THE ECOLOGY OF THE ROCKY SHORE INTERTIDAL BARNACLE *Chamaesipho tasmanica* IN NEW SOUTH WALES

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DECLARATION

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

Signed: [redacted]

Date: 12/8/97

"The task is not so much to see what no one else has yet seen; but to think what no one has yet thought about what everybody sees."

Arthur Schopenhauer, 1890

The honeycomb barnacle *Chamaesipho tasmanica* Foster & Anderson

ABSTRACT

The small honeycomb barnacle *Chamaesipho tasmanica* occurs in patches on exposed rocky shores and higher up the shore, but often carpets the substratum at mid-shore levels of sheltered shores of south-eastern Australia. This thesis investigates the effects of *initial settlement* and *post-settlement mortality* on stages of the life-history of populations of *C. tasmanica* at Cape Banks in New South Wales. The relative importance of the individual stages of the life-cycle in determining the demography of adult populations was interpreted by simultaneous studies of juveniles and adults.

Larval supply was studied experimentally using plankton traps in a nested design on two heights within *Chamaesipho's* distribution at sheltered Site 4. An intensive daily sampling of plankton from 1990 to 1993 (over five to six successive days during new and full moons from the end of July to mid December each year) and concurrent monitoring of settlement from 1991 to 1993, revealed that larval arrival and settlement were typified by trickles of larvae from late July to December. During this period, major pulses of arriving cyprids were also recorded once or twice each year.

A consistent spatial pattern of larval arrival was measured at sheltered Site 4 from 1990 to 1993, with one set of traps low on the shore always capturing more cyprid larvae during major peaks of arrival than all other traps. While the different numbers of cyprids in these different places cannot be explained by cyprids arriving first on lower shores, longer periods of submersion nor aggregations of larvae in the plankton, these recurrent patterns of arrival of larvae suggest that local site-specific characteristics have much more influence on the demography of populations of this species than was previously thought.

Because cyprids of *Chamaesipho* and *T. purpurascens* were caught in plankton traps together but different patterns of larval distribution were evident, it may therefore be that cyprids of *Chamaesipho* and *T. purpurascens* occur in different positions in the water column. Larvae arrive in different numbers at different places on the shore even though water-flow across the substratum and through traps is similar. Water-flow is therefore not implicated in determining differences in larval supply. While direction of water-flow and small-scale turbulence were not measured in this study, they may contribute to the different numbers recorded in different places. Major peaks of larval arrival, however, were always associated with high velocity Southerly winds and specific wind speeds and wave heights during new and full moons. Variations in larval supply were also found to be responsible for the variations in distributions of juveniles on the substratum.

Hypotheses pertaining to models explaining settlement as a function of larval choice were tested by experimental manipulations in the field. Once larvae arrive, larval choice will modify the numbers that settle in response to particular environmental cues. That is, cyprids do not act as passive particles at settlement but will actively select the habitat on which they settle. For example, larval supply, enhanced by the gregarious response of larvae to the presence and proximity of adult conspecifics and older recruits, determined distributions of juvenile populations of *Chamaesipho* at Cape Banks. In areas where there were small clear patches among aggregations of barnacles there was greater settlement and larger densities of barnacles. It seems that larval supply and larval choice also determine adult distributions because a strong relationship was found between annual total settlers and annual total adults at six sites and three heights (Low, Mid, Upper) of *Chamaesipho's* distribution studied from 1989 to 1993. Recruitment each year was not sufficient to maintain densities of *Chamaesipho* so that populations at Cape Banks were observed to decrease at all sites and heights studied from 1989 to 1993.

Mortality of juveniles and of adults were also compared. Despite great post-settlement mortality of juveniles, spatial patterns of settlers and adults were similar and were not altered by juvenile nor adult mortality. These juvenile spatial patterns were retained by adults. Post-settlement mortality merely acted on settlers evenly across the six sites studied, despite differences in height and exposure. Differential mortality was therefore rejected as a model for causing the sparse populations of barnacles on exposed and upper shores. There were, however, isolated incidences of intense mortality. For example, predation by the whelk *Morula marginalba* was considered to maintain the uniform small size of *Chamaesipho* at Site 3, low on the shore so that populations consisted of only one or two cohorts at any one time. When the limpet *Cellana tramoserica* was added to, or excluded from plots low on the shore at sheltered Site 4, although survival of juvenile barnacles was affected, *Cellana* did not influence survival of adults. Because the spatial patterns of settlers were the same as adults and because mortality was similar at all sites and heights, *initial settlement* was found to be more important than *post-settlement mortality* in determining the abundance and distribution of *Chamaesipho.*

Because *Chamaesipho* varied in size among sites, and because size was not necessarily representative of age, three growth models were proposed to explain this size differential. While rates of growth and periods of growth did not differ, differences in longevity were found to influence size of *Chamaesipho* in some places at Cape Banks. In fact, when barnacles were aged, it was found that a greater proportion of older barnacles (> 3 years of age) occupied areas predominated by large barnacles, especially on exposed shores. That is, site-specific characteristics influenced longevity in some places so that larger *Chamaesipho* continued to predominate in these areas. Size distributions of *Chamaesipho* were therefore influenced by site-specific characteristics.

Overall, this study found that *initial settlement*, which included the processes of larval supply and larval choice at settlement, was integral in determining the demography of *Chamaesipho* at Cape Banks. The alternative model that *post-settlement mortality* determined the distributions and abundance of juveniles and adults was discounted by experimental tests of the prediction for differential mortality on exposed and sheltered shores and at different heights within shores to match eventual numbers of adults. Post-settlement mortality merely modified densities of barnacles; patterns of juvenile density were retained by adults.

Long-term ecological studies of larval supply, settlement and recruitment of *Chamaesipho* at various sites and shores on the eastern Australian coast are necessary to determine processes governing demographic trends of this barnacle at larger spatial scales. Effects of *site-specific characteristics* on larval supply, settlement and on longevity after settlement will then become even more apparent as major causative mechanisms for the demography of *Chamaesipho*. Future research on *Chamaesipho* also needs to address the issues of larval dispersal (including hydrodynamics at small and large spatial scales), the fate of larvae in the plankton and the genetic origins of populations.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Ecological Theory

"Do the populations at a site consist of all those that happened to arrive there, or of only a special subset - those with properties allowing their coexistence?" (Roughgarden, 1989). This question is fundamental to ecology and the answer to this question will be very different for populations in open or closed systems.

Closed populations receive their recruits from adults within them, whereas open populations rely on the influx of recruits from an outside source (Roughgarden & Iwasa, 1986; Roughgarden et al., 1987). Source habitats are occupied by species that maintain their populations without immigration, whereas sink habitats are occupied by species that require immigration to maintain their populations (Roughgarden & Iwasa, 1986; Pulliam, 1988; McPeek & Holt, 1992). Therefore, reproductive surpluses from source habitats can help to maintain "deficient" populations in sink habitats which have relatively poor reproductive success in those habitats, compared with their rates of mortality (Pulliam, 1988).

In closed systems, density may influence the structure of a population by affecting survivorship and fecundity due to interactions such as competition for food and space (Krebs, 1972; Valiela, 1984). For example, Branch (1975) showed that there was a relationship between large densities of adult limpets and mortality of young limpets due to limited space available for settlement of these juveniles. Also, at large densities, competition for food reduced rates of growth and resulted in smaller individuals with reduced fecundities (Branch, 1975; Valiela, 1984). That is, with limited food and space, fertility and longevity would decrease and eventually the population would stop growing (Krebs, 1972).

Most population models in ecology are based on closed populations (Roughgarden & Iwasa, 1986) whereas many marine species have open populations with sessile adults and long-lived dispersive larval stages. Consequently, in marine studies, it is often uncertain whether adults being investigated are parents of larvae arriving, or whether new populations are derived from another source. Current research is addressing this issue (Black & Johnson, 1981; Johnson & Black, 1982, 1984a, 1984b; Ayre, 1985, 1990; Grosberg, 1987; Hunt & Ayre, 1989; Levin, 1990; Young, 1990; Hurlbut, 1992). The number of recruits, rather than their source, should, however, be the most important factor in determining population densities in any population (Denley & Underwood, 1979; Underwood et al., 1983; Connell, 1985; Roughgarden et al., 1987; Ayre, 1990).

