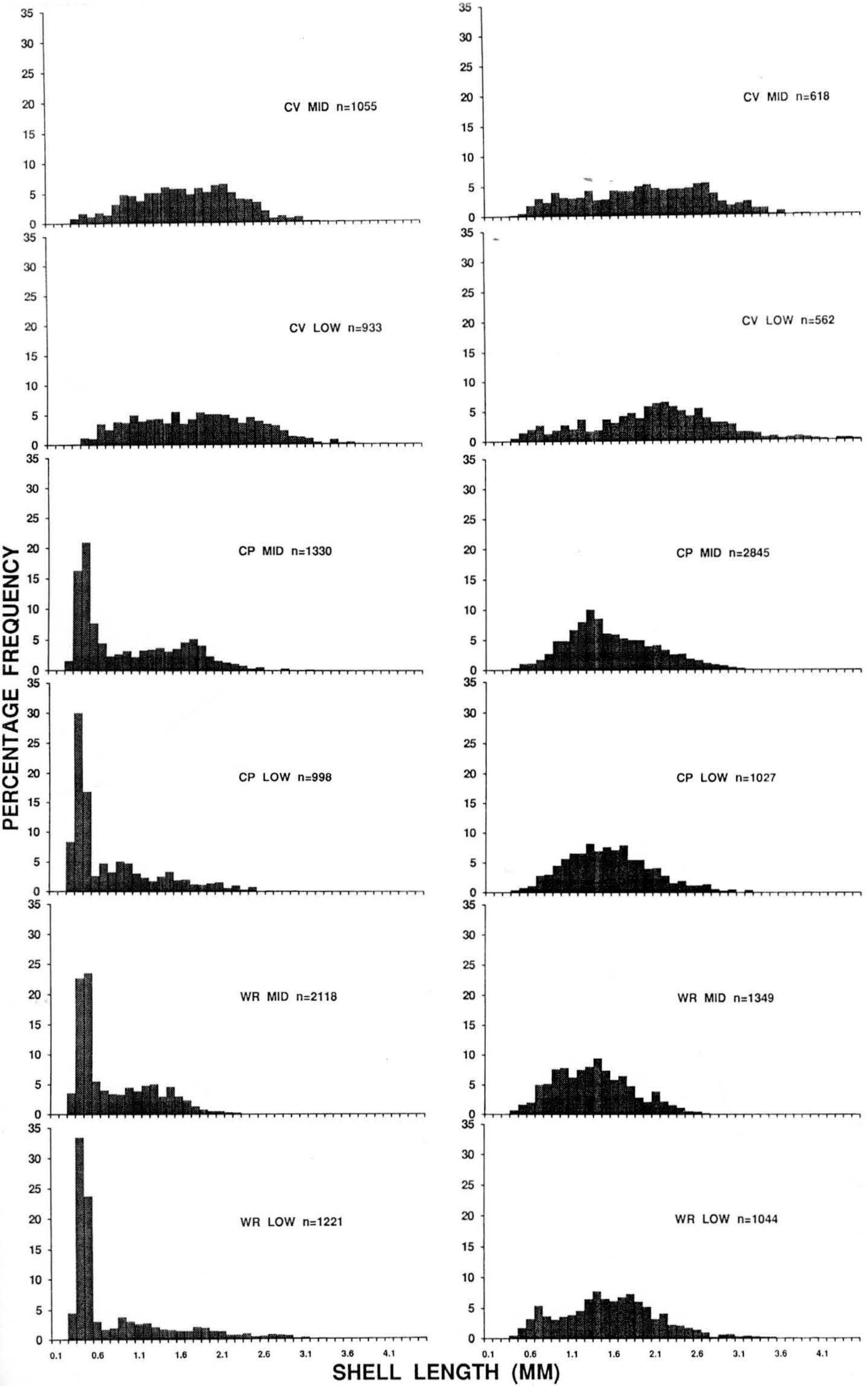
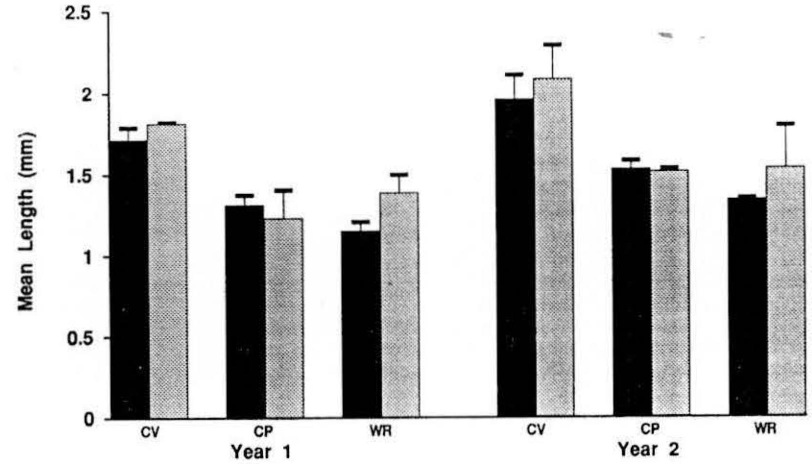
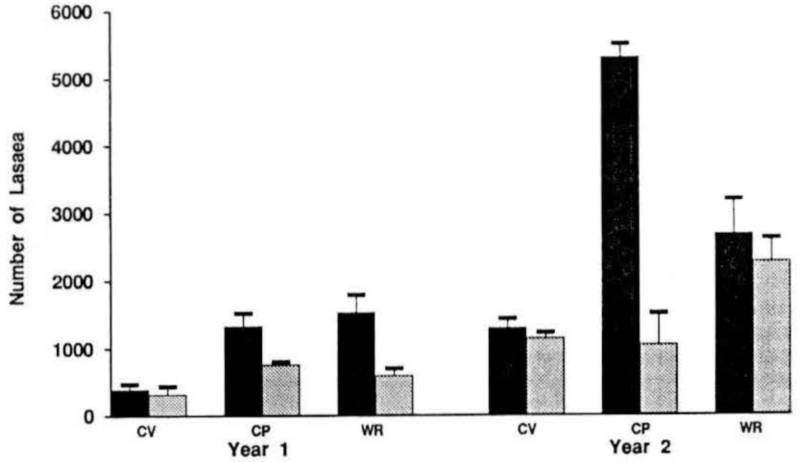

CV MID n=1055
CV MID n=618
CV LOW n=933
CV LOW n=562
CP MID n=1330
CP MID n=2845
CP LOW n=998
CP LOW n=1027
WR MID n=2118
WR MID n=1349
WR LOW n=1221
WR LOW n=1044
PERCENTAGE FREQUENCY
0
5
10
15
20
25
30
35
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
SHELL LENGTH (MM)

Figure 4.15. Mean (+ S.E.) shell length of *Lasaea* (>0.5 mm) from one-year and two-year Supergrasse squares in the mid (black) and low (stippled) areas at the three study sites.

Figure 4.16. Mean (+ S.E.) number of *Lasaea* (>0.5 mm) collected in one-year and two-year Supergrasse squares in the mid (black) and low (stippled) areas at the three study sites. Data were pooled from two plots.

Figure 4.17. Mean (+ S.E.) weight of sediment collected in one-year and two-year Supergrasse squares in the mid (black) and low (stippled) areas at the three study sites. Data were pooled from two plots.


Mean Length (mm)
2.5
2
1.5
1
0.5
0
CV
CP
WR
Year 1
CV
CP
WR
Year 2


Number of Lasaea
6000
5000
4000
3000
2000
1000
0
CV
CP
WR
Year 1
CV
CP
WR
Year 2

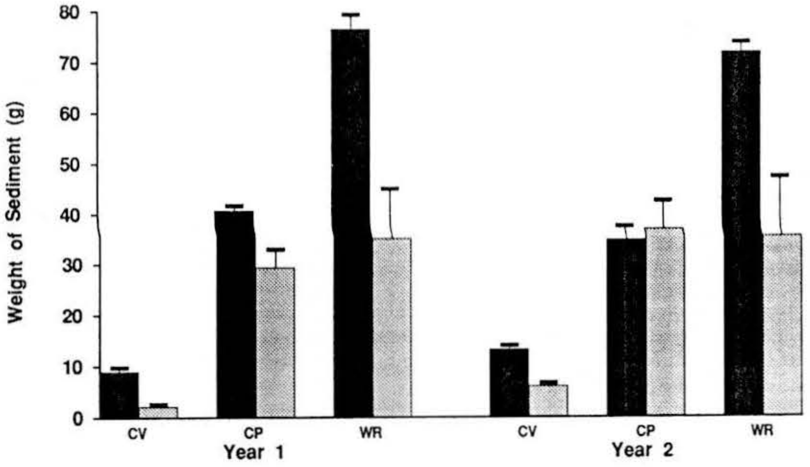

Weight of Sediment (g)
80
70
60
50
40
30
20
10
0
CV
CP
WR
Year 1
CV
CP
WR
Year 2

Figure 4.18. Relationship between biomass of sediment and the number of *Lasaea* collected in one-year (left) and two-year (right) Supergrasse squares from the mid (▲) and low (❐) areas.

a. Site CV

b. Site CP

c. Site WR

d. Site CV

e. Site CP

f. Site WR

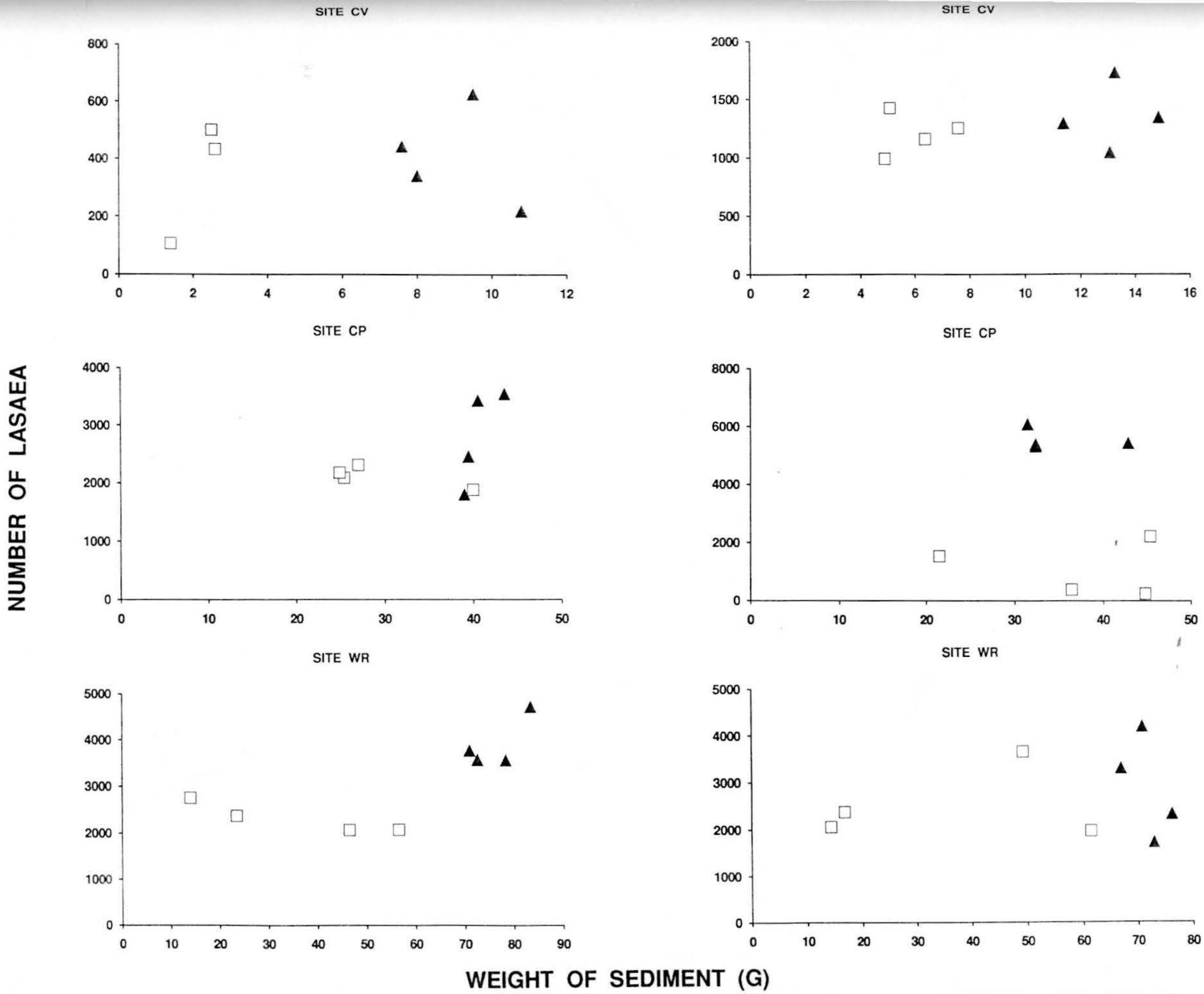
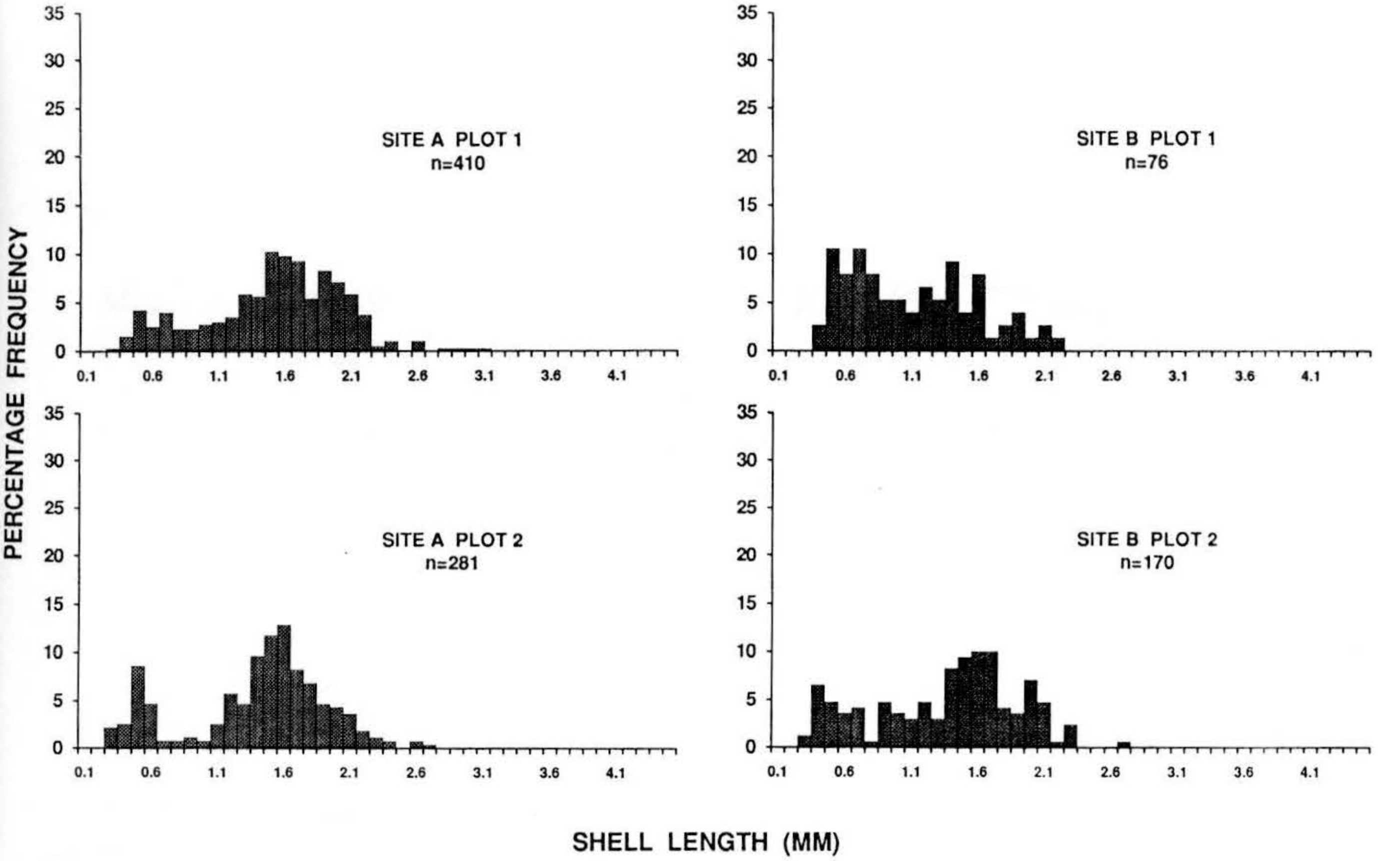

SITE CV
SITE CV
SITE CP
SITE CP
SITE WR
SITE WR
NUMBER OF LASAEA
WEIGHT OF SEDIMENT (G)
0
200
400
600
800
0
2
4
6
8
10
12
0
500
1000
1500
2000
0
2
4
6
8
10
12
14
16
0
1000
2000
3000
4000
0
10
20
30
40
50
0
2000
4000
6000
8000
0
10
20
30
40
50
0
1000
2000
3000
4000
5000
0
10
20
30
40
50
60
70
80
90
0
1000
2000
3000
4000
5000
0
10
20
30
40
50
60
70
80

Figure 4.19. Size-frequency histograms of *Lasaea* from regenerated *Corallina*. Data were pooled from two replicates.