Most models in the literature are space-limited and free space is emphasised as the main determinant of demography (Roughgarden et al., 1985, 1988; Possingham & Roughgarden, 1990). That is, the amount of free space determines survivorship in space-limited populations. For example, Gaines and Roughgarden (1985) found that, among populations of barnacles, free space generally occurs in patches which are filled by cyprid larvae from the same generation, resulting in patches of similarly-sized barnacles. At locations where settlement was intense, mortality was cover-dependent due to increased predation by starfish. They further suggested a new model for demography and population dynamics of an open population with space-limited recruitment by proposing that rate of larval settlement acts to determine the structure of assemblages in intertidal habitats. That is, small rates of settlement give populations with steady-state abundance whereas large rates of settlement result in temporal oscillations in numbers in a population (Gaines & Roughgarden, 1985).

In open systems, due to variable mortality in the plankton, hydrodynamics responsible for transporting larvae, larval selection of habitat (Butman, 1987) and the pattern of already existing adults (Chesson, 1982a, 1982b, 1985), the effects of density and their associated interactions will vary for each batch of new arrivals and subsequent survivors. If there is large recruitment, density-dependent processes may operate whereas density-independence may be a function of small recruitment (Underwood & Denley, 1984; Connell, 1985). Once these new individuals are established, interactions among mixed cohorts, or the same cohort, may bear no relationship to future densities of adults (especially if larvae arrive from another source) or to the numbers of larvae arriving to settle. The numbers of already established adults may, however, influence the numbers of larvae that do settle due to available space or to specific physical and chemical cues. Therefore the importance of long-term ecological studies is stressed. Research should encompass spatial and temporal patterns of distribution and abundance of adult populations and should monitor selected individuals from the larval through to the adult stage.

Early ecological studies emphasised the adult stage (Connell, 1961a, 1961b, 1970; Paine 1969, 1974, 1984; Dayton, 1971; Menge & Sutherland, 1976; Lubchenco & Menge, 1978). These early studies of adults attempted to explain patterns of abundance and distribution of various intertidal marine assemblages. Physical factors such as temperature and desiccation were considered to determine the upper limits of vertical distribution and caused fluctuations of densities within these populations (Connell, 1961a, 1961b, 1975; Lewis, 1963; Brown, 1967; Kensler, 1967; Kennedy & Mihursky, 1971; Vermeij, 1971). Lower limits were said to be determined by biological factors such as competition and predation which also influenced population densities and thus explained population dynamics (Connell, 1961a, 1961b; Dayton, 1971; Menge, 1976, 1992; Menge & Sutherland, 1976; Paine, 1974, 1984).

In the late 70's, several studies confirmed that predation and disturbance could operate to maintain local diversity of intertidal species (Paine, 1974; Lubchenco, 1978; Sousa, 1979; Menge & Lubchenco, 1981). Experimental studies on intertidal rocky shores in North America have shown that predation (Paine 1966, 1974; Connell, 1972; Gaines & Roughgarden, 1985), grazing (Lubchenco, 1978, 1980) and physical disturbances (Dayton, 1971) cause mortality and maintain relatively small densities while opening space for new recruits and influencing diversity of species (Valiela, 1984). Similar patterns of distribution of intertidal organisms are found along much of the coast of New South Wales, Australia. The predatory starfish *Pisaster ochraceus* which apparently acts as a keystone species and prevents competitively dominant species from monopolizing intertidal areas in some parts of the west coast of the

United States (Paine, 1974, 1984) does not exist in Australia and there is no similar major predator. Predation by whelks is, however, important on rocky shores in Australia but comparisons cannot be made due to the complex and uncertain, as yet, results of field experiments (Underwood, 1994). Therefore models based on major predators which would explain the observed American patterns would not explain the Australian situation: how intertidal communities are structured in one area cannot be generalized to other marine environments (Underwood & Denley, 1984; Underwood, 1985). The role of predation and disturbance as a general model for promoting diversity of species was largely unchallenged until Underwood et al. (1983) found that the abundance of various species in several rocky intertidal areas in New South Wales, Australia was not determined primarily by disturbance or predation, but by the number of recruits. That is, patterns of distribution could also be due to processes of settlement or recruitment. Other studies support this association of larval settlement and assemblages of species (Denley & Underwood, 1979; Grosberg, 1982; Keough, 1983; Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985, 1987; Roughgarden et al., 1985; Roughgarden & Iwasa, 1986; Raimondi, 1988a, 1988b, 1990, 1991; Minchinton & Scheibling, 1991; Bertness et al., 1992; Hurlbut, 1992; Gaines & Bertness, 1993; Pineda, 1994a).

Currently, there is controversy about the relative importance of juvenile and adult stages in processes causing distributions of populations in sessile marine invertebrates (Denley & Underwood, 1979; Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985). For example, Connell (1985) indicated that post-settlement mortality modifies barnacle densities to determine adult distributions. Underwood and Denley (1984), however, emphasised that mechanisms influencing settlement of larvae, *not* post-settlement mortality, can be primarily important in determining distributions of barnacles.

Underwood (1979, 1994) stressed that the study of biological interactions such as larval recruitment, pre-emption of space, competition for food and space, predation and mutualism is essential to explain patterns of distribution on local rocky shores. Similarly, it is important to emphasise that the patterns of distribution and abundance of sessile populations such as barnacles are governed by dynamic complex processes, and that the processes of initial settlement and recruitment are different and not necessarily closely related (Underwood, 1979; Caffey, 1985). Larvae may arrive to settle, but selection of habitat and post-settlement mortality and various site-specific characteristics will influence the numbers of recruits that settle and survive. The models of *larval delivery* (larval supply) versus *larval behaviour* (larval choice) have recently been proposed by Raimondi (1991) to explain the distributions of adult barnacles, whereas Connell (1985) emphasised the effects of *post-settlement mortality* on survival and ultimate distributions of adults. Hence the dynamics of a marine intertidal population will be determined by the arrival of larvae and their successful settlement and recruitment (Underwood, 1979; Underwood & Denley, 1984; Keough, 1986).

The **physical processes** which determine **larval supply**, including meteorological conditions and associated hydrodynamics over large spatial scales and micro-hydrodynamics at small spatial scales, (Shanks, 1983, 1986; Kingsford & Choat, 1986; Butman, 1987; Shanks & Wright, 1987; Denny & Shibata, 1989; Epifanio et al., 1989; Farrell et al., 1991; Kingsford et al., 1991; Mullineaux & Butman, 1991; Roughgarden et al., 1991, 1994; Mullineaux & Garland, 1993; Milicich, 1994; Alexander & Roughgarden, 1996), and the behavioural responses of larvae at settlement (**larval choice**) (Knight-Jones, 1953; Moyse & Hui, 1981; Crisp, 1984; Wethey, 1984, 1986a; Gaines & Roughgarden, 1985; Chabot & Bourget, 1988; Raimondi, 1988a, 1988b, 1990, 1991), are now considered to have primary roles in determining the abundance and distribution of open populations: the concept of *supply-side ecology* has only recently been introduced (Underwood & Denley, 1984; Gaines & Roughgarden, 1985; Lewin, 1986; Butman, 1987; Roughgarden et al., 1987, 1988; Underwood & Fairweather, 1989; Sutherland, 1990; Hurlbut, 1992; Gaines & Bertness, 1993).

Terrestrial ecologists also accept the importance of the transport of propagules in maintaining assemblages of organisms which, in turn, are governed by population dynamics, including interactions among species (Roughgarden, 1989; Underwood & Fairweather, 1989).

If *initial settlement* of larvae (larval supply and larval choice) determines adult distributions, the prevalence of greater numbers of adults on lower areas of shores may occur because more larvae arrive here first and leave fewer to settle on upper areas (Roughgarden et al., 1988). Denley and Underwood (1979) and Underwood and Denley (1984) proposed that times of submersion determined these differences in vertical distribution of the barnacle *Tesseropora rosea.* Aggregations of cyprids in the plankton (de Wolf, 1973; Gaines et al., 1985; Roughgarden et al., 1987, 1988) and/or the position of larvae in the water column (Grosberg, 1982; Gaines et al., 1985) may also be responsible for differences in abundances of barnacle populations.

Connell (1961a, 1961b), Underwood and Denley (1984), Caffey (1985) and Gaines and Roughgarden (1985) indicated that variable input (settlement) and early survival (leading to recruitment) of juveniles largely determine the initial, but variable conditions of post-settlement processes. That is, the processes of settlement and recruitment should organise patterns of distribution and abundance of intertidal organisms on relatively exposed shores.

Further, Connell (1985) stated that, in sessile species such as barnacles, only mortality can affect density after settlement. He stated that zonation of barnacles is determined by patterns of settlement by cyprids, but post-settlement processes primarily influence adult distributions. Underwood and Denley (1984), however, emphasised that processes influencing settlement of larvae, *not* post-settlement mortality, often determine the upper limit of distribution of barnacles. Clearly there is dissension in the literature (Denley & Underwood, 1979; Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985) about the relative importance of juvenile and adult stages in processes causing distributions of populations in sessile marine invertebrates. What then is the relative importance of *initial settlement* versus *post-settlement mortality* in determining the demography of these populations?

1.2 This Study

As mentioned previously, past ecological intertidal studies were concerned with post-settlement processes, especially competition and predation (Connell, 1961a, 1961b; Dayton, 1971; Menge & Sutherland, 1976). Currently there is a push for pre-settlement processes such as larval dispersal and survival, and for habitat selection during settlement (Strathmann et al., 1981; Grosberg, 1982; Keough, 1983; Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985, 1987; Gaines et al., 1985; Butman, 1987; Bushek, 1988; Minchinton & Scheibling, 1991, 1993; Bertness et al., 1992; Hurlbut, 1992; Milicich et al., 1992; Gaines & Bertness, 1993; Pineda, 1994a, 1994b; Alexander & Roughgarden, 1996).

There have been few studies which connect larval supply, settlement, recruitment, adults and reproductive output (Yoshioka, 1982; Roughgarden et al., 1988; Hurlbut, 1992; Ross, 1992; Carlon & Olson, 1993; Meekan et al., 1993). Hence, this study was established to determine the importance of these processes, except reproductive output, on the demography of the Chthamaloid honeycomb barnacle, *Chamaesipho tasmanica* (throughout this thesis referred to as *Chamaesipho*), a species which varies enormously in density within a relatively small spatial scale on one shore. *Chamaesipho* varies in density from crowded to patchy to sparse aggregations on the mid littoral zones of relatively exposed rocky shores in Eastern Australia. It is very abundant in some areas, and, because it occurs higher up the shore usually in more protected areas, it is emersed for longer periods than most other barnacles.

Previous studies have shown spatial and temporal variation in recruitment of populations of *Chamaesipho* (Caffey 1983, 1985; Fairweather et al., 1984; Moran et al., 1984; Otaiza, 1989). In 1974, *Chamaesipho* recruited heavily at Green Point in New South Wales but since 1979, insignificant recruitment was recorded on most shores studied (Moran et al., 1984). Underwood (pers. comm.) also observed no settlement at all on most shores studied in New South Wales between 1980 and 1983. Otaiza (1989), however, found that new settlers of *Chamaesipho* were abundant in the

Cape Banks Scientific Marine Research Area, Botany Bay, New South Wales from August to November, 1986 and from August to October, 1987.

Post-settlement mortality has also been implicated in determining populations of adult barnacles (Connell, 1985). The physical effects of temperature and desiccation on survival of young barnacles have been well documented (Connell, 1961a, 1961b; Dayton, 1971; Denley & Underwood, 1979). Earlier studies have also shown that limpets can affect densities and survival of barnacles after settlement (Hatton, 1938; Connell, 1961b). The limpet *Cellana tramoserica* is numerous on sheltered mid-shore heights on rocky shores in New South Wales (Underwood et al., 1983) and can influence survival of juvenile barnacles (Denley & Underwood, 1979; Caffey, 1983; Underwood et al., 1983). During feeding on microalgal spores, *Cellana* can accidentally destroy or bulldoze cyprid larvae of the barnacle *T. rosea* (Denley & Underwood, 1979; Underwood et al., 1983). Caffey (1983) also found that the presence of *Cellana* had a deleterious effect on survival of young *T. rosea* less than 30 days old. Because *Cellana* also grazes in patches within populations of neighbouring *Chamaesipho*, it is proposed that *Cellana* may also influence distributions of *Chamaesipho* at Cape Banks by killing newly-settled barnacles. There are also studies on the effects of predation on adult barnacles (Fairweather et al., 1984; Moran et al., 1984; Fairweather, 1988a, 1988b). Connell (1985) stated that if juvenile or adult mortality of barnacles was density-independent, the numbers of adults would be determined by the numbers of larvae that settled initially. Intense predation, however, could negate the effect of initial settlement. Otaiza (1989) further suggested that differences in total recruitment, survival or both were implicated in determining densities of *Chamaesipho.*

Because early observations in this study in May 1989 at Cape Banks indicated that *Chamaesipho* has abundant free space for settlement although few cyprids arrive to fill these spaces and because most prior research was based on space-limited species which had unlimited numbers of larvae arriving, *Chamaesipho* was considered to be a suitable organism for research into extending the accepted ecological principles that determine the demography of sessile populations. All stages of *Chamaesipho's* life-history, apart from the naupliar stages (unpubl. data), were studied to determine the relative importance of each stage on the structure of populations of adults. This demographic study was designed to determine the processes affecting the spatial and temporal distributions and abundance of the barnacle *Chamaesipho*. In particular, the relative importance of *initial settlement* versus *post-settlement mortality* in determining the abundance and distribution of populations of these barnacles at Cape Banks were investigated. The variables measured include larval supply, settlement, recruitment, rates of growth and mortality.

Aims of This Study

1. To describe spatial and temporal patterns of distribution of *Chamaesipho tasmanica*
2. To test hypotheses about the influence of larval supply on population densities
3. To test hypotheses about the association of larval supply with water-flow, wind direction, wind speed, and wave height
4. To test hypotheses about the influence of cues on settlement of larvae: manipulated cues include the presence or absence of barnacle abstract, new recruits and already existing adults
5. To test hypotheses about the influence of mortality on distributions of juveniles and adults
6. To test hypotheses about the influence of the limpet *Cellana tramoserica* on post-settlement mortality of new recruits
7. To test hypotheses about the influence of growth of juvenile and adult barnacles on differential sizes of barnacles at different sites and different heights on the shore

Central to this investigation was the need to describe and explain spatial and temporal patterns of distribution and abundance of the adult barnacle (**Chapters 2 and 5**). The role of the larval phase in determining juvenile and adult patterns was studied (**Chapters 3, 4 and 5**), including some factors which influenced larval supply and selection of habitat (**Chapters 3 and 4**), as was the influence of post-settlement mortality on barnacle populations (**Chapter 5**). Growth was also studied to determine the influence on the size differential of *Chamaesipho* at Cape Banks (**Chapter 6**).

Models were formulated and results of data on larval supply (**Chapters 3, 4 and 5**), recruitment (**Chapters 4 and 5**), mortality (**Chapter 5**) and growth (**Chapter 6**) have been discussed in **Chapter 7** in an attempt to explain the relative importance of these processes on the demography of *Chamaesipho* on intertidal rocky shores.

CHAPTER 2

GENERAL METHODS

2.1 Fauna and Flora at Cape Banks

This study was done at the Cape Banks Scientific Marine Research Area, Botany Bay, New South Wales (34° 00'S, 150° 15'E), a relatively undisturbed location with highly diversified marine flora and fauna. Descriptions of species diversity can be extrapolated to other areas on the NSW coast. The following information (**2.1.1 Fauna, 2.1.2 Flora**) represents personal observations from a study of the barnacle *Chamaesipho tasmanica* Foster & Anderson (throughout this thesis referred to as *Chamaesipho*) at Cape Banks, and details gained from a variety of references. These include **keys** (Pope, 1945, 1965; Newman & Ross, 1976; Underwood, 1977a; Borowitzska et al., 1982; Shepherd & Thomas, 1982, 1989), **descriptions** (Dakin, 1952; Dakin et al., 1948; Endean et al., 1956; Fuhrer et al., 1981; Caffey, 1983; Foster & Anderson, 1986; Bennett, 1987, 1992; Underwood & Chapman, 1993; Jones & Morgan, 1994), and **experimental studies** (Underwood, 1975, 1980, 1994; Denley & Underwood, 1979; Creese, 1982; Underwood et al., 1983; Underwood & McFadyen, 1983; Fairweather et al., 1984; Underwood & Jernakoff, 1984; Jernakoff, 1985a, 1985b; Moran, 1985a).

2.1.1 Fauna

General patterns of assemblages of organisms are evident on the rocky substratum at Cape Banks although some degree of overlap of species occurs. Furthest up the shore the gastropods *Littorina unifasciata* (Gray) and *Nodilittorina pyramidalis* (Quoy & Gaimard) predominate. Below this area are various species of barnacles and further down, masses of tube worms, especially *Galeolaria caespitosa* (Lamarck). Most of the space below this area is occupied by the tunicate *Pyura stolonifera* (Heller) (Underwood, 1981, 1994; Bennett, 1992; Underwood & Chapman, 1993).