Figure 4.20. Mean (+ S.E.) shell length of *Lasaea* from regenerated *Corallina* in Plot 1 (black) and Plot 2 (stippled) at the two study sites.


PERCENTAGE FREQUENCY
SITE A PLOT 1
n=410
SITE B PLOT 1
n=76
SITE A PLOT 2
n=281
SITE B PLOT 2
n=170
35
30
25
20
15
10
5
0
0.1
0.6
1.1
1.6
2.1
2.6
3.1
3.6
4.1
SHELL LENGTH (MM)

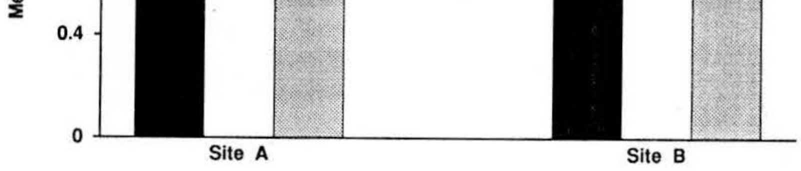

Mean Length (mm)
1.6
1.2
0.8
0.4
0
Site A
Site B

Table 4.1.

The mean height (m above chart datum) (S.D., n=2) of the experimental areas.

	CV	CP	WR	PB
Mid	1.48(0.03)	0.76(0.06)	0.70(0.05)	1.08(0.01)
Low	1.05(0.02)	0.59(0.04)	0.59(0.01)	0.64(0.01)

Table 4.2.

Analysis of numbers of *Lasaea* from Supergrasse squares at Site PB. Cochran's test was not significant ($P > 0.05$). In this and subsequent tables, ns denotes $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

SOURCE	DF	MS	*F*
Week	3	267977	40.9 ***
Height	1	186737	28.5 ***
Wk X Ht	3	37299	5.7 **
Residual	16	6551	
Total	23		

SNK-test on the means for significant effect of Wk X Ht:

	mid		low
for Wk 1:	81		50
for Wk 2:	139		89
for Wk 4:	563	>	259
for Wk 11:	650	>	328

at mid:	Wk 1	Wk 2	<	Wk4	Wk 11
at low:	Wk 1	Wk 2	<	Wk4	Wk 11

(values underlined are not significantly different at $P = 0.05$ in this and subsequent tables)

Table 4.3.

Analysis of weight of sediment from Supergrasse squares at Site PB.
Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Week	3	1651.60	14.45 ***
Height	1	0.07	0.001
Wk X Ht	3	134.77	1.18
Residual	16	114.30	
Total	23		

SNK-test on the means for significant effect of Week:

Wk 1	Wk 2		Wk 4		Wk 11
7.8	12.8	<	27.4	<	44.7

Table 4.4.

Analysis of mean log shell length of *Lasaea* from Supergrasse squares at Site PB. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Week	1	0.0804	270.3 ***
Height	1	0.0024	8.0 *
Wk X Ht	1	0.0062	20.7 *
Residual	4	0.0003	
Total	7		

SNK-test on the means for significant effect of Wk X Ht:

	Wk 2		Wk 11
at mid:	2.597	<	2.853
at low:	2.687	<	2.832
for Wk 2:	mid	<	low
for Wk 11:	mid		low

Table 4.5.

Analysis of numbers of marked *Lasaea* remaining in the Supergrasse squares over twelve weeks. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Week	3	4.56	0.11 ns
Residual	8	40.17	
Total	11		

Table 4.6.

Analysis of weight of sediment from Supergrasse squares set up near Site CB. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Week	3	743	4.78 *
Residual	8	155	
Total	11		

SNK-test on the means:

Wk 1		Wk 2	Wk 4	Wk 12
38.4	<	65.4	70.5	72.1

Table 4.7.

Analysis of numbers of *Lasaea* from Supergrasse squares set up near Site CB. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Week	3	47586	34.3 ***
Residual	8	1386	
Total	11		

SNK-test on the means:

Wk 1	Wk 2		Wk 4		Wk 12
53	104	<	239	<	329

Table 4.8.

Analysis of mean log shell length of *Lasaea* from two-week-old Supergrasse squares. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Site	2	0.0017	0.66 ns
Height	1	0.0086	8.60 ns
Si X Ht	2	0.0010	0.40 ns
Residual	6	0.0025	
Total	11		

Table 4.9.

Analysis of numbers of *Lasaea* from two-week-old Supergrasse squares (Plots were nested within Site X Height interaction). All data were transformed as square-root(x+1) to homogenize the variance (Cochran's test).

SOURCE	DF	MS	*F*
Site	2	525.26	34.68 **
Height	1	655.75	6.71
Si X Ht	2	97.71	6.45 *
Plot (Si X Ht)	6	15.15	13.64 ***
Residual	24	1.11	
Total	35		

SNK-test on the means for significant effect of Si X Ht:

	mid		low
at CV:	5.4		2.7
at CP:	17.1	>	8.3
at WR:	24.1	>	10.0

at mid:	CV	<	CP	<	WR
at low:	CV	<	CP		WR

Table 4.10.

Analysis of weight of sediment from two-week-old Supergrasse squares (Plots were nested within Site X Height interaction). Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Site	2	6009.7	109.68 ***
Height	1	13288.3	3.80
Si X Ht	2	3496.5	63.81 ***
Plot (Si X Ht)	6	54.8	4.53 **
Residual	24	12.1	
Total	35		

SNK-test on the means for significant effect of Si X Ht:

	mid		low		
at CV:	0.5		0.2		
at CP:	50.9	>	2.3		
at WR:	78.0	>	11.7		
at mid:	CV	<	CP	<	WR
at low:	CV		CP		WR

Table 4.11.

Analysis of mean shell length of *Lasaea* (>0.5 mm) from long-term Supergrasse squares. Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Year	1	0.2904	64.00 *
Site	2	0.7301	23.30 ***
Height	1	0.0523	1.49
Yr X Si	2	0.0045	0.14
Yr X Ht	1	0.0004	0.30
Si X Ht	2	0.0350	1.12
Yr X Si X Ht	2	0.0014	0.05
Residual	12	0.0313	
Total	23		

SNK-test on the means for significant effect of Site:

WR	CP		CV
1.35	1.39	<	1.89

SNK-test on the means for significant effect of Year:

Year 1		Year 2
1.43	<	1.65

Table 4.12.

Analysis of numbers of *Lasaea* (>0.5 mm) from long-term Supergrasse squares (Plots were nested within Year X Site X Height interaction). Cochran's test was significant ($0.05 > P > 0.01$). Therefore, the *F*-ratio is considered to be significant only when $P < 0.01$. (^{a}: loss of one degree of freedom due to missing value)

SOURCE	DF	MS	*F*
Year	1	25163800	17.21
Site	2	7110691	20.65 ***
Height	1	13328300	2.44
Yr X Si	2	1462118	4.25 *
Yr X Ht	1	3258905	0.63
Si X Ht	2	5460393	15.86 ***
Yr X Si X Ht	2	5176137	15.03 **
Plot (Yr X Si X Ht)	12	344395	1.47
Residual	23^a	234408	
Total	46		

Table 4.12 (continued).

SNK-test on the means for significant effect of Yr X Si X Ht interaction:

	Yr 1		Yr 2
at CV mid:	392	<	1297
at CV low:	264		1140
at CP mid:	1327	<	5298
at CP low:	755		1039
at WR mid:	1525	<	2677
at WR low:	593	<	2271

for CV Yr 1:	mid		low
for CV Yr 2:	mid		low
for CP Yr 1:	mid		low
for CP Yr 2:	mid	>	low
for WR Yr 1:	mid	>	low
for WR Yr 2:	mid		low

for Yr 1 mid:	CV	<	CP		WR
for Yr 1 low:	CV		WR		CP
for Yr 2 mid:	CV	<	WR	<	CP
for Yr 2 low:	CP		CV	<	WR

Table 4.13.

Analysis of weight of sediment from long-term Supergrasse squares (Plots were nested within Year X Site X Height interaction). Cochran's test was not significant (*P* > 0.05) ([a]: loss of one degree of freedom due to missing value)

SOURCE	DF	MS	*F*
Year	1	10.67	0.29
Site	2	8423.80	32.06 ***
Height	1	3253.02	2.27
Yr X Si	2	36.78	0.14
Yr X Ht	1	106.87	2.32
Si X Ht	2	1431.09	5.45 *
Yr X Si X Ht	2	46.11	0.18
Plot (Yr X Si X Ht)	12	262.73	12.87 ***
Residual	23[a]	20.41	
Total	46		

SNK-test on the means for significant effect of Si X Ht:

mid low

at CV: $\underline{11.1 \qquad\qquad 4.0}$

at CP: $\underline{37.7 \qquad\qquad 33.2}$

at WR: 74.1 > 35.4

at mid: CV < CP < WR

at low: CV < $\underline{\text{CP} \qquad\qquad \text{WR}}$

Table 4.14.

Analysis of mean log shell length of *Lasaea* from regenerated *Corallina*. Cochran's test was not significant ($P > 0.05$). ([a]: effect of Site was tested by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site[a]	1	0.0117	2.88 ns
Plot	2	0.0043	1.08 ns
Residual	4	0.0040	
Total	7		

CHAPTER FIVE *LASAEA* IN ARTIFICIAL SUBSTRATA

5.1 Introduction

In the past, the process of selection of habitat was believed to be important in determining the local distribution of marine invertebrates (Meadows & Campbell, 1972; Gray, 1974; but see Moore, 1975). Recently, the role played by hydrodynamic process has been given more attention (Eckman, 1983; Hannan, 1984; Roughgarden *et al.*, 1987, 1988; Butman, 1989). Butman (1987) has pointed out that the two hypotheses regarding larval settlement, namely passive deposition and habitat selection, are not mutually exclusive. Hydrodynamic process can govern the broad-scale distribution before the fine adjustment via habitat choice can operate. The pattern of colonization of soft sediment by juvenile and adult meiofauna also involves passive recruitment and active selection processes. Field experiments have shown that neither mechanism alone can serve to explain the small-scale spatial distribution of meiofauna (Kern & Taghon, 1986; Palmer, 1988; Savidge & Taghon, 1988; DePatra & Levin, 1989).

In Chapter 4, I described the colonization of Supergrasse by *Lasaea* as postlarval individuals. The observed correlation between the amount of sediment and the number of *Lasaea* in each experimental square could be the result of purely physical phenomena. Being in the water column with the sediment, the transport of *Lasaea* and the sediment might be under similar hydrodynamic influences. Alternatively, this could be a causal response of *Lasaea* towards the amount of sediment present in each square. I therefore attempted to distinguish between these two possibilities in probably one of the few such studies on rocky shores.

5.2 Materials and methods

Supergrasse squares (12 X 12 cm^2) were used for all the experiments. As described in Section 4.2, the material brushed out from each square was filtered through a series of 1 mm, 265 µm and 75 µm sieves. After the *Lasaea* were removed from each fraction, the sediment was oven-dried before weighing to the nearest 0.01 g.

In order to study the spatial variation in the numbers of *Lasaea*, squares were set up in the mid and low areas at Sites CV, PB, CP and WR (see Fig. 3.1 & Table 4.1 for their respective heights). At each height, there were two plots 3-40 m apart and within each of these 1-2.5 m^2 plots there were three replicates. At Sites CP and WR, the same plots were used for all the experiments. This experiment was run for two weeks in February 1989 (n.b. part of this experiment has been described in Chapter 4).

The numbers of *Lasaea* collected in the squares were linearly correlated with the amount of sediment present (see Sections 4.3.1, 4.3.3 & 5.3.1) suggesting that *Lasaea* might behave like passive sediment particles. To test this, the Supergrasse squares were manipulated to reduce the amounts of sediment they could retain. If *Lasaea* colonized squares like passive particles, the pattern of collection of sediment in the Treated and Control squares would be mirrored by that of *Lasaea*. Here, I assume that the weight of sediment is directly proportional to the number of sediment particles present and then compare the distribution pattern of sediment by weight with the corresponding numerical pattern of *Lasaea*.

In the first experiment, the tufts of Supergrasse in every row in the squares were cut to reduce their height from 7-8 mm to about 4 mm. Two Treated and two Control squares were set up at each of the two plots in the mid and low areas at Sites PB, CP and WR. Site CV was not included in this study because too few *Lasaea* would be collected there within a two-week period. This experiment was run for two weeks in April 1989.

In the second experiment, the density of the tufts was reduced by cutting alternate tufts in every row to about 2-3 mm height. Three Treated and three Control squares were set up at each of the two plots at the mid levels at Sites CP and WR. This design halved the total number of squares to be examined, while increasing the number of replicates (in fewer areas) from two to three. The squares were left on the rock platform for two weeks in August 1989.

To reduce the amount of natural sediment that could accumulate in the squares, they were first seeded with some reddish-brown mineral ballast (used in hobbies and model-making). The ballast was 0.265-1 mm, which was similar in size to the major fraction of the sediment collected by Supergrasse. The density of ballast was about half that of the natural sediment (ballast: 1.23 ± 0.02 g.cm^{-3}; sediment: 2.51 ± 0.02 g.cm^{-3}; mean $\pm$ S.D., n=3). 30-70 g of sediment had been found to accumulate in the squares in previous experiments. Therefore, 17.5 ± 0.5 g of ballast was addded to each experimental square. This amount of ballast had a volume equivalent to about 35 g of natural sediment. Three Treated and three Control squares were set up at each of the two plots at Sites CP Mid and WR Mid in October 1989. After two weeks, the squares were retrieved. The amount of sediment in the dried 0.265-1 mm fraction actually arriving from the water column was determined by removing the ballast using chloroform (density:

1.47 $g.cm^{-3}$) as a buoyant medium to wash it out of the sediment. I was unable to purchase the original type of Supergrasse for this experiment. The material used was therefore different and had fewer strips of material per tuft than the ones normally used (October: 16.6 ± 2.4; Normal: 23.0 ± 3.5; mean ± S.D., n=5; t-test: $P < 0.05$). The experiment was therefore repeated in November 1989 using the original type of Supergrasse and increasing the amount of seeded ballast to 25 ± 0.5 g per square.