In the area dominated by barnacles, *Chthamalus antennatus* (Darwin) are found on uppermost shores, while *Tesseropora rosea* (Krauss) and *Catomerus polymerus* (Darwin) (on very exposed shores only) are found lower down the shore. *Chamaesipho* range from the level of *C. antennatus* down to *T. rosea* and degrees of overlap occur with each species on either boundary. Overgrowth of *Chamaesipho* by *C. antennatus* and *T. rosea* occurs at upper and lower shores respectively (pers. obs.). Variations in density are associated with gradients of exposure and more *T. rosea* and *C. antennatus* are found on exposed than on sheltered shores. *Tetraclitella purpurascens* (Wood) can also be found among other barnacles, typically scattered in groups in shaded areas (Underwood, 1981, 1994; Bennett, 1992; Underwood & Chapman, 1993; pers. obs.).

Crevices and rockpools abound throughout the mid-shore area where *Chamaesipho* predominate, and many limpets and other gastropods are dispersed throughout this area. Obvious species seen near *Chamaesipho* include the gastropods *Cellana tramoserica* (Sowerby), *Patelloida latistrigata* (Angas), *Notoacmaea petterdi* (T. Woods), *Bembicium nanum* (Lamarck), *Nerita atramentosa* Reeve, *Austrocochlea porcata* (Lamarck) and *Morula marginalba* Blainville (pers. obs.).

2.1.2 Flora

Encrusting and foliose algae are found in the mid-shore area, especially in rockpools, while on the substratum, foliose algae are positively correlated with the density of sessile species (Underwood, 1981). Seasonal patterns in algal distributions are prevalent and extensions into higher shore levels during winter in some species may occur (Underwood, 1981; pers. obs.). The brown alga *Colpomenia sinuosa* is present all year round, but is more common in summer (Fuhrer et al., 1981; Bennett, 1992). It was particularly prominent throughout distributions of *Chamaesipho* at Cape Banks in the summer of 1992. In some areas, the algae nearly covered aggregations of these barnacles (pers. obs.).

Other seasonal algae closely associated with *Chamaesipho* at Cape Banks during this study include the Cyanophyte *Aphanothece pallida*, the Phaeophytes *Petrospongium rugosum* and *Petalonia fascia*, and the Chlorophyte *Ulva lactuca* (L.).

The Phaeophyte *Hormosira banksii* (Turn.) Decne is the most obvious local algal species (Borowitzka et al., 1982). It dominates rockpools throughout the study area on sheltered shores and occurs on rocks among barnacles on lower exposed shores. For further information on algal abundance and diversity at Cape Banks see Jernakoff (1985a, 1985b).

2.2 *Chamaesipho tasmanica*

2.2.1 Classification

The Chthamaloid honeycomb barnacle *Chamaesipho tasmanica* Foster & Anderson has recently been distinguished from the New Zealand species *Chamaesipho columna* Spengler (Foster & Anderson, 1986). All earlier keys and descriptions (Pope, 1945, 1965; Dakin, 1952; Newman & Ross, 1976; Underwood, 1977a; Bennett, 1987) refer to the former name.

2.2.2 Geographical Distribution

Chamaesipho form dense aggregations along the more sheltered areas of the east Australian coast from Cape Byron in northern New South Wales to Tasmania, including Lord Howe Island and westwards to Point Sinclair in the Great Australian Bight (Pope, 1965; Foster, 1967; Foster & Anderson, 1986).

The barnacle occurs in patches on exposed rocky shores, but often forms continuous sheets covering the substratum at mid-shore levels of sheltered areas. Individual sutures of each barnacle are generally not visible in these joined forms. Adults are found on rocks in sunny areas exposed to relatively mild wave-action (Underwood et al., 1983) and solitary individuals at Cape Banks have been observed to reach 9 mm basal-length and 5 mm height (Otaiza, 1989). In this study, aperture-lengths ranged from 0.27 mm to 7.19 mm. From upper to lower levels on sheltered shores, there is a generally progressive decrease in size and increase in density (see **Chapters 5 and 6**). *Chamaesipho* are larger in Victoria and southern New South Wales (Bennett, 1992).

For descriptions of habitat and distribution see Pope (1943, 1945, 1965), Dakin (1952), Dakin et al., (1948), Bennett (1992), Bennett and Pope (1953, 1960), Endean et al., (1956), Womersley and Edmonds (1958), Underwood (1977a, 1981), Underwood et al., (1983), Fairweather et al., (1984) and Otaiza (1989).

2.2.3 Life-History

Chamaesipho mainly breed from April to November with maximally gravid animals from June to August (Egan & Anderson, 1989). Wisely and Blick (1964) recorded naupliar release from the mantle cavity into the plankton from July to October. This period for naupliar release should be expanded from April to December because Egan and Anderson (1989) found mature nauplii ready for release in dissected barnacles from May, and April, to December in 1982, and 1983, respectively, and because during this study, mature pale-blue eyed nauplii were also seen in the mantle cavities of adult *Chamaesipho* in May 1989 and 1990. In some of these barnacles, there were small numbers of fully-developed eyed nauplii, and, in others, empty mantle cavities, indicating that naupliar release had already occurred. Eggs were also seen in great numbers in February 1990 in barnacles from Low and Mid heights, and in January 1990 from Upper heights, within *Chamaesipho*'s distribution (unpubl. data). Egan and Anderson (1989) also found mature eyed nauplii in February 1984. This indicates that some larvae are also released during summer.

Chamaesipho cyprids arrive at Cape Banks from late July to December, with a few arriving in January and February during each year of this study (see **Chapters 3 and 4**). There are usually two peaks of settlement (although only one peak was recorded in September 1992 and in November 1993), generally in September and November associated with new and full moons (see **Chapter 3**). Time of arrival varies from year to year (Caffey, 1983; Otaiza, pers. comm.) and it is not known whether metamorphosed larvae are returning to Cape Banks or are from another source.

In the laboratory, Egan and Anderson (1989) found metamorphosis from the egg to the cyprid stage to be twenty days, and from the fully mature nauplius to the cyprid stage to be seven days. This is probably irrelevant in real life; delayed metamorphosis of larvae can occur in the plankton (Wilson, 1968; Crisp, 1974, 1984). The length of larval life of broadcast larvae of *Chamaesipho* is not known.

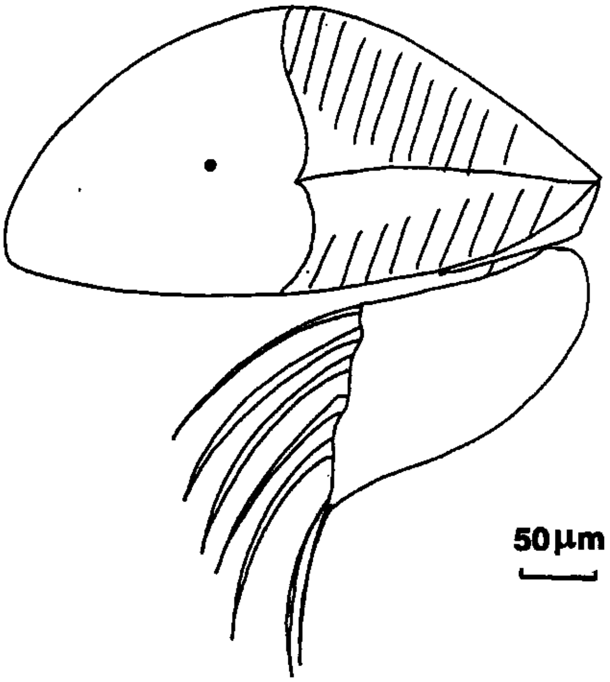

Fig. 2.1
Cyprid of *Chamaesipho tasmanica.*

C. tasmanica cyprids (0.42 mm x 0.22 mm (Egan & Anderson, 1989)) are dark-blue posteriorally and transparent anteriorally (Figs. 2.1, 2.2, 2.3, 2.4). They appear identical to cyprids of another coexisting intertidal barnacle *C. antennatus* except that *Chthamalus* has a brown posterior (pers. obs.). The cyprid stage lasts for about one day on the substratum, during which the larva actively selects its habitat and orientates itself.