5.3 Results

5.3.1 Spatial variation

Although Site PB was included in this analysis, the general pattern of accumulation of *Lasaea* was similar to that described in Section 4.3.3. Irrespective of height on the shore, the least *Lasaea* were always collected at Site CV (Fig. 5.1; Table 5.1). Among the three other sites, there was more *Lasaea* at the mid level at Site WR, but there was no significant difference in the low shore. At Sites CP and WR, the numbers of *Lasaea* in the mid shore squares were greater than in the low shore ones, while no comparable difference was detected at Sites CV and PB. Additionally, there was a significant Plot effect. At Site CP, Plot 1 had more *Lasaea* than Plot 2 at the mid level but the two plots in the low shore had similar numbers. At Site WR, there were more *Lasaea* in Plot 1 than in Plot 2 and the reverse was observed lower down the shore. These patterns of collection were quite consistent throughout all the experiments.

The pattern of accumulation of sediment was similar to that of *Lasaea* (Fig. 5.2; Table 5.2) except that no significant difference was detected among the four sites in the low shore. The amount of sediment collected also varied with the Plots concerned. There was no significant difference between the two plots at each height at Site CP. At Site WR, the pattern was similar to that of *Lasaea;* there was more sediment at Plot 1 and at Plot 2 respectively at the mid and low levels.

At Site PB, the number of *Lasaea* collected in the squares was also linearly correlated with the amount of sediment present (Fig. 5.3). This pattern was similar to the situation at the three other study sites (see Fig. 4.13).

Since most of the samples were dominated by particles 0.265-1 mm (Fig. 5.4), this fraction was used in the following analyses. The proportion (by number) of *Lasaea* in the squares remained similar irrespective of the height of the plots and the study sites concerned (Table 5.3). The sediment fraction also showed a similar pattern except that the proportion (by weight) could vary significantly between the two plots at a particular area (Table 5.4). Despite the absolute quantity of either *Lasaea* or the sediment collected being different between the two heights and among the study sites, the proportion of *Lasaea* or sediment in the range 0.265-1 mm did not differ significantly.

5.3.2 Variation with the height of the tufts

As predicted, the amount of sediment collected was greater in the Control squares than in the squares with shortened tufts, especially in the mid shore (Fig. 5.5; Table 5.5). Again, more sediment accumulated at the mid level than at the low level at Site CP and Site WR irrespective of the type of squares concerned. Among the three study sites, mid shore Supergrasse squares at Site WR also collected the maximal amount of sediment, while the difference was less drastic in the low shore. At WR Mid, more sediment was collected in Plot 1 than in Plot 2, which was similar to the pattern observed in February 1989.

Depending on the plot under consideration, there were either more *Lasaea* in the Control than in the Treated squares or similar numbers were present in the two sets (Fig. 5.6; Table 5.6). At each of the heights of Site CP and Site WR, where the same two plots were used throughout the study, the relative number of *Lasaea* in the two plots was identical to that observed in February 1989. Furthermore, there were consistently more *Lasaea* at the mid level than at the low level at Sites CP and WR, but no difference was detected between the two heights at Site PB. In the mid zone, *Lasaea* was again most numerous at Site WR while similar numbers were found in the low shore squares in the three sites.

Because the quantity of sediment collected in the low shore squares was minute (less than 7 g), the manipulated squares (*i.e.* with tufts of reduced height) were not very successful in creating a difference in the sediment content between the two Treatments. Hence, only the results of the mid shore squares were interpreted. In general, no significant difference was observed in the number of *Lasaea* collected in the two Treatments, despite more sediment being accumulated in the Control squares (except for Plot 1 at PB Mid and for Plot 1 at WR Mid; Fig. 5.7; Tables 5.5 & 5.6).

Both *Lasaea* and the sediment particles responded differently to the Treatments. The percentage of 0.265-1 mm *Lasaea* in the sample did not vary between the Treated and Control squares (Figs 5.8; Table 5.7). The proportion of similar-sized sediment was, however, greater in the Control ones (Table 5.8). This was due to the greater proportion of >1 mm sediment collected in the squares with shortened tufts.

5.3.3 Variation with the density of the tufts

As predicted, the amount of sediment was significantly greater in the Control than in the Treated squares (Fig. 5.9; Table 5.9). Similar to the results in previous experiments, the squares in Plot 1 at WR Mid collected more sediment than those in Plot 2.

In contrast with the pattern of sediment, more *Lasaea* were collected in the squares with tufts of reduced density (Fig. 5.10; Table 5.10). Again, more *Lasaea* were collected in Plot 1 than in Plot 2 at WR Mid.

At the two sites, the fractions of 0.265-1 mm *Lasaea* were greater in the samples from Control than from Treated squares, except for Plot 1 at CP Mid (Fig. 5.11; Table 5.11). This fraction of sediment particles was also greater in the Control squares (Table 5.12) because Treated squares tended to collect more sediment greater than 1 mm.

5.3.4 Variation with the amount of sediment seeded among the tufts

In the October experiment, the ballast treatment was effective because the amount of sediment was significantly less in the Treated squares (Fig. 5.12; Table 5.13, $P < 0.001$). *Lasaea* were also less numerous in the Treated squares (Fig. 5.13; Table 5.14, $P < 0.05$). This similarity in response for the sediment and *Lasaea* towards the two Treatments was at variance with the results from previous experiments. At Site WR, the squares at Plot 1 collected more sediment and *Lasaea* than at Plot 2, which was similar to the patterns observed in the earlier experiments.

The proportion of 0.265-1 mm *Lasaea* in the sample was similar for the two types of squares (Fig. 5.14; Table 5.15). There was, however, a Treatment effect on sediment, with a greater proportion of medium-sized particles in the Control squares for one plot at each site (Table 5.16).

From an initial amount of 17.5 g , the ballast remaining in the Supergrasse squares was reduced respectively to 9.6 ± 2.3 g and 2.6 ± 3.2 g (mean ± S.D., n=6) at Site CP and Site WR. The experiment was therefore repeated in November 1989 by increasing the amount of seeded ballast to 25 g.

In November, the amounts of sediment collected in the two Treatments were similar at Site CP, but at Site WR, there was more sediment in the Control squares as predicted (Fig. 5.15; Table 5.17). The ballast still residing in the squares after the two weeks was 17.1 ± 1.0 g and 9.7 ± 5.2 g (mean ± S.D., n=6) at Sites CP and WR, respectively. The failure to obtain different quantities of sediment between the two Treatments at Site CP was presumably due to the scarcity of exogenous sediment actually collected there (less than 10 g). Interestingly, a greater quantity of sediment was also collected at Site WR than at Site CP.

There was, however, no significant difference in the numbers of *Lasaea* collected in the Treated and the Control squares (Fig. 5.16; Table 5.18). This variation in response of the sediment and *Lasaea* towards the two

Treatments at Site WR is illustrated in Fig. 5.17. Within a plot, the numbers of *Lasaea* in the two types of squares were found to be similar, despite a significant difference in the amount of sediment present. At Site WR, the amount of sediment and the number of *Lasaea* in the Control squares were consistently greater at Plot 1 than at Plot 2.

When the proportion of 0.265-1 mm *Lasaea* was analysed, a significant Treatment effect was only evident in one of the four plots (Fig. 5.18; Table 5.19). The proportion of similar-sized sediment in the sample was, however, different between the Control and the Treated squares in all four plots (Table 5.20).

5.4 Discussion

All the experiments were designed to reduce the amount of sediment retained in the Treated Supergrasse squares. If *Lasaea* was behaving like a passive sediment particle, the pattern of collection of *Lasaea* in the two Treatments would mirror that of the sediment irrespective of the success of the experimental manipulation. A different pattern of accumulation for *Lasaea* and the sediment would indicate that *Lasaea* was not responding like a passive particle.

In the Reduced Height experiment, no significant difference was recorded for *Lasaea* in the two Treatments, despite a greater quantity of sediment being found in the Control squares for four of the six tested plots in the mid shore. Lower down, *Lasaea* had a different pattern of accumulation from the sediment for only half of the experimental plots. Since the quantities of sediment and *Lasaea* collected during the two weeks were not large, the results from the low shore might not be very reliable. When the 0.265-1 mm proportion of each sample was examined, a more distinct pattern emerged. There was a consistently smaller proportion of sediment in this size range in the Treated squares, because they tended to collect particles larger than 1 mm, presumably due to the wider spacing among the tufts. Unlike the sediment, the proportions of *Lasaea* in the range 0.265-1 mm were not different between the two Treatments. Although the results from the various plots were inconsistent, this experiment did show that *Lasaea* was not behaving like a passive sediment particle.

When the density of the Supergrasse tufts was reduced, less sediment was again collected in these squares, but *Lasaea* were found in greater numbers. Therefore, this experiment showed that *Lasaea* did not behave like passive particles, although, on a proportional basis, both *Lasaea* and sediment in the range 0.265-1 mm responded similarly to the two Treatments.

In the Ballast I experiment, both the quantities of sediment and *Lasaea* were greater in the Control squares (sediment: $P < 0.001$; *Lasaea*: $P < 0.05$). Proportionally, there was a slight difference in response between the medium-sized *Lasaea* and the sediment towards the two Treatments. When the experiment was repeated in November, the numbers of *Lasaea* collected in the squares at site WR were found to be independent of the amount of sediment present. Moreover, *Lasaea* in the range 0.265-1 mm showed no Treatment effect while the sediment responded otherwise. Unfortunately, too little material was collected at Site CP over the experimental period to allow any meaningful conclusion to be drawn. These two experiments did, however, demonstrate a similar trend for *Lasaea* to respond differently from the sediment, but they might have been confounded by the presence of ballast in only one type of experimental square.

Although the patterns of accumulation of the sediment and *Lasaea* were shown to be different in the experiments, they did not imply that the bivalve could not have arrived at the Supergrasse in a manner similar to a sediment particle. Studies have demonstrated that invertebrate larvae can sink through the water like passive particles in turbulent near-bed flows (Hannan, 1984; Butman, 1989). Similarly, the transport of the sediment and *Lasaea* could be under the influence of boundary-layer flow dynamics (Jumars & Nowell, 1984; Nowell & Jumars, 1984) or other physical processes such as waves and currents (Connell, 1985).

The role played by hydrodynamic processes in the transport of *Lasaea* and the sediment could be inferred from the following non-random patterns of accumulation. On a broad spatial scale, the maximal amount of sediment and *Lasaea* were collected in the mid shore at Site WR in all experiments while Site CV ranked lowest when tested. There was always a tendency for more material to be accumulated in the mid than low shore at Site CP and Site WR. Furthermore, the relative amount of sediment or *Lasaea* between the experimental plots at Site WR was quite consistent over time (Plot 1 > Plot 2 at mid shore; Plot 2 > Plot 1 at low shore).

The difference in the quantity of trapped sediment between the Shortened/Thinned and Control squares can be partly explained by hydrodynamic forces. Eckman (1983) has shown that the rate of fluid transport and the degree of boundary layer scouring can vary with the numerical density of the protruding structures. The difference in height or density of the tufts might create dissimilar hydrodynamic regimes, thus affecting the collection of particles in the two Treatments.

Lasaea had some association with Supergrasse that had tufts of reduced density, because this was the only occasion when they were more abundant than in the Control squares. There have been similar patterns in the distribution of fauna in other habitats. For example, some fish in seagrass beds increased in numbers when the seagrass leaves were thinned out experimentally (Bell & Westoby, 1986).

The influences of biological interactions have not been taken into account in these experiments. Predators of *Lasaea* such as juvenile *Thais orbita* and *Morula marginalba* (Fairweather, 1985; pers. obs.) were only collected in a few squares over the whole study period although they might be preying on *Lasaea* at other times. Normally, juvenile *Morula* reside amongst the *Corallina* bed in the low-shore (Moran, 1985). They possibly disliked the texture of Supergrasse because they crawled away soon after being seeded into squares. The effect of predation on *Lasaea* in these experimental squares was, therefore, assumed to be unimportant.

A second model can be proposed to explain the correlation between the number of *Lasaea* and the amount of sediment in the Supergrasse. *Lasaea* might be responding to the sediment particles themselves (Meadows & Campbell, 1972; Gray, 1974). Under this model, there will be a faster colonization of *Lasaea* in areas with accumulated sediment than in areas where the sediment have to be accumulated first. To test this, the Supergrasse can be seeded with natural sediment but the experiment has to be terminated before the amounts of sediment in the Control squares reach the same quantity as in the Treated ones. A greater number of *Lasaea* present in the

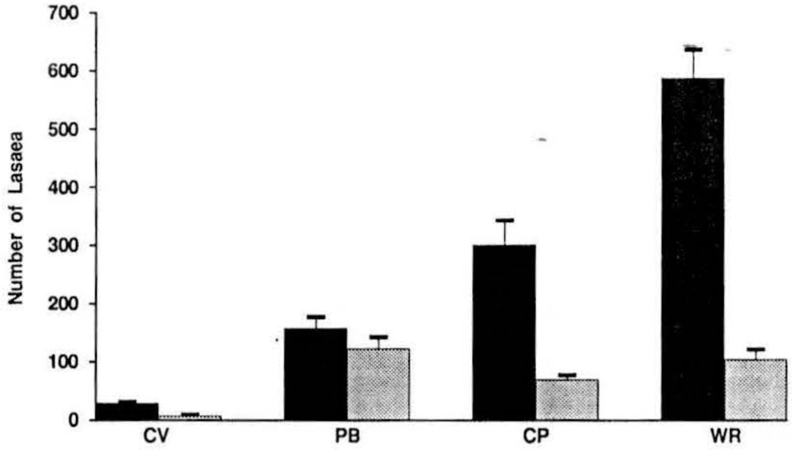
Treated squares will then support this model. Due to the shortage of time, this model is left unexamined.

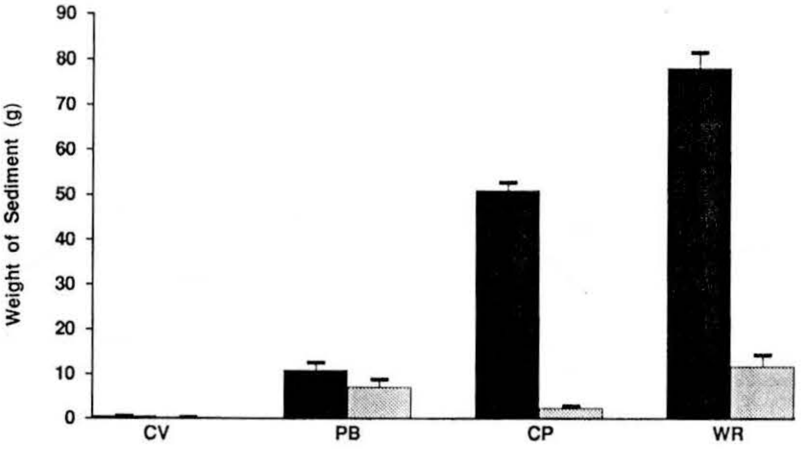
From the above results, I suggest that the arrival of *Lasaea* and the sediment into the Supergrasse squares were governed by similar hydrodynamic processes. After their arrival, *Lasaea* because of their ability to attach themselves by a byssal thread managed to remain among the tufts while the sediment particles were susceptible to water-dislodgement. Hence, their final patterns of accumulation in the experimental squares were different. Experiments using a laboratory flume would enable test of this hypothesis.