Metamorphosis of the cyprid results in a six-plate metamorph stage (Figs. 2.2, 2.4, 2.5) which lasts about two to three days. The shells of these six-plate metamorphs are transparent and greyish and the body remains dark-blue (pers. obs.). Further metamorphosis and fusion of the rostro-lateral and lateral plates (Foster &

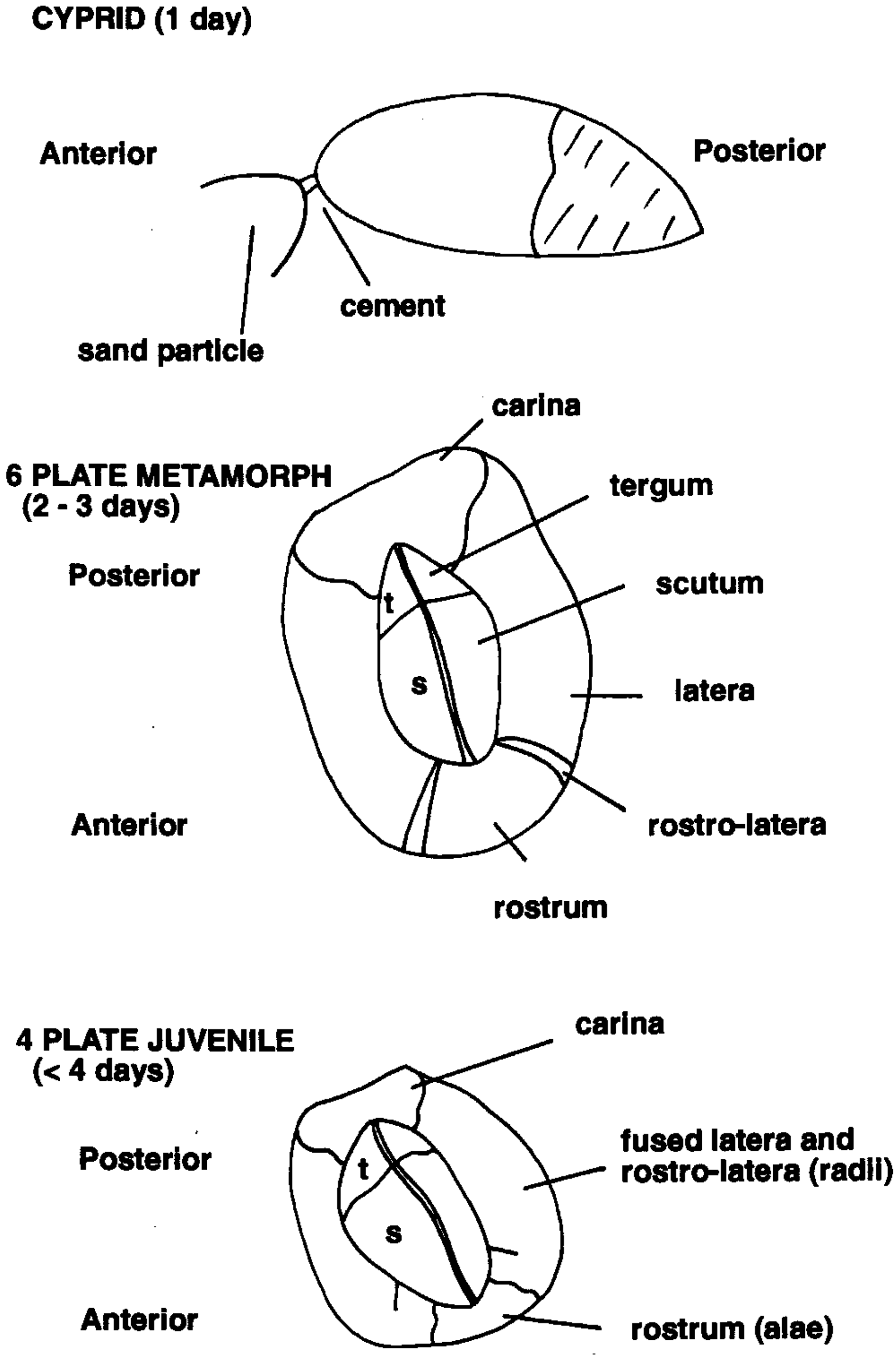

Fig. 2.2

Attached cyprid, 6-plate metamorph and 4-plate juvenile

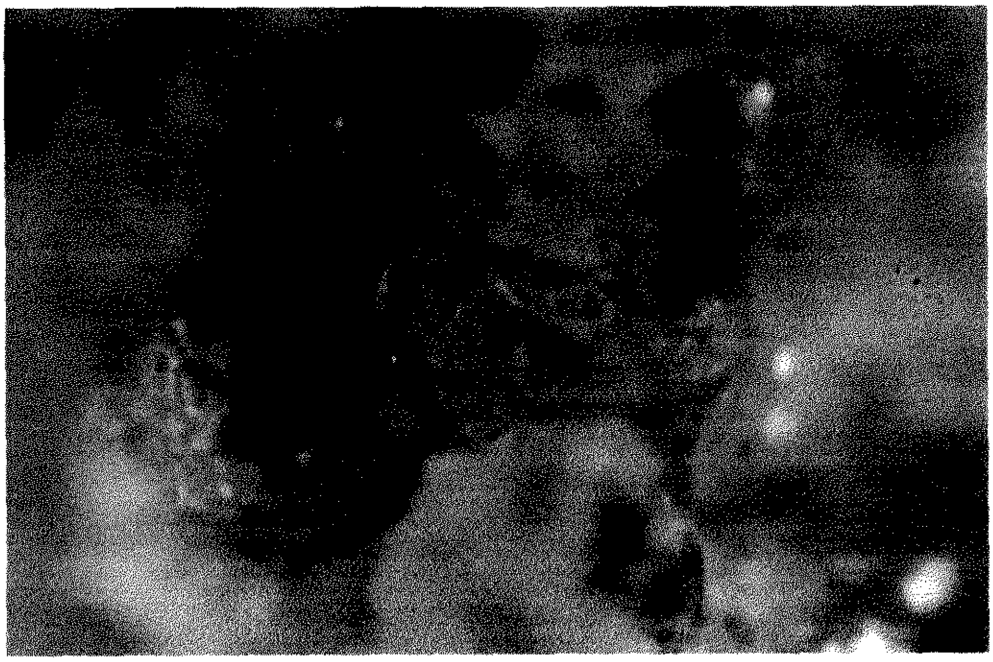

Fig. 2.3

Cyprid.

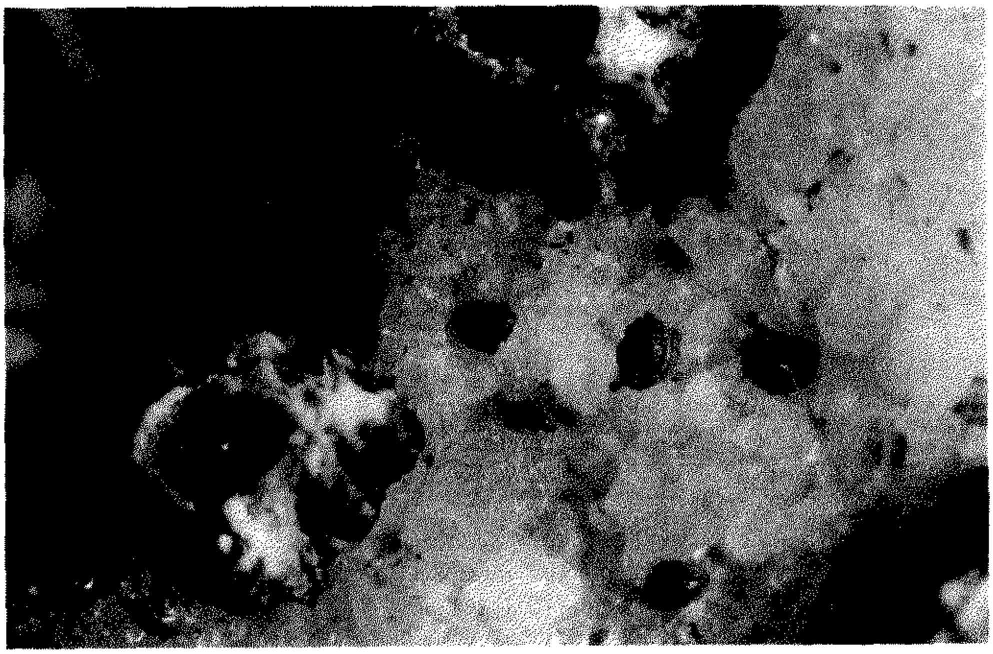

Fig. 2.4

Cyprid, Adults and metamorphs.

Fig. 2.5

6-plate metamorph.

Fig. 2.6

4-plate juvenile.

Anderson, 1986) results in the less than four-day four-plate juvenile stage (Figs. 2.2, 2.4, 2.6) which has a dark-blue body and grey plates. Older juveniles and adults (Fig. 2.4) have pale-grey shell plates.

2.3 Study Area

Chamaesipho was studied from May 1989 until July 1994 in the Cape Banks Scientific Marine Research Area at the northern head of Botany Bay (Fig. 2.7). The study area faces south and is prone to the influence of South-East swells which can produce more than 3 metre waves during the winter months (Short & Trenaman, 1992). During these conditions there is no low tide and field work is impossible. Tides are semi-diurnal and range over 2 metres.

During outgoing tides in Botany Bay, strong ebbjet currents form on the northern head at Cape Banks with some recirculation back to the coast north and south. During late ebb tides, an intense narrow ebbjet forms which is strongest near the surface and flows from the northern half of Botany Bay to about 2 kilometres offshore. Drogues released on the southern entrance of Botany Bay travel in a south-easterly direction and are then caught in the southern circulation (Cox et al., 1993). At Malabar, just north of Cape Banks and the entrance to Botany Bay, currents flow in a northerly direction up to 100 metres offshore, in an easterly direction up to 150 metres offshore and southwards after 150 metres. The East Australian Current flows southwards and seems to be involved in driving nutrient-rich water towards the Sydney coast (Cresswell, 1994). Generally North-East waves occur in summer whereas South-East waves occur anytime with heights peaking in May and November. The general trend is for an increase in South-East waves from February to August followed by a decrease in frequency from August (Short & Trenaman, 1992). Cold water upwelling is associated with eddies of the East Australian Current which are known to drive nutrient-rich intrusions towards the Sydney coast (Cresswell, 1994). Incursions on the Sydney continental shelf, originating from 200 m to 400 m depth, have been recorded from September to December (Rochford, 1958) and major peaks of *Chamaesipho* larvae were registered from 1989 to 1993 during these months (see **Chapter 3**). When cyclonic eddies are inshore from the East Australian Current

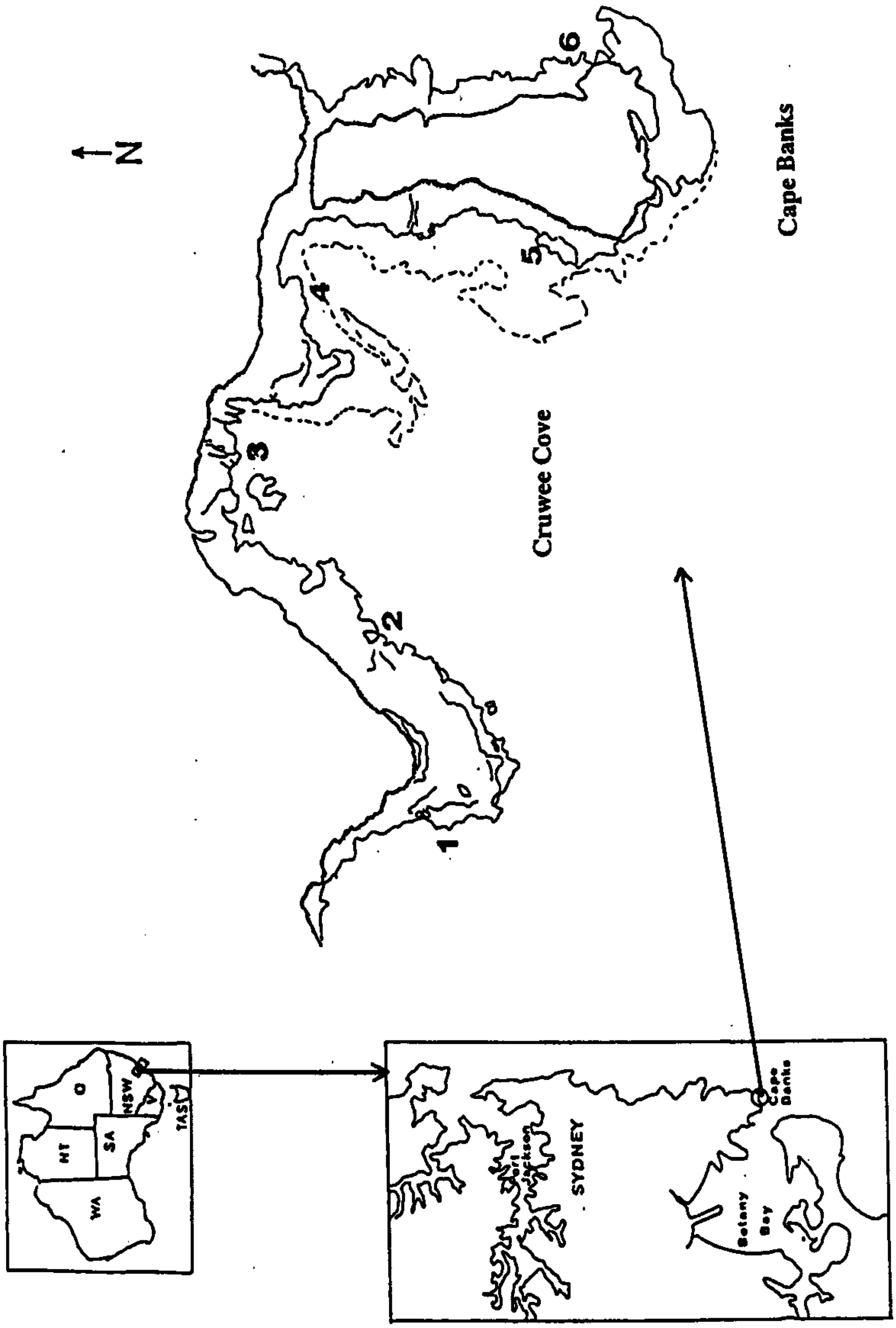

Fig. 2.7

Map of Cape Banks on the New South Wales coast showing the six sites studied: Sites 1, 2 and 6 are exposed, Site 5 is semi-exposed and Sites 3 and 4 are sheltered.

they may dominate the effects of wind to force water towards the New South Wales coast (Cresswell, 1994). This information has important implications for larval dispersal, although currently very little is known about dispersal patterns of broadcast nauplii and cyprid larvae.

The rock platform at Cape Banks consists of Hawkesbury sandstone which is pitted with 500 μm pits (Caffey, 1983). On the more exposed areas, sandstone particles are weathered so that the substratum is less pitted than at sheltered sites.