Figure 5.1. Mean (+ S.E.) number of *Lasaea* collected in two-week Supergrasse squares in the mid (black) and low (stippled) areas at the four study sites. Data were pooled from two plots.

Figure 5.2. Mean (+ S.E.) weight of sediment collected in two-week Supergrasse squares in the mid (black) and low (stippled) areas at the four study sites. Data were pooled from two plots.

Figure 5.3. Relationship between biomass of sediment and the number of *Lasaea* collected in two-week Supergrasse squares in the mid (▲) and low (❒) areas at Site PB.


Number of Lasaea
700
600
500
400
300
200
100
0
CV
PB
CP
WR


Weight of Sediment (g)
90
80
70
60
50
40
30
20
10
0
CV
PB
CP
WR

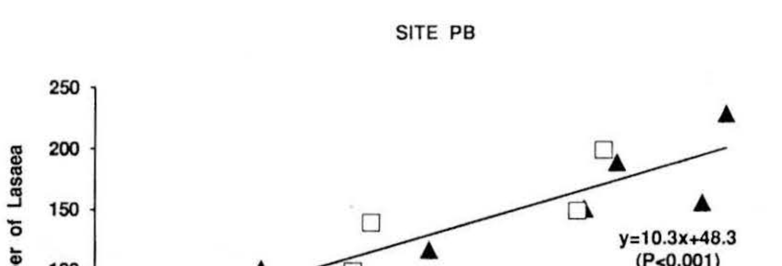

SITE PB
Number of Lasaea
250
200
150
100
50
0
0
2
4
6
8
10
12
14
16
Weight of Sediment (g)
y=10.3x+48.3
(P<0.001)

Figure 5.4. Mean (+ S.E.) percentage of different-sized *Lasaea* and sediment collected in two-week Supergrasse squares in the mid (black) and low (stippled) areas. Data were pooled from two plots.

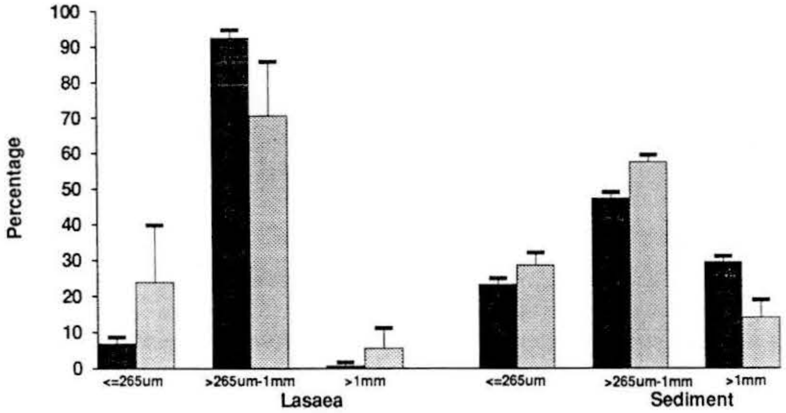
a. Site CV

b. Site PB

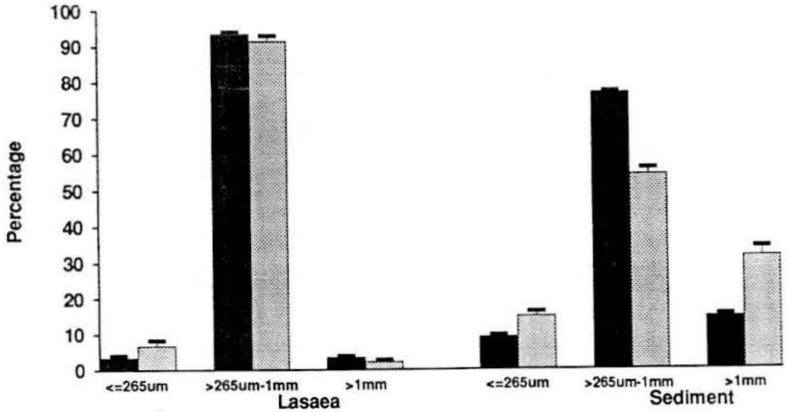
c. Site CP

d. Site WR

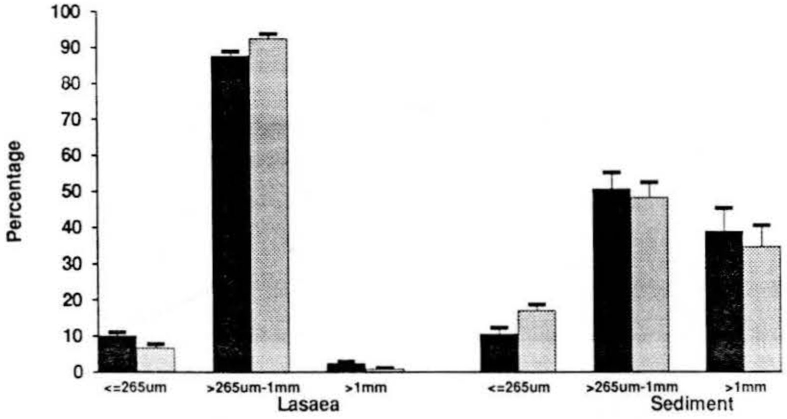
SITE CV



SITE CP



SITE PB



SITE WR

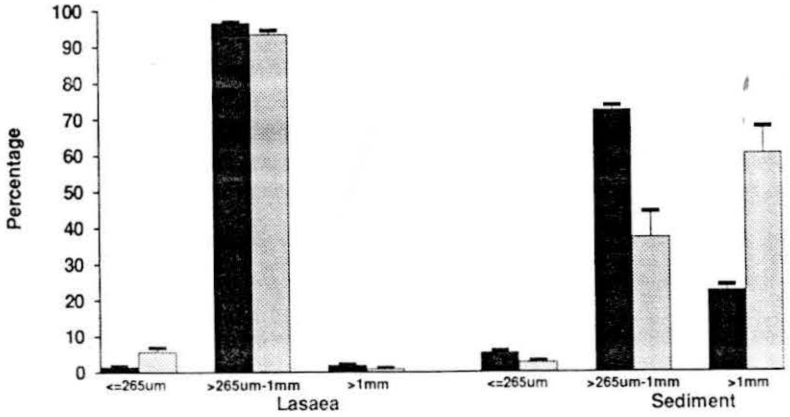
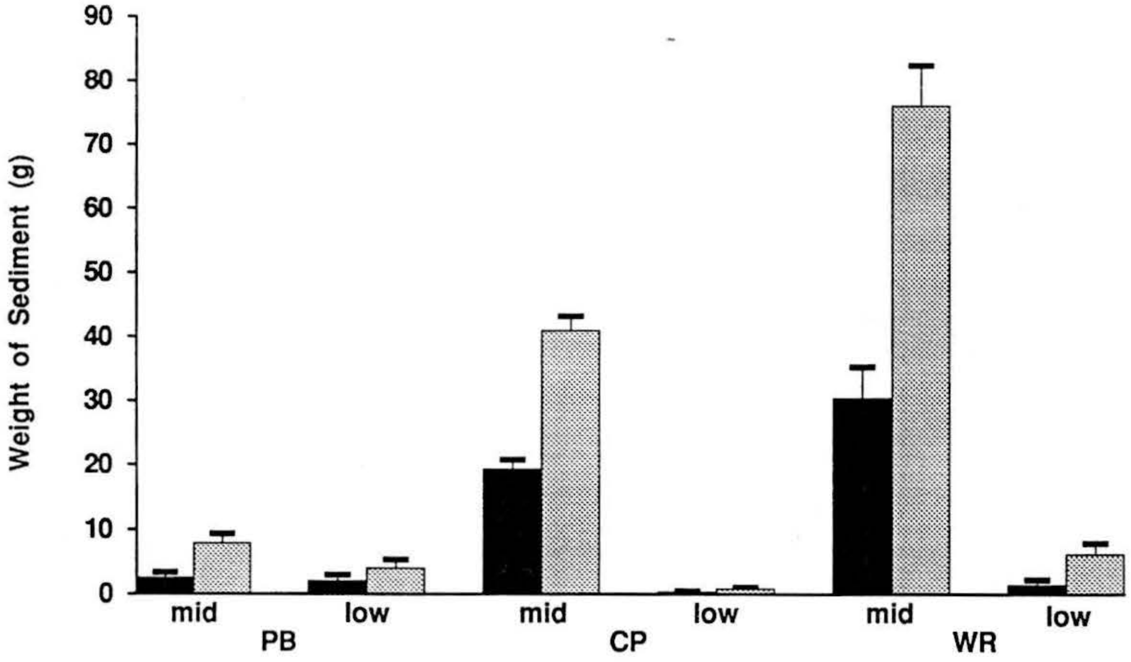


Figure 5.5. Mean (+ S.E.) weight of sediment collected in Shortened (black) and Control (stippled) Supergrasse squares at the two heights of the three study sites. Data were pooled from two plots.

Figure 5.6. Mean (+ S.E.) number of *Lasaea* collected in Shortened (black) and Control (stippled) Supergrasse squares at the two heights of the three study sites. Data were pooled from two plots.


90
80
70
60
50
40
30
20
10
0
Weight of Sediment (g)
mid
low
mid
low
mid
low
PB
CP
WR

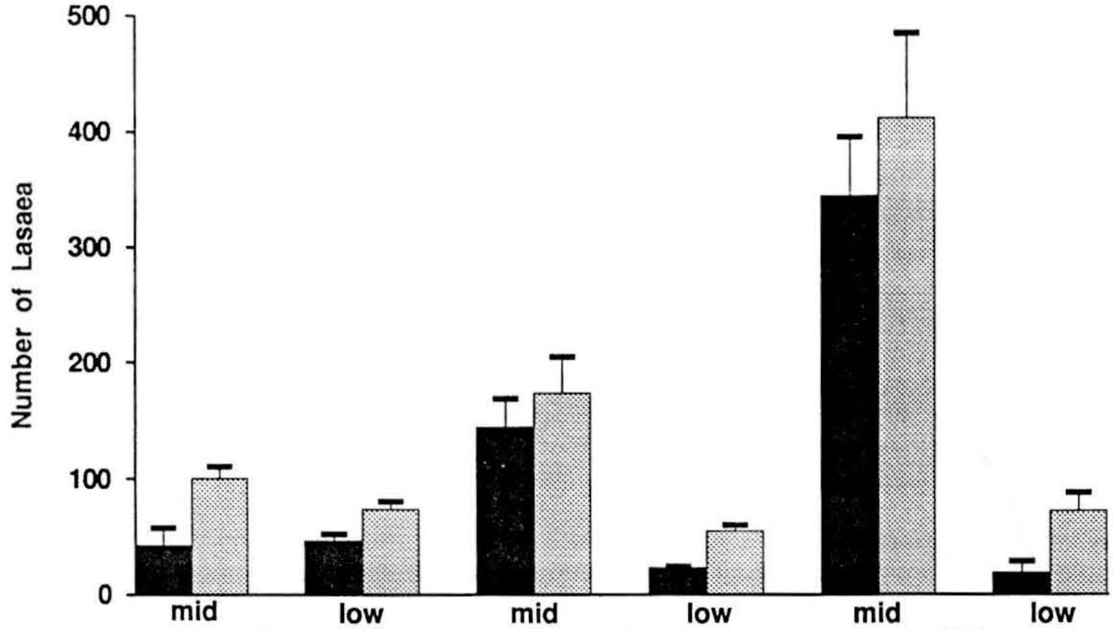
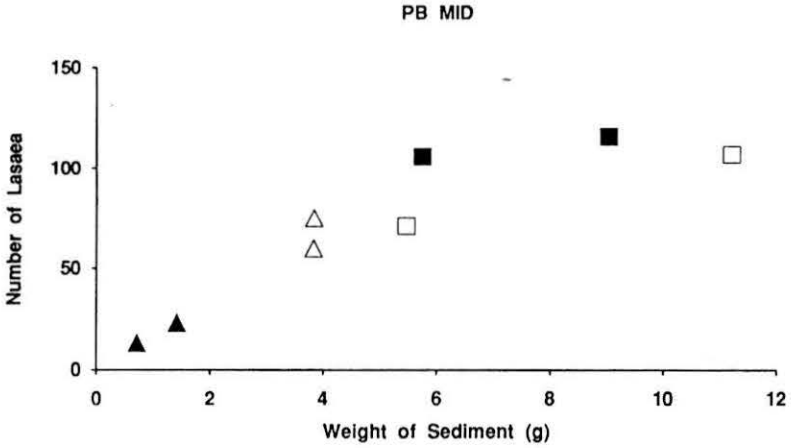

500
400
300
200
100
0
Number of Lasaea
mid
low
mid
low
mid
low
PB
CP
WR

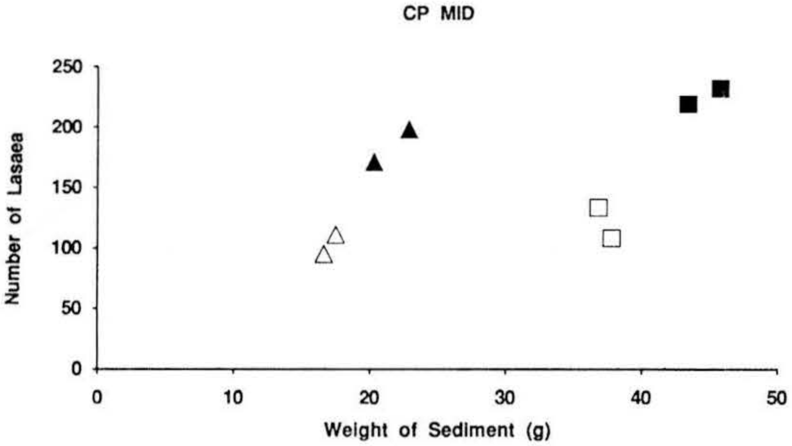
Figure 5.7. Relationship between biomass of sediment and the number of *Lasaea* collected in Shortened (triangles) and Control (squares) Supergrasse squares. Solid and open symbols represent data from Plot 1 and Plot 2 respectively.

a. Site PB Mid

b. Site CP Mid

c. Site WR Mid


PB MID
Number of Lasaea
Weight of Sediment (g)
0
50
100
150
0
2
4
6
8
10
12


CP MID
Number of Lasaea
Weight of Sediment (g)
0
50
100
150
200
250
0
10
20
30
40
50

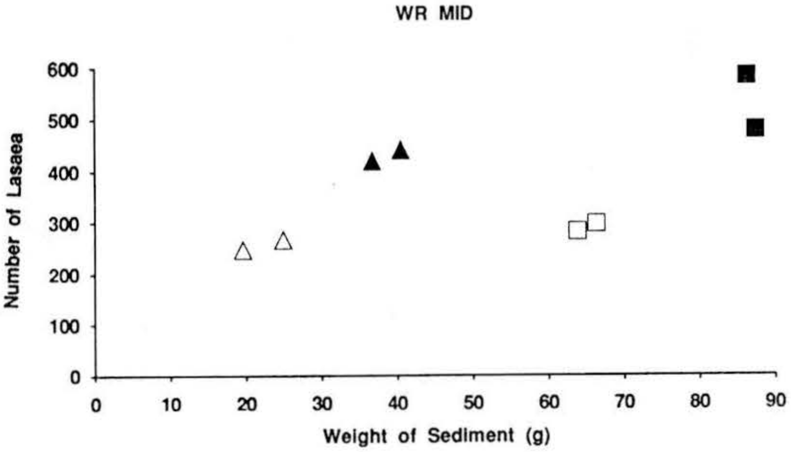

WR MID
Number of Lasaea
Weight of Sediment (g)
0
100
200
300
400
500
600
0
10
20
30
40
50
60
70
80
90

Figure 5.8. Mean (+ S.E.) percentage of different-sized *Lasaea* and sediment collected in Shortened (black) and Control (stippled) Supergrasse squares. Data were pooled from two plots.

a. Site PB Mid

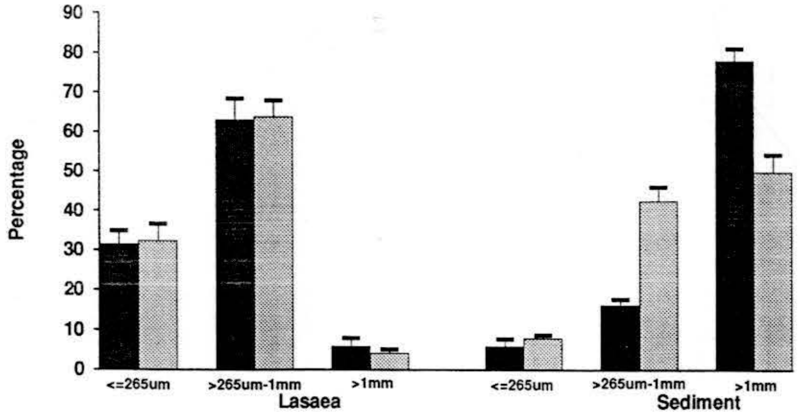
b. Site PB Low

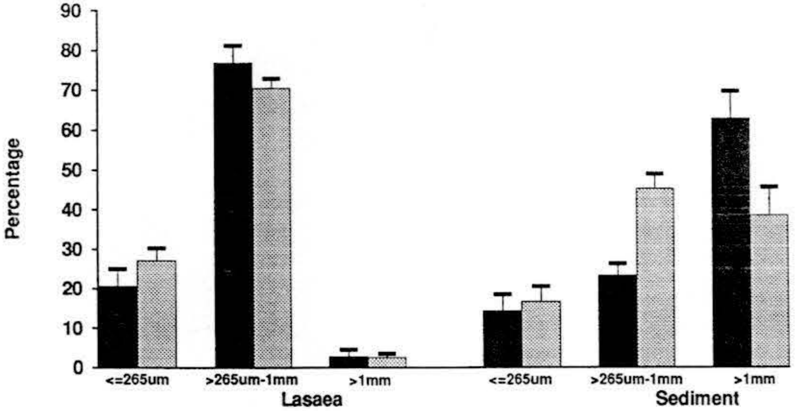
c. Site CP Mid

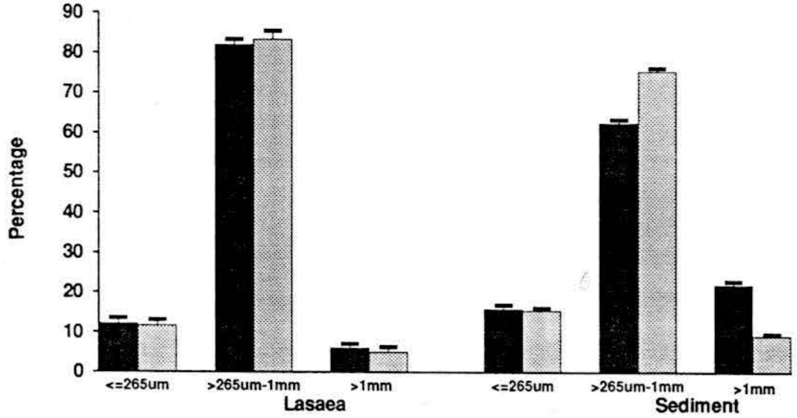
d. Site CP Low

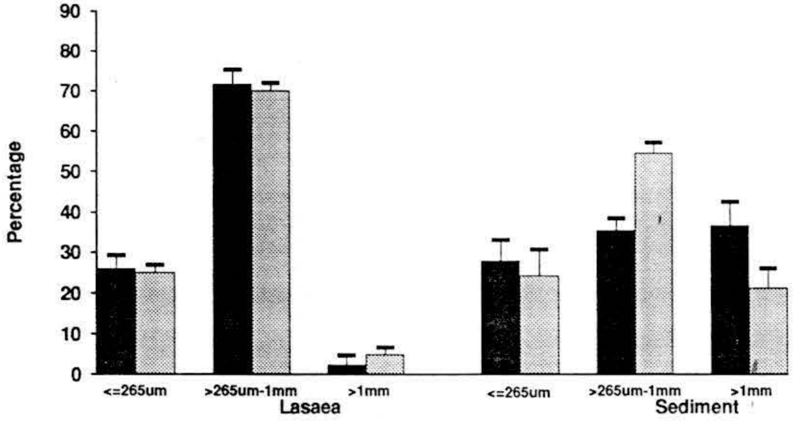
e. Site WR Mid

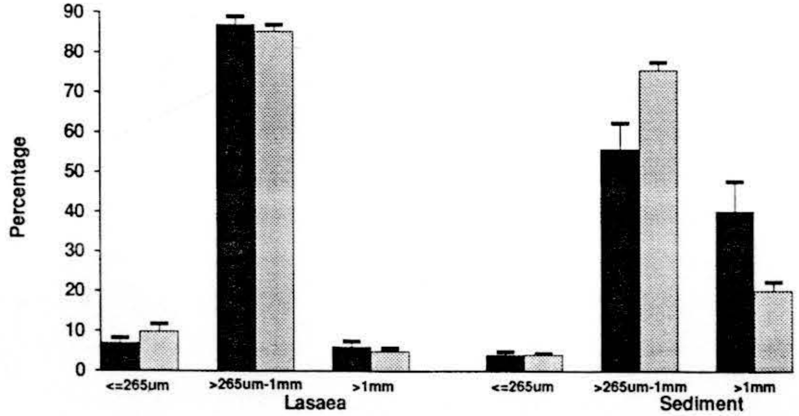
f. Site WR Low


PB MID


PB LOW


CP MID


CP LOW


WR MID

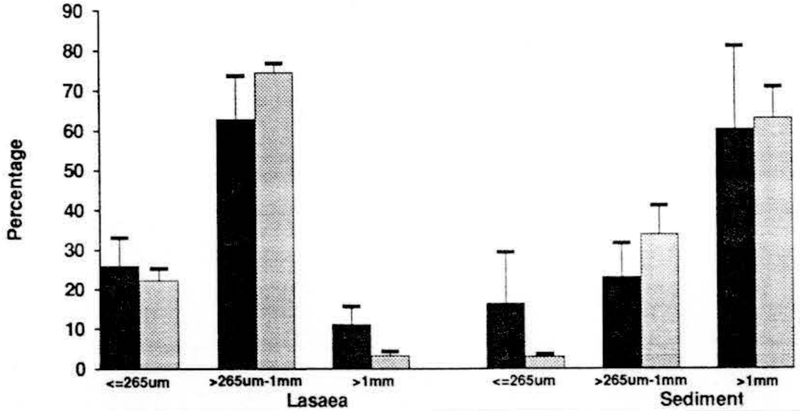
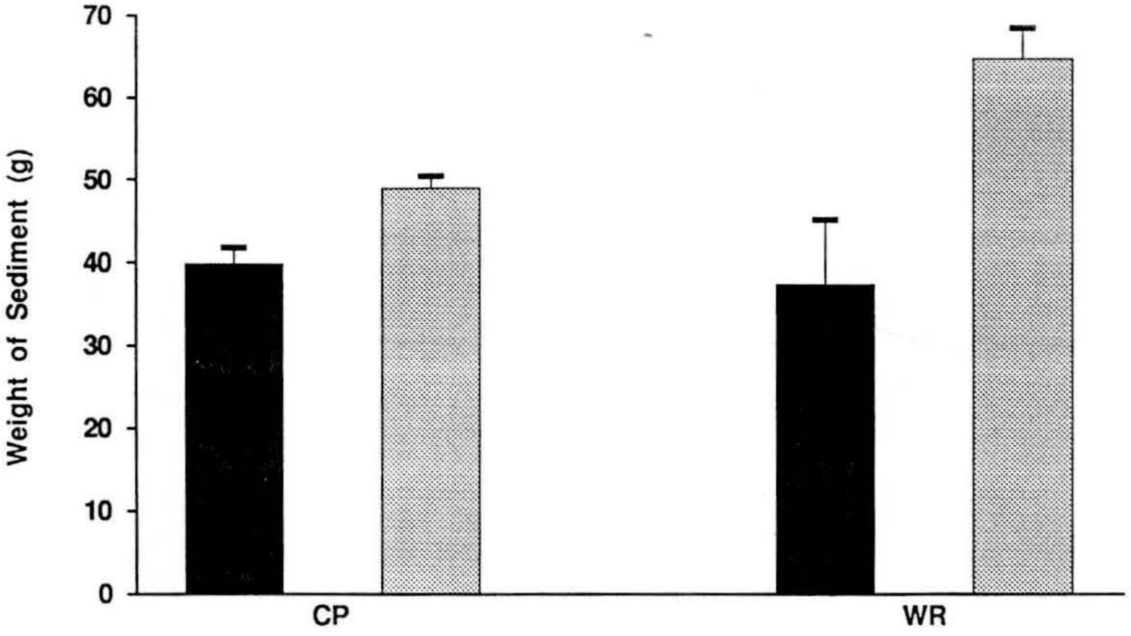
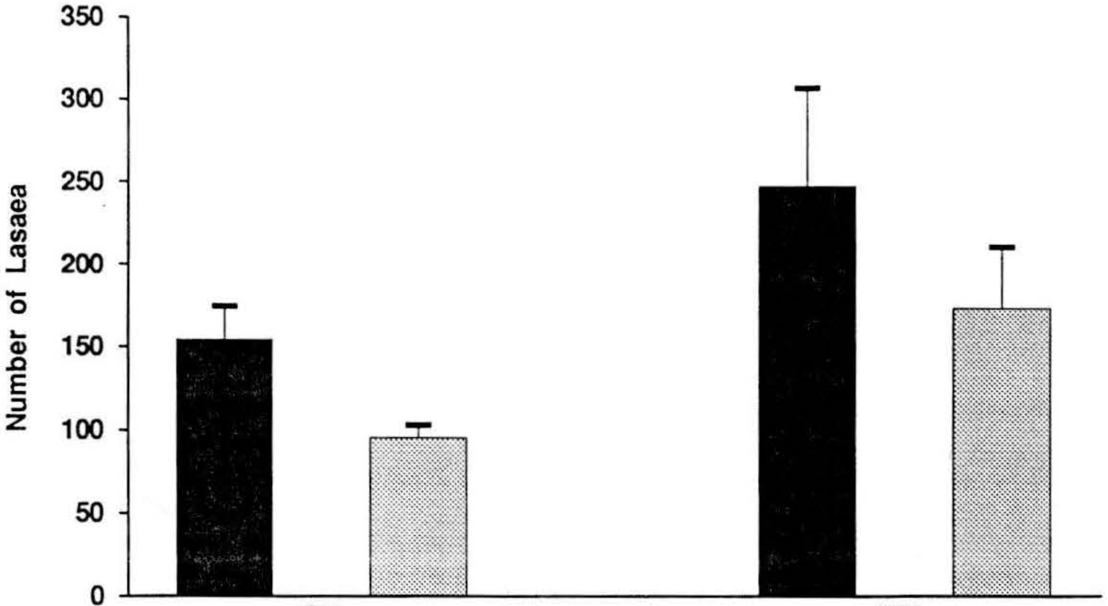

WR LOW

Figure 5.9. Mean (+ S.E.) weight of sediment collected in Thinned (black) and Control (stippled) Supergrasse squares at the two study sites. Data were pooled from two plots.

Figure 5.10. Mean (+ S.E.) number of *Lasaea* collected in Thinned (black) and Control (stippled) Supergrasse squares at the two study sites. Data were pooled from two plots.



Weight of Sediment (g)
70
60
50
40
30
20
10
0
CP
WR

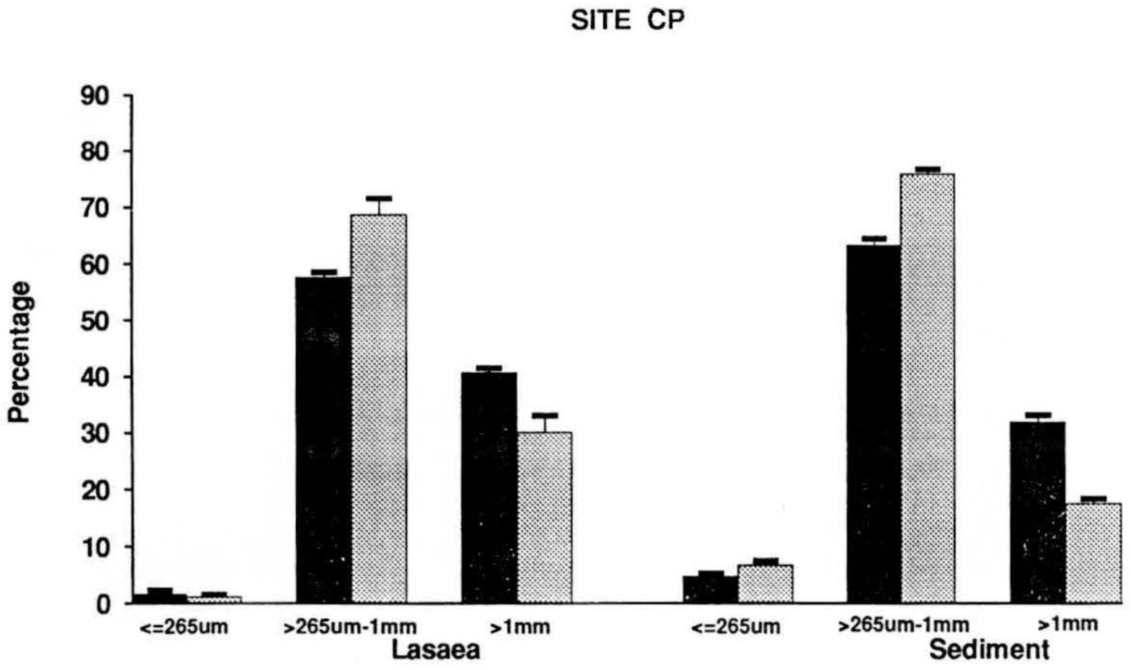


Number of Lasaea
350
300
250
200
150
100
50
0
CP
WR

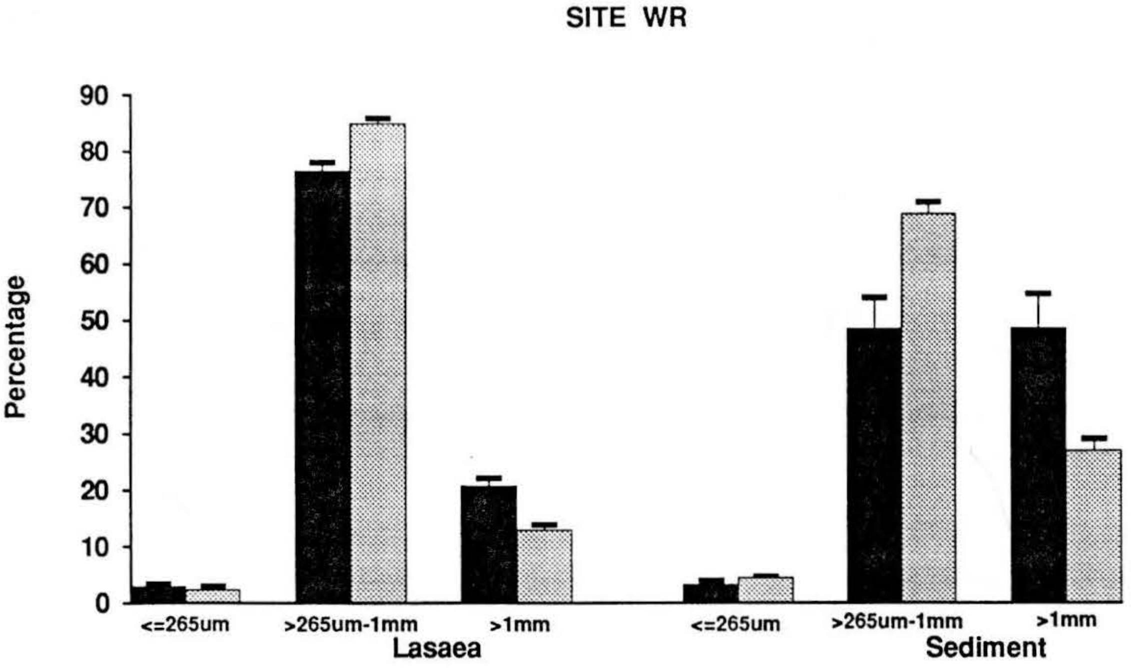
Figure 5.11. Mean (+ S.E.) percentage of different-sized *Lasaea* and sediment collected in Thinned (black) and Control (stippled) Supergrasse squares. Data were pooled from two plots.