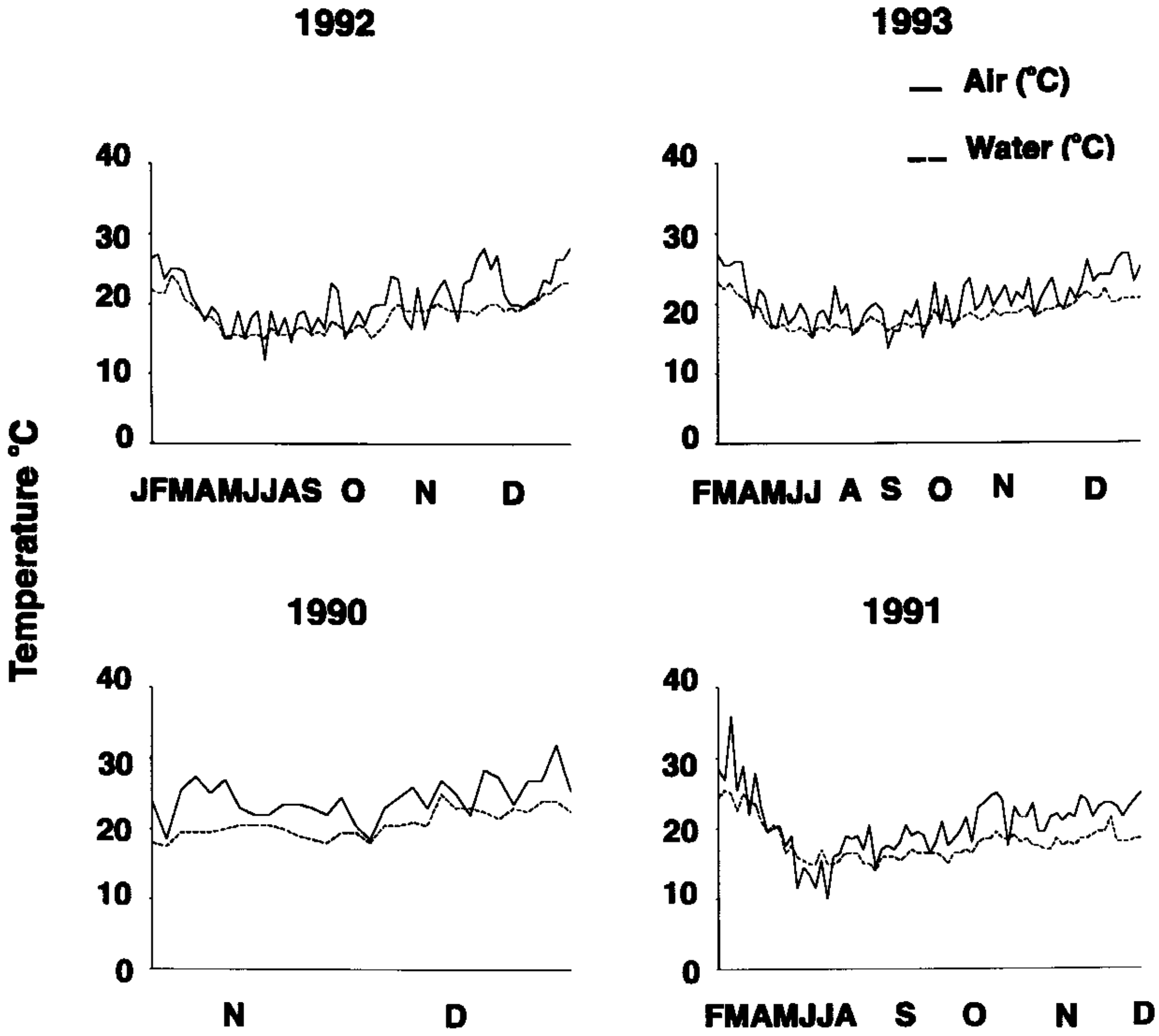

Fig. 2.8

Temperature (°C) of — Air and – – Surface Water. Months when barnacles were sampled are indicated on the X-axis.

During this study, air temperatures varied from 10°C to 36°C and surface water temperatures near the rock platform ranged from 14°C to 25.5°C. All of these measurements were recorded in 1991 (Fig. 2.8). Salinity varied very little (in 1991) and ranged from 35 to 39.5 ppm (Fig. 2.9).

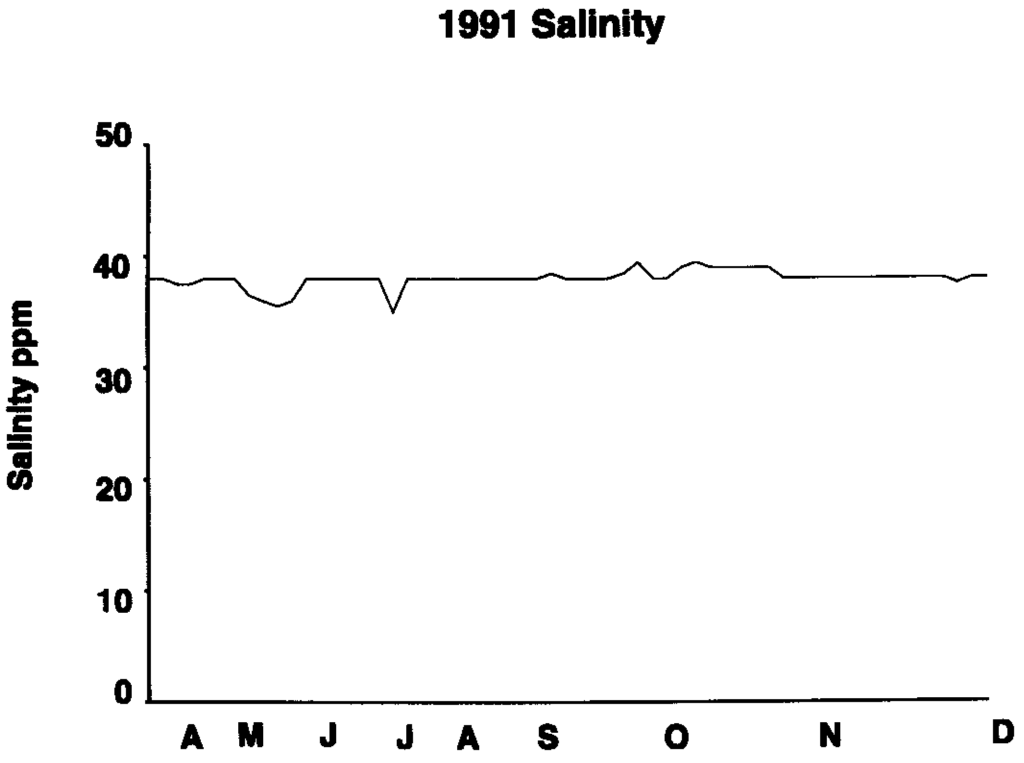

Fig. 2.9

Salinity readings for 1991. Months when barnacles were sampled are indicated on the X-axis.

It was not considered necessary to sample at more than one geographical location, because considerable variation in distribution and abundance of populations of *Chamaesipho* exists from place to place in the area studied. *Chamaesipho* were therefore studied at six sites (Fig. 2.7) with different degrees of exposure, varying from exposed to semi-exposed to protected sites. The six sites varied in height from 0.08 m above MLWS at low sheltered sites, to 3.00 m above MLWS at upper exposed sites (Table 2.1).

Sites 1 and 2, exposed sites, were located on the western side of Cruwee Cove, facing south-west and south-east, respectively. Sites 3 and 4 were at sheltered sites in Cruwee Cove and faced south. Site 5, near the Wreck on the sheltered side of the headland, faced west and was semi-exposed. Site 6, an exposed site, was located "outside" on the eastern side of the northern headland of Botany Bay (Fig. 2.7).

Each site in the mid-shore area was divided into three vertical zones (Low, Mid and Upper), determined by the distribution of *Chamaesipho*: the lower and upper levels delimited the distribution of this barnacle. These levels were not at the same sea level for each site (Table 2.1), due to differences in exposure to wave-action. Barnacles were at higher levels on exposed shores with greater wave-action (Underwood, 1981).

Table 2.1

Height of Sites Sampled (m above Low Water Spring)

	SITE 1	**SITE 2**	**SITE 3**	**SITE 4**	**SITE 5**	**SITE 6**
LOW	2.07	1.64	0.08	1.02	1.17	2.95
MID	2.29	1.74	1.31	1.17	1.24	3.00
UPPER	2.25	1.85	1.34	1.37	1.32	2.96

2.4 Field Methodology

2.4.1 General Methods

Chamaesipho were sampled from May 1989 to July 1994. Throughout the study, settlement and recruitment were defined after Underwood (1979), Underwood and Denley (1984) and Connell (1985). Settlement includes the period of attachment and metamorphosis of cyprid larvae; recruitment is measured as the number of metamorphosed barnacles surviving after settlement. Settlement in *Chamaesipho* is considered to include the cyprid stage, which lasts less than one day after attachment to the substratum, the 2-3 day six-plate metamorph stage and the four-plate juvenile stage, which is formed about 4 days after initial attachment of the cyprid (see Figs. 2.1 - 2.6).

Various procedures were repeated throughout this study. Undisturbed Control barnacles were monitored at three heights of *Chamaesipho's* distribution (Low, Mid, Upper) in six sites (Fig. 2.7) from August 1989 until the end of December 1993.

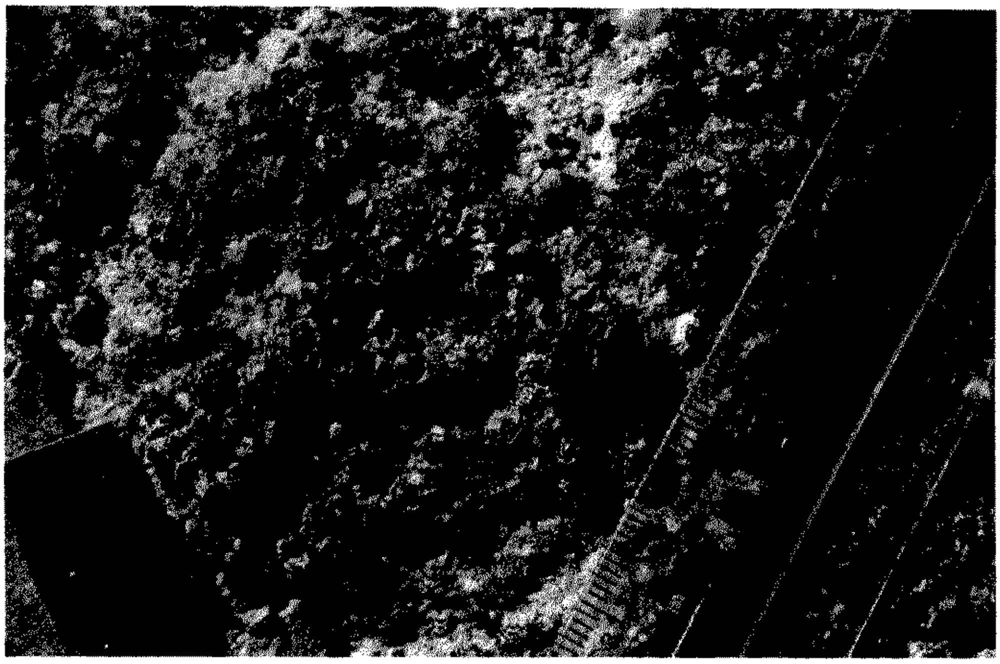

Fig. 2.10

Replicate with metal tag from Mid height of *Chamaesipho's* distribution at Site 4.