a. Site CP

b. Site WR



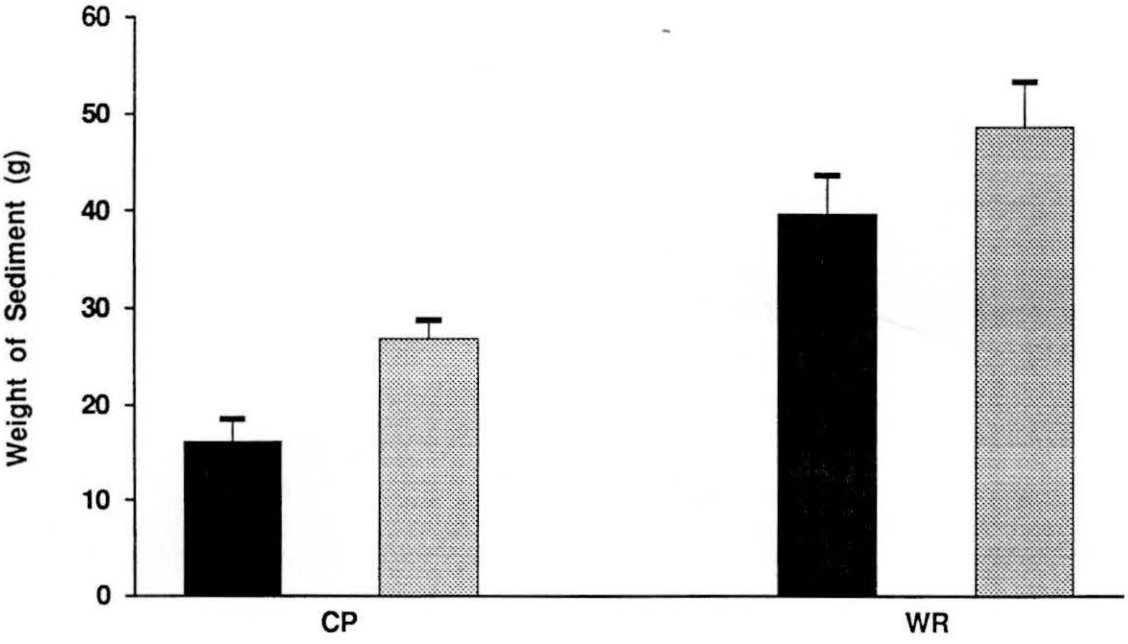
SITE CP



SITE WR

Figure 5.12. Mean (+ S.E.) weight of sediment collected in Seeded (black) and Control (stippled) Supergrasse squares in the Ballast I experiment at the two study sites. Data were pooled from two plots.

Figure 5.13. Mean (+ S.E.) number of *Lasaea* collected in Seeded (black) and Control (stippled) Supergrasse squares in the Ballast I experiment at the two study sites. Data were pooled from two plots.


60
50
40
30
20
10
0
Weight of Sediment (g)
CP
WR

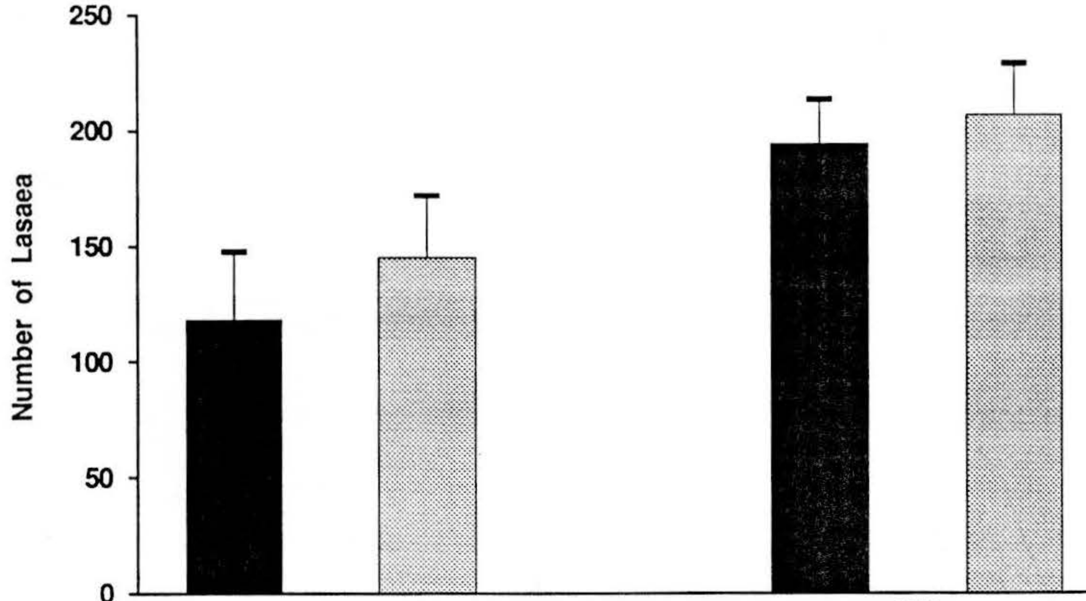
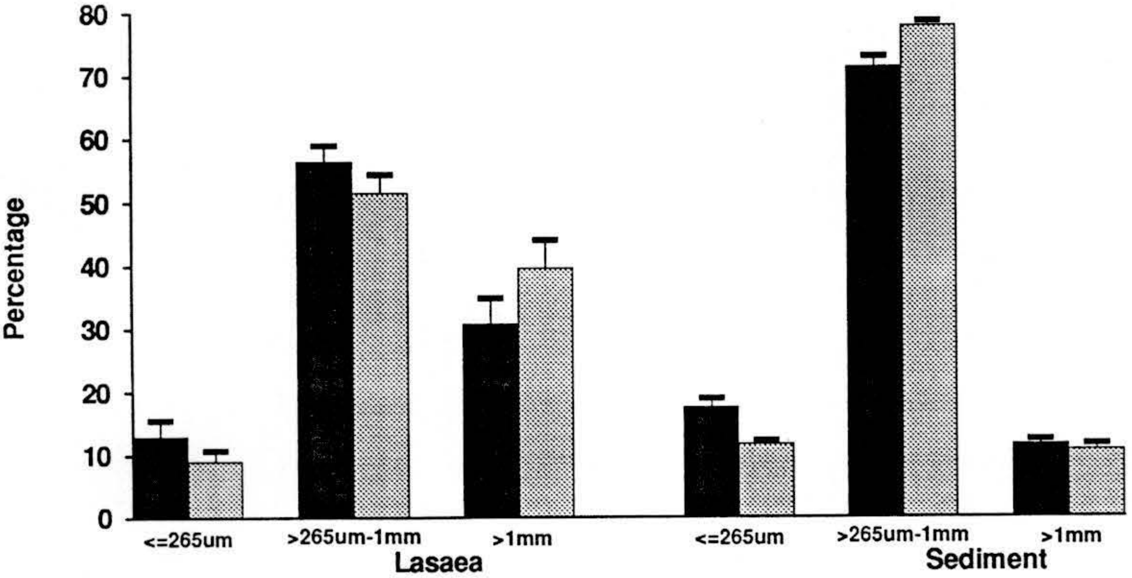

250
200
150
100
50
0
Number of Lasaea
CP
WR

Figure 5.14. Mean (+ S.E.) percentage of different-sized *Lasaea* and sediment collected in Seeded (black) and Control (stippled) Supergrasse squares in the Ballast I experiment. Data were pooled from two plots.

a. Site CP

b. Site WR


SITE CP

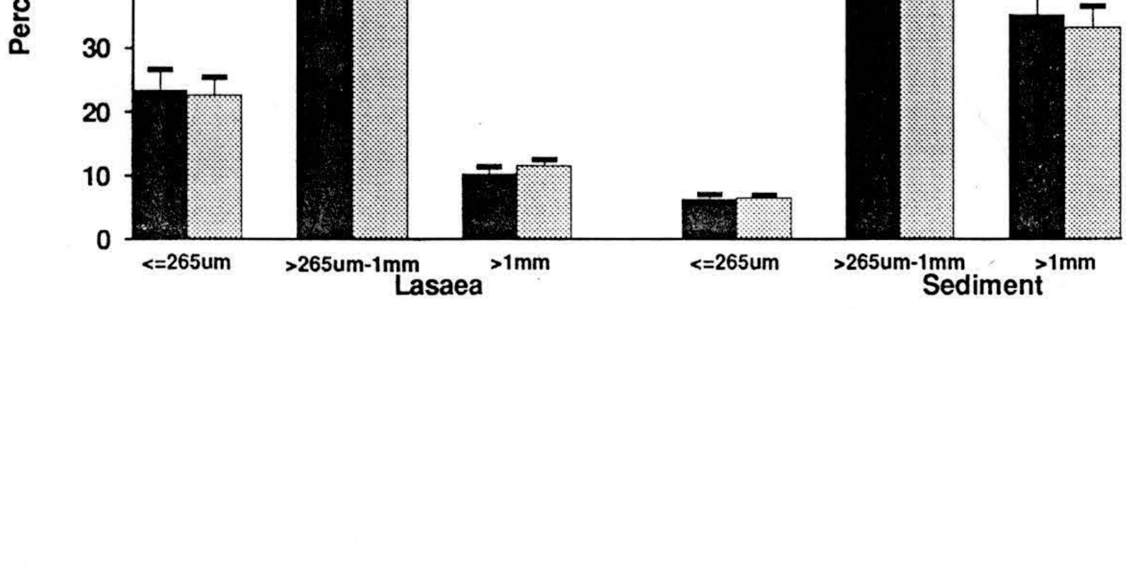
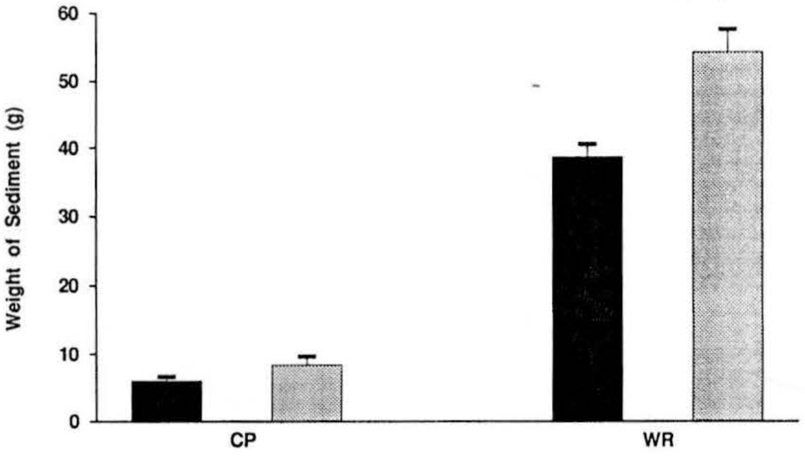
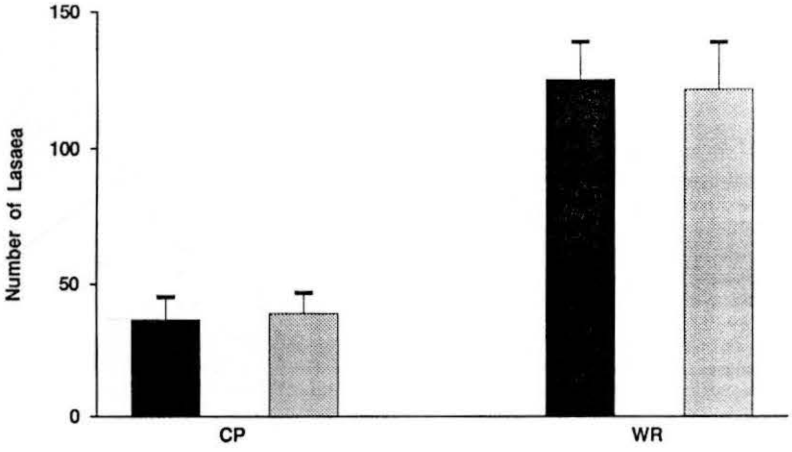

SITE WR

Figure 5.15. Mean (+ S.E.) weight of sediment collected in Seeded (black) and Control (stippled) Supergrasse squares in the Ballast II experiment at the two study sites. Data were pooled from two plots.

Figure 5.16. Mean (+ S.E.) number of *Lasaea* collected in Seeded (black) and Control (stippled) Supergrasse squares in the Ballast II experiment at the two study sites. Data were pooled from two plots.

Figure 5.17. Relationship between biomass of sediment and the number of *Lasaea* collected in Seeded (triangles) and Control (squares) Supergrasse squares at Site WR. Solid and open symbols represent data from Plot 1 and Plot 2 respectively.


Weight of Sediment (g)
0
10
20
30
40
50
60
CP
WR


Number of Lasaea
0
50
100
150
CP
WR

WR MID

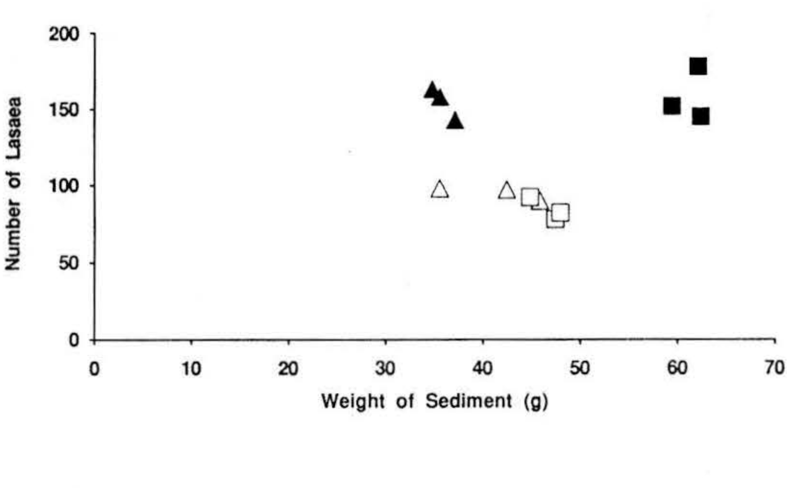
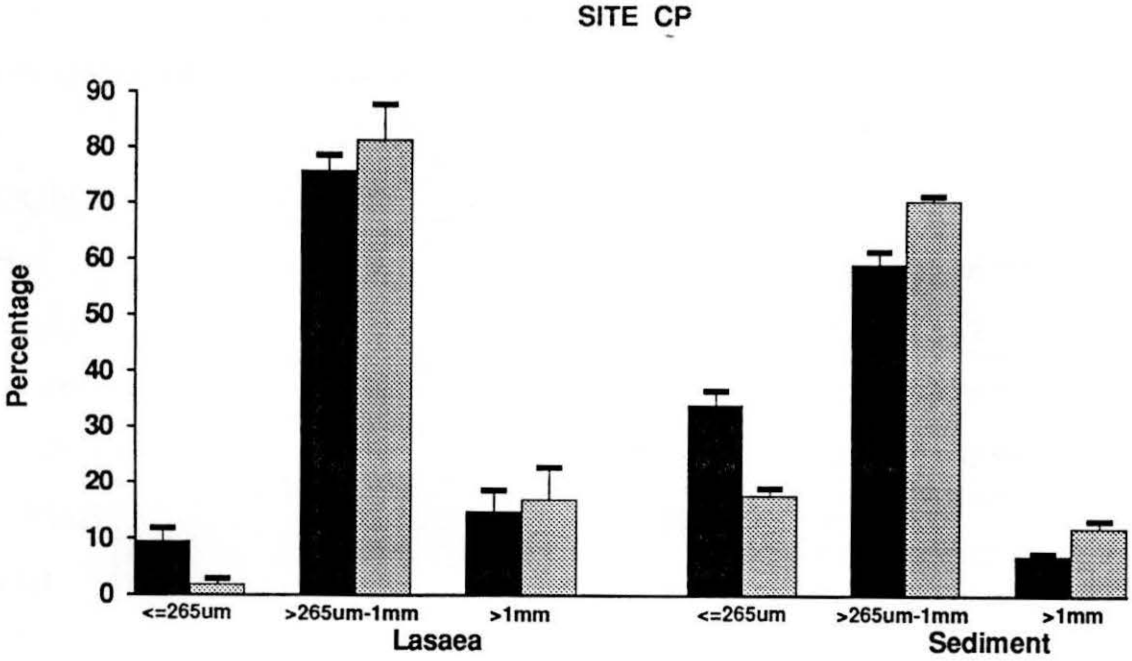

Number of Lasaea
0
50
100
150
200
0
10
20
30
40
50
60
70
Weight of Sediment (g)

Figure 5.18. Mean (+ S.E.) percentage of different-sized *Lasaea* and sediment collected in Seeded (black) and Control (stippled) Supergrasse squares in the Ballast II experiment. Data were pooled from two plots.

a. Site CP

b. Site WR


SITE CP
Percentage
90
80
70
60
50
40
30
20
10
0
<=265um
>265um-1mm
>1mm
<=265um
>265um-1mm
>1mm
Lasaea
Sediment

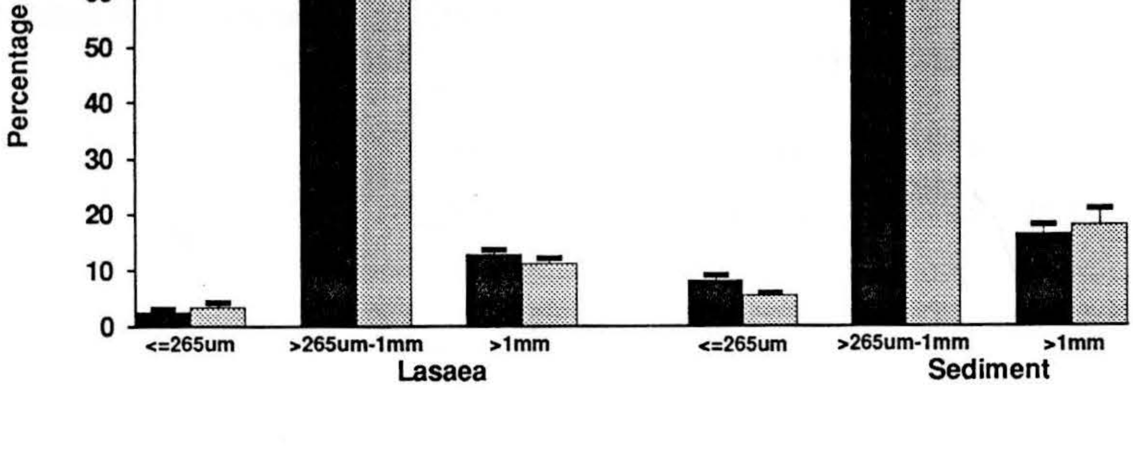

SITE WR
Percentage
90
80
70
60
50
40
30
20
10
0
<=265um
>265um-1mm
>1mm
<=265um
>265um-1mm
>1mm
Lasaea
Sediment

Table 5.1.

Analysis of numbers of *Lasaea* from two-week-old Supergrasse squares (Plots were nested within Site X Height interaction). All data were transformed as square-root(x+1) to homogenize the variance (Cochran's test). In this and subsequent tables, * denotes $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

SOURCE	DF	MS	*F*
Site	3	350.73	23.26 ***
Height	1	552.29	5.42
Si X Ht	3	101.97	6.76 *
Plot (Si X Ht)	8	15.08	12.67 ***
Residual	32	1.19	
Total	47		

SNK-test on the means for significant effect of Plot (Si X Ht):

	P1		P2		P1		P2
at mid CV:	5.7		5.1	at low CV:	2.9		2.5
PB:	13.8	>	11.2	PB:	12.7	>	9.1
CP:	19.9	>	14.3	CP:	8.9		7.8
WR:	26.1	>	22.1	WR:	8.2	<	11.8

SNK-test on the means for significant effect of Si X Ht:

	mid		low		mid		low
at CV:	5.4		2.7	at CP:	17.1	>	8.3
at PB:	12.5		10.9	at WR:	24.1	>	10.0

at mid: CV < PB CP < WR

at low: CV < CP WR PB

(values underlined are not significantly different at $P = 0.05$ in this and subsequent tables)

Table 5.2.

Analysis of weight of sediment from two-week-old Supergrasse squares (Plots were nested within Site X Height interaction). Cochran's test was not significant (*P* > 0.05).

SOURCE	DF	MS	*F*
Site	3	4682.81	92.33 ***
Height	1	10624.58	3.29
Si X Ht	3	3232.91	63.74 ***
Plot (Si X Ht)	8	50.72	4.32 **
Residual	32	11.75	
Total	47		

SNK-test on the means for significant effect of Plot (Si X Ht):

	P1		P2		P1		P2
at mid CV:	0.46		0.54	at low CV:	0.19		0.10
PB:	12.9		8.7	PB:	9.9	>	4.1
CP:	52.7		49.0	CP:	1.8		2.7
WR:	84.4	>	71.6	WR:	8.6	<	14.8

SNK-test on the means for significant effect of Si X Ht:

	mid		low		mid		low
at CV:	0.5		0.2	at CP:	50.9	>	2.3
at PB:	10.8		7.0	at WR:	78.0	>	11.7

at mid: CV < PB < CP < WR

at low: CV CP PB WR

Table 5.3.

Analysis of proportions of 0.265-1 mm *Lasaea* from two-week-old Supergrasse squares (Plots were nested within Site X Height interaction). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was significant ($P < 0.01$). Therefore, the F-ratio is considered to be significant only when $P < 0.001$.
(^{a}: effect of Height was tested by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site	3	0.059	0.71
Height^{a}	1	0.065	0.82
Si X Ht	3	0.068	0.82
Plot (Si X Ht)	8	0.083	2.24 *
Residual	32	0.037	
Total	47		

Table 5.4.

Analysis of proportions of 0.265-1 mm sediment from two-week-old Supergrasse squares (Plots were nested within Site X Height interaction). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was significant (0.05 > P > 0.01). Therefore, the F-ratio is considered to be significant only when $P < 0.01$.

SOURCE	DF	MS	*F*
Site	3	0.0628	1.78
Height	1	0.2115	1.57
Si X Ht	3	0.1348	3.82
Plot (Si X Ht)	8	0.0353	25.21 ***
Residual	32	0.0014	
Total	47		

Table 5.5.

Analysis of weight of sediment from Supergrasse squares in the Reduced Height experiment (Plots were nested within Site X Height interaction). Cochran's test was not significant ($P > 0.05$). ([a]: loss of one degree of freedom due to missing value)

SOURCE	DF	MS	*F*
Site	2	2239.08	17.42 **
Height	1	8417.92	3.93
Treatment	1	2041.82	4.59
Si X Ht	2	2140.07	16.65 **
Si X T	2	444.58	135.13 ***
Ht X T	1	1365.27	4.16
Si X Ht X T	2	328.35	99.80 ***
Plot (Si X Ht)	6	128.55	28.25 ***
T X Plot (Si X Ht)	6	3.29	0.72
Residual	23[a]	4.55	
Total	46		

Table 5.5 (Continued).

SNK-test on the means for significant effect of Plot (Si X Ht):

	P1 P2		P1 P2
at mid PB:	$\underline{4.2 \quad 6.1}$	at low PB:	$\underline{1.7 \quad 4.4}$
CP:	33.1 > 27.2	CP:	$\underline{0.7 \quad 0.4}$
WR:	62.7 > 43.7	WR:	$\underline{3.6 \quad 4.0}$

SNK-test on the means for significant effect of Si X Ht X T:

	T'ment Control		T'ment Control
at mid PB:	2.5 < 7.9	at low PB:	$\underline{2.0 \quad 4.0}$
CP:	19.3 < 40.9	CP:	$\underline{0.3 \quad 0.8}$
WR:	30.4 < 76.0	WR:	1.4 < 6.2

T'ment:	at PB:	$\underline{\text{mid} \quad \text{low}}$	Control: at PB:	mid > low
	at CP:	mid > low	at CP:	mid > low
	at WR:	mid > low	at WR:	mid > low

for T'ment:	at mid:	PB < CP < WR
	at low:	$\underline{\text{CP} \quad \text{WR} \quad \text{PB}}$
for Control:	at mid:	PB < CP < WR
	at low:	CP < $\underline{\text{PB} \quad \text{WR}}$

Table 5.6.

Analysis of numbers of *Lasaea* from Supergrasse squares in the Reduced Height experiment (Plots were nested within Site X Height interaction). All data were transformed as square-root(x+1) to homogenize the variance (Cochran's test). ([a]: loss of one degree of freedom due to missing value)

SOURCE	DF	MS	*F*
Site	2	89.71	5.67 *
Height	1	500.93	3.32
Treatment	1	74.93	48.03 *
Si X Ht	2	150.88	9.53 *
Si X T	2	1.56	0.55
Ht X T	1	1.75	0.30
Si X Ht X T	2	5.87	2.07
Plot (Si X Ht)	6	15.83	23.63 ***
T X Plot (Si X Ht)	6	2.83	4.22 **
Residual	23[a]	0.67	
Total	46		

Table 5.6 (Continued).

SNK-test on the means for significant effect of T X Plot (Si X Ht):

		T'ment		Control
at PB	mid P1:	4.3	<	10.6
		^		ll
	P2:	8.3		9.4
	low P1:	6.2	<	9.2
		ll		ll
	P2:	7.5		8.0
at CP	mid P1:	13.6		15.0
		v		v
	P2:	10.2		11.0
	low P1:	5.0	<	7.9
		ll		ll
	P2:	4.8	<	7.0
at WR	mid P1:	20.8	<	23.1
		v		v
	P2:	16.1		17.1
	low P1:	3.0	<	7.2
		^		^
	P2:	4.9	<	9.6

SNK-test on the means for significant effect of Si X Ht:

	mid		low
at PB:	8.2		7.7
at CP:	12.5	>	6.2
at WR:	19.3	>	6.2

at mid:	PB	CP	<	WR
at low:	CP	WR		PB

Table 5.7.

Analysis of proportions of 0.265-1 mm *Lasaea* from Supergrasse squares in the Reduced Height experiment (Plots were nested within Site X Height interaction). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was significant ($P < 0.01$). Therefore, the *F*-ratio is considered to be significant only when $P < 0.001$. (^{a}: test of Effect by pooling Mean Squares; ^{b}: loss of one degree of freedom due to missing value)

SOURCE	DF	MS	*F*
Site	2	0.0487	2.40
Height	1	0.0815	0.69
Treatment	1	0.0009	0.10
Si X Ht	2	0.1177	5.80 *
Si X T^a	2	0.0092	1.88
Ht X T	1	0.0008	0.04
Si X Ht X T^a	2	0.0181	3.69
Plot (Si X Ht)	6	0.0203	3.90 **
T X Plot (Si X Ht)	6	0.0037	0.71
Residual	23^b	0.0052	
Total	46		

Table 5.8.

Analysis of proportions of 0.265-1 mm sediment from Supergrasse squares in the Reduced Height experiment (Plots were nested within Site X Height interaction). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was not significant ($P > 0.05$). ([a]: test of Effect by pooling Mean Squares; [b]: loss of one degree of freedom due to missing value)

SOURCE	DF	MS	*F*
Site	2	0.2902	7.74 *
Height	1	0.4887	2.16
Treatment	1	0.5080	50.30 *
Si X Ht	2	0.2260	6.03 *
Si X T[a]	2	0.0101	4.04 *
Ht X T[a]	1	0.0003	0.12
Si X Ht X T[a]	2	0.0032	1.28
Plot (Si X Ht)	6	0.0375	15.00 ***
T X Plot (Si X Ht)	6	0.0028	1.12
Residual	23[b]	0.0025	
Total	46		

SNK-test on the means for significant effect of Si X T:

	T'ment		Control
at PB:	0.46	<	0.72
at CP:	0.78	<	0.94
at WR:	0.64	<	0.84

Table 5.9.

Analysis of weight of sediment from Supergrasse squares in the Reduced Density experiment (Plots were nested within Sites). Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Site	1	264.38	0.29
Treatment	1	1997.32	4.04
Si X T	1	494.53	4.68
Plot (Si)	2	897.93	36.46 ***
T X Plot (Si)	2	105.68	4.29 *
Residual	16	24.63	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	40.6	<	50.1
	ll		ll
P2:	38.9	<	47.8
at WR P1:	53.7	<	72.7
	V		V
P2:	20.9	<	56.7

Table 5.10.

Analysis of numbers of *Lasaea* from Supergrasse squares in the Reduced Density experiment (Plots were nested within Sites). All data were transformed as square-root(x+1) to homogenize the variance (Cochran's test). (^{a}: effect of Si X T was tested by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site	1	52.379	0.69
Treatment	1	36.435	2429.00 *
Si X T^a	1	0.015	0.007
Plot (Si)	2	76.300	30.85 ***
T X Plot (Si)	2	0.698	0.28
Residual	16	2.473	
Total	23		

SNK-test on the means for significant effect of Plot (Si):

	P1		P2
at CP:	<u>12.0</u>	<u> </u>	<u>10.1</u>
at WR:	17.4	>	10.6

SNK-test on the means for significant effect of Treatment:

T'ment	>	Control
13.7		11.3

Table 5.11.

Analysis of proportions of 0.265-1 mm *Lasaea* from Supergrasse squares in the Reduced Density experiment (Plots were nested within Sites). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Site	1	0.23469	66.48 *
Treatment	1	0.07514	626.17 *
Si X T	1	0.00012	0.02
Plot (Si)	2	0.00353	2.28
T X Plot (Si)	2	0.00781	5.04 *
Residual	16	0.00155	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	0.88		0.93
P2:	0.85	<	1.03
at WR P1:	1.09	<	1.18
P2:	1.05	<	1.16

Table 5.12.

Analysis of proportions of 0.265-1 mm sediment from Supergrasse squares in the Reduced Density experiment (Plots were nested within Sites). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was significant ($0.05 > P > 0.01$). Therefore, the *F*-ratio is considered to be significant only when $P < 0.01$.

SOURCE	DF	MS	*F*
Site	1	0.0788	1.90
Treatment	1	0.1800	21.95 *
Si X T	1	0.0082	1.01
Plot (Si)	2	0.0414	34.50 ***
T X Plot (Si)	2	0.0081	6.75 **
Residual	16	0.0012	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	0.93	<	1.04
P2:	0.92	<	1.07
at WR P1:	0.89	<	1.03
P2:	0.65	<	0.93

Table 5.13.

Analysis of weight of sediment from Supergrasse squares in the Ballast I experiment (Plots were nested within Sites). Cochran's test was significant ($0.05 > P > 0.01$). Therefore, the *F*-ratio is considered to be significant only when $P < 0.01$. ([a]: test of Effect by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site	1	3067.79	4.32
Treatment[a]	1	584.08	34.93 ***
Si X T[a]	1	4.59	0.26
Plot (Si)	2	709.65	39.76 ***
T X Plot (Si)	2	13.72	0.77
Residual	16	17.85	
Total	23		

SNK-test on the means for significant effect of Plot (Si):

	P1		P2
at CP:	25.4	>	17.6
at WR:	54.2	>	34.0

SNK-test on the means for significant effect of Treatment:

T'ment		Control
27.9	<	37.7

Table 5.14.

Analysis of numbers of *Lasaea* from Supergrasse squares in the Ballast I experiment (Plots were nested within Sites). Cochran's test was not significant ($P > 0.05$). (^{a}: test of Effect by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site	1	28428.17	0.87
Treatment^a	1	2400.00	4.60 *
Si X T^a	1	337.50	0.63
Plot (Si)	2	32730.42	55.61 ***
T X Plot (Si)	2	84.42	0.14
Residual	16	588.54	
Total	23		

SNK-test on the means for significant effect of Plot (Si):

	P1		P2
at CP:	191	>	72
at WR:	244	>	157

SNK-test on the means for significant effect of Treatment:

T'ment	<	Control
156		176

Table 5.15.

Analysis of proportions of 0.265-1 mm *Lasaea* from Supergrasse squares in the Ballast I experiment (Plots were nested within Sites). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was not significant ($P > 0.05$). ([a]: test of Effect by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site	1	0.09563	4.78
Treatment[a]	1	0.00474	1.74
Si X T[a]	1	0.00273	1.01
Plot (Si)	2	0.02000	6.78 **
T X Plot (Si)	2	0.00083	0.28
Residual	16	0.00295	
Total	23		

Table 5.16.

Analysis of proportions of 0.265-1 mm sediment from Supergrasse squares in the Ballast I experiment (Plots were nested within Sites). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Site	1	0.15910	3.45
Treatment	1	0.01241	2.39
Si X T	1	0.00519	1.17
Plot (Si)	2	0.04613	38.76 ***
T X Plot (Si)	2	0.00443	3.72 *
Residual	16	0.00119	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	1.04		1.09
P2:	0.97	<	1.07
at WR P1:	0.98		0.95
P2:	0.76	<	0.83

Table 5.17.

Analysis of weight of sediment from Supergrasse squares in the Ballast II experiment (Plots were nested within Sites). Cochran's test was significant ($0.05 > P > 0.01$). Therefore, the *F*-ratio is considered to be significant only when $P < 0.01$.

SOURCE	DF	MS	*F*
Site	1	9156.80	223.50 **
Treatment	1	477.76	1.85
Si X T	1	258.62	1.72
Plot (Si)	2	40.97	6.28 **
T X Plot (Si)	2	150.19	23.04 ***
Residual	16	6.52	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	7.3		9.7
	ll		ll
P2:	4.7		7.1
at WR P1:	35.8	<	61.3
	^		V
P2:	41.3	<	46.8

SNK-test on the means for significant effect of Site:

CP	<	WR
7.2		46.3

Table 5.18.

Analysis of numbers of *Lasaea* from Supergrasse squares in the Ballast II experiment (Plots were nested within Sites). Cochran's test was not significant ($P > 0.05$). ([a]: test of Effect by pooling Mean Squares)

SOURCE	DF	MS	*F*
Site	1	43861.50	5.18
Treatment[a]	1	2.67	0.03
Si X T[a]	1	54.00	0.58
Plot (Si)	2	8467.50	89.01 ***
T X Plot (Si)	2	80.67	0.85
Residual	16	95.13	
Total	23		

SNK-test on the means for significant effect of Plot (Si):

	P1		P2
at CP:	55	>	21
at WR:	157	>	90

Table 5.19.

Analysis of proportions of 0.265-1 mm *Lasaea* from Supergrasse squares in the Ballast II experiment (Plots were nested within Sites). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was significant ($0.05 > P > 0.01$). Therefore, the *F*-ratio is considered to be significant only when $P < 0.01$.

SOURCE	DF	MS	*F*
Site	1	0.0201	0.19
Treatment	1	0.0240	1.43
Si X T	1	0.0168	0.45
Plot (Si)	2	0.1032	17.79 ***
T X Plot (Si)	2	0.0374	6.45 **
Residual	16	0.0058	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	1.01		0.97
P2:	1.11	<	1.39
at WR P1:	1.17		1.18
P2:	1.17		1.19

Table 5.20.

Analysis of proportions of 0.265-1 mm sediment from Supergrasse squares in the Ballast II experiment (Plots were nested within Sites). All data were transformed as $\sin^{-1}$(square-root x). Cochran's test was not significant ($P > 0.05$).

SOURCE	DF	MS	*F*
Site	1	0.0950	6.99
Treatment	1	0.0265	1.63
Si X T	1	0.0163	2.06
Plot (Si)	2	0.0136	22.67 ***
T X Plot (Si)	2	0.0079	13.17 ***
Residual	16	0.0006	
Total	23		

SNK-test on the means for significant effect of T X Plot (Si):

	T'ment		Control
at CP P1:	0.92	<	1.00
P2:	0.83	<	1.00
at WR P1:	1.07	<	1.14
P2:	1.04	>	1.00

CHAPTER SIX GENERAL DISCUSSION

The structure of a population is affected by the reproduction, mortality, growth and dispersion of its individuals (Krebs, 1972). The recruitment of young *Lasaea* (less than 0.5 mm in shell length) to the population mainly occurred in summer between November and March for the two years of sampling (Section 3.3.1). Besides recruitment from planktonic larvae, the population also received juvenile and adult immigrants. *Corallina* algae were quite susceptible to this form of colonization, as was shown in the Regenerated *Corallina* experiment (Section 4.3.5). Unfortunately, this process has not been assessed in the *Galeolaria* substratum. *Lasaea* could probably colonize *Galeolaria* by seeking refuge among the surface irregularities of the worm tubes.

The mean sizes of the *Lasaea* populations were not dependent on their respective shore height at each site (Section 3.3.1). This is quite unusual for a filter-feeder whose feeding-time is directly related to the period of submersion and hence a decrease in rate of growth with shore height is expected (Seed, 1976; Griffiths, 1981; Butler, 1987). Besides the possible causes discussed in Section 3.4, the constant influx of *Lasaea* from a distant source might have masked the response of growth of the resident population to the tidal height. This, however, assumes that the mean size of organisms represents their rate of growth. The actual magnitude of growth of *Lasaea* at different tidal heights has to be evaluated by monitoring marked individuals.

The rate of growth of marked *Lasaea* has not been determined in this study. The only information available was a comparison of the mean sizes of *Lasaea* from Supergrasse squares at the two heights of the three study sites (Section 4.3.4). The increase of 0.15-0.28 mm from Year 1 to Year 2 is a rough estimate because animals less than 0.5 mm were not included in this analysis and there were always *Lasaea* of unknown origin deposited into the squares. They were more slow-growing than their Victorian counterparts whose rate of growth was 0.8 and 0.4 mm per year in the mussel bed and *Galeolaria* bed respectively (Polz, 1986).

Although *Lasaea australis* are tiny (usually smaller than 5 mm) and cryptic, they can be numerically important on a rock platform. The mean density per core from the various *Corallina* sites ranged from 9-105 (Fig. 3.7). This is equivalent to a mean of 7-79 X 10^3 *Lasaea* per square metre of the *Corallina* bed. In the *Galeolaria* substratum, the mean density ranged from 10-18 per ml of the worm tubes. This is equivalent to a density of 10-18 X 10^4 *Lasaea* per square metre of the *Galeolaria* bed of thickness 1 cm. These are crude estimates, but they indicate that the density of *Lasaea* in these substrata were much greater than that reported in Western Australia (1.5-2 X 10^3 per square metre underneath the rock surface; Roberts, 1984).

Corallina at Cape Banks exhibited two recognizable growth forms: the compact, turf form and the long, pendant form described in Johansen & Colthart (1975). The turf form was not a very stable substratum because it could get scoured off from the surface of rocks by trampling (pers. obs.). *Galeolaria* also exhibited two growth forms: the upright form where worms are dense and the prostrate form where they are sparse (O'Donnell, 1986). *Galeolaria* could also be an unstable substratum. The upright form was susceptible to removal by storms, during which *Lasaea* and other associated invertebrates were washed away. Moreover, *Lasaea* were found amongst algal substrata such as *Hormosira* holdfasts and underneath encrusting *Hildenbrandia*, where they were vulnerable to dislodgement by waves. These dislodged animals could serve as the source for colonization of experimental squares or other new surfaces. Over a period of two weeks, 50-600 *Lasaea* could accumulate in a Supergrasse square of 12 X 12 cm^2 (Chapters 4 & 5). The number increased progressively with time and, after two years, 250-6000 bivalves (including recruits from larvae) could be collected in a square.

The association between *Lasaea* and *Corallina* or *Galeolaria* was only a facultative one, because *Lasaea* could occur in other substrata, for example, inside empty barnacle tests, underneath encrusting algae or among brown algal holdfasts. They could be associated with artificial structures such as inside Supergrasse or underneath synthetic foam secured to the rock surface. Presumably, *Lasaea* would gain some degree of protection from physical stress such as desiccation and wave shock in these cryptic microhabitats. Various studies on phytal invertebrates have also emphasized their dependence on the algal hosts for shelter and food (Wigham, 1975; Fretter & Manly, 1977; Hayward, 1980). When Supergrasse squares were set up at a tidal height of 2.2 m C.D. which is above the upper limit of its natural substrata, *Lasaea* could still establish there (pers. obs.). This suggests that *Lasaea* can extend its vertical distribution when a suitable shelter is provided.

The spatial patterns of accumulation of *Lasaea* and sediment in the Supergrasse squares were consistent over time (Chapters 4 & 5). Sites WR and CV were, respectively, the highest and lowest ranked site in terms of the quantity of accumulated material. There was always more material collected at the mid than low shore at most of the sites. This is comparable to the pattern of accumulation of sediment in plastic algal mats reported by Gibbons (1988). The relative amount of accumulated material between the tested plots in an area was also quite consistent over the study period. Similar to the distribution in Supergrasse squares, there were consistently more *Lasaea* from the high zone than the low zone of each of the *Corallina* and *Galeolaria* bed (Sections 3.3.2 & 3.3.3). It is very likely that local physical conditions such as coastal geomorphology, shore waves or tidal currents were responsible for causing these non-random patterns of distribution (Connell, 1985).

Although the arrival pattern of *Lasaea* and sediment might be governed by similar hydrodynamic forces, the series of Supergrasse manipulative experiments demonstrated that *Lasaea* did not behave exactly like passive sediment particles (Chapter 5). Presumably, they could withstand some degree of water-dislodgement due to byssal attachment. Therefore, the marked *Lasaea* that disappeared at the initial stage of the Retention experiment were likely to be individuals that had not yet properly attached (Section 4.3.2). Once established, *Lasaea* could survive in these sediment-packed Supergrasse microhabitats and can be treated as a group of stress-tolerant strategist (Littler *et al.*, 1983).

Lasaea species that lack planktonic larvae can be dispersed by byssal drifting or rafting (Ó Foighil, 1989). Similarly, *L. australis* is capable of being transported while as juveniles or as adults. This alternative mode of dispersal is likely to be a side-product of wave-dislodgement rather than by the active choice of the bivalve as suggested by Bayne (1964) and Prezant & Chalermwat (1984). When dislodged from its natural substrata, *Lasaea* is transported in the water and deposited in areas of reduced water flow (Dean & Connell, 1986c). This is comparable to the situation with meiofauna in soft sediments. They are liable to suspension by water disturbance, transported in the water column before their subsequent settlement (Bell & Sherman, 1980; Palmer, 1984, 1988).

Due to its size and cryptic habit, *Lasaea australis* does not have the potential to dominate intertidal shores as mussels do (Seed, 1976; Suchanek, 1985). Mussels are capable of monopolizing the space and eventually form a monostand unless their competitive exclusion of barnacles and algae can be checked by predation or disturbance (Paine, 1966, 1971, 1974; Dayton, 1971; Menge, 1976; Menge & Sutherland, 1976). Sometimes, mussels can acquire size-refuge by reaching a size too large to be eaten by starfish or predatory gastropods (Dayton, 1971; Paine, 1974). These existing theories, though widely accepted, do not seeem to apply to *Lasaea* because they are small and non-sessile. More work, however, has to be done before the effect of predation on *Lasaea* can be assessed.

This study shows that the process of recruitment, especially of adults, can be quite important in determining the pattern of distribution of an intertidal organism. This adds support to the role played by recruitment in community structuring, although early emphasis was on larval recruitment of sessile organisms (Underwood & Denley, 1984; Underwood & Fairweather, 1989). Recruitment is known to be influenced by physical transport processes in hard-shore and soft-shore environment (Butman, 1987; Roughgarden *et al.*, 1987, 1988). These involve mechanisms such as internal waves, shore waves, tidal currents or boundary-layer flow (Shanks, 1983; Jumars & Nowell, 1984; Nowell & Jumars, 1984; Connell, 1985; Scheltema, 1986) and may account for the consistent patterns of distribution of *Lasaea* in natural and artificial substrata.

Biological interactions involving predation and competition have been shown to be important in structuring intertidal communities. This study, however, demonstrates that adult recruitment under the effect of hydrodynamic processes can be important in determining the distribution and abundance of an intertidal bivalve on a rocky shore.

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