Replicates (Fig. 2.10) were originally outlined with a hammer and cold chisel and some were marked with an inscribed metal tag cemented into the substratum (Selleys Quick Crete). Other replicates were identified from marks made on the substratum with a hammer and cold chisel. Replicates were photographed with a 35 mm camera attached to a 26 cm high brass tripod and the metal tags, or identification marks, were used to match up and identify individual barnacles on black and white negatives in the laboratory. Generally, each replicate with barnacles was photographed and counted monthly in each site from January until mid July, and fortnightly from the end of July until the end of December during settlement.

In areas where settlement of cyprids was to be studied, patches were cleared of barnacles in July each year before an expected settlement. A hammer and cold chisel were used to remove any deep seated remnants of adults in the rocky substratum. Each replicate was washed after preparation to remove any fine particles of sand.

A hand lens (x 5) was used to count the number of cyprids, metamorphs and young juveniles. All replicates in two sheltered sites (Sites 3 and 4; Fig. 2.7) were mapped daily over a period of 5-7 days every fortnight, to coincide with new and full moons, during settlement from late July until late December, weather and tide permitting. Maps were done with different coloured permanent pens on acetate sheets. Replicates in other sites (Sites 1, 2, 5 and 6; Fig 2.7) were mapped fortnightly from late July until late December. Numbers of recruits in each replicate for all six sites were recorded monthly from January until mid July.

A petrol drill or a hand-held battery-operated drill was used to drill holes in the sandstone for attachment of plankton traps, clod cards and fences. Plastic rawl plugs were inserted in these holes and stainless steel screws were used to attach this equipment. Fences were held down with lead washers. Heights on the midshore (Low, Mid, Upper) at the six sites were surveyed with a surveyor's level (Table 2.1).

A 100^{0}C thermometer was used to measure air temperature and temperature of surface water for most sampling times from October 1990. A temperature compensated hand refractometer was used to measure salinity in 1991. Other environmental factors sampled throughout the study included tidal amplitude, wind direction and estimates of wave height.

2.4.2 Larval Supply

Plankton traps (Otaiza, 1989; Figs. 2.11, 2.12, 3.1) were used to estimate the numbers of larvae arriving at Site 4 and two heights on the shore (Low and Mid/Upper) within *Chamaesipho's* distribution. Each trap consisted of a top half made from a 90% PVC elbow, 90 mm in diameter, secured by a bracket and two screws into rawl plugs in the substratum. The bottom half of the trap, containing a modified PVC filter funnel to prevent backflow of water, was a PVC cup, 90 mm in diameter and 100 mm high, inserted underneath the elbow and secured by three

Fig. 2.11

Plankton trap.

rubber bands. The sides of the PVC cup had eight 2.5 cm circular holes covered with 100 µm plankton mesh to allow water to drain. The top part of the trap faced the incoming waves and traps were placed so that the bottom edge of the opening of the upper part was flush with the substratum. This was done by putting traps on the edge of crevices, so that the PVC cup extended below the substratum (for all details, see Otaiza, 1989).

2.4.3 Water-Flow

Clod cards (Figs. 2.12, 2.13) have been used to measure water-flow; weight lost from each card is proportional to water velocity over a wide range of measurements (Jokiel & Morrissey, 1993). To determine the relative amount of water flowing near and through plankton traps, hemispherical clods of Velmix Dental Stone (7 water: 23 powder) were prepared in the laboratory (see Doty, 1971; Caffey,1983; Bushek, 1988; Otaiza, 1989; Jokiel & Morrissey, 1993). The % loss of dry weight from each of these over a 24 hour period was a measure of water-flow.

Large clods (4.2 cm in diameter and 2.0 cm high) were attached to 9 cm x 6 cm x 0.1 cm aluminium plates with Selleys Silicone R.T.V. Marine Sealant and the plates were secured to the substratum next to each plankton trap with screws in rawl plugs (Fig. 2.12). To determine the relative amount of water passing through plankton traps, small hemispherical clods of dental cement (1.7 cm in diameter and 1.5 cm high) were each glued to a 2 cm x 2 cm x 0.1 cm aluminium plate and then one of these glued to the bottom of each removable filtering cup of the plankton trap (Fig. 2.13).

All clods were dried at 60°C for 24 hours and reweighed to ascertain the % mass lost from each clod in the field over 24 hours, that is over two tides, to indicate water-flow over the substratum and through plankton traps.

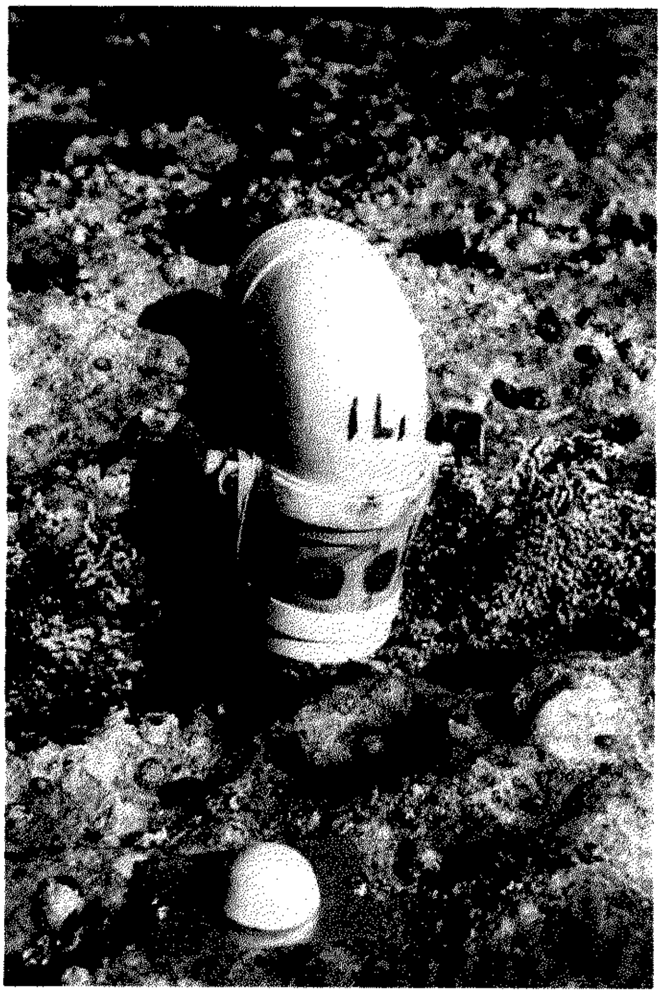

Fig. 2.12

Clod card secured to the substratum next to plankton trap.

Fig. 2.13

Clod card secured to bottom of plankton trap.

CHAPTER THREE

LARVAL SUPPLY

3.1 Introduction

Early models to explain settlement of sessile marine invertebrates, especially barnacles, were based on populations with large numbers of larvae arriving to settle (Connell, 1961a, 1961b; Dayton, 1971; Paine, 1974; Lewin, 1986). Because larval supply was considered to be unlimited, these early models emphasised that competition, predation and physical disturbance in the adult stage determined intertidal marine assemblages (Connell, 1961a, 1961b, 1970; Paine, 1974, 1984; Dayton, 1971; Menge, 1976; Menge & Sutherland, 1976; Lubchenco & Menge, 1978; Menge & Lubchenco, 1981). More recent studies on the eastern Australian coast (Underwood et al., 1983; Underwood & Denley, 1984) have emphasised that the processes of settlement or recruitment determine the patterns of distribution of marine assemblages: where larval settlement was low, very different patterns emerged than from areas where larval settlement was large.

As discussed in Chapter 1, *larval delivery* (larval supply) (Raimondi, 1991) is considered integral to the formation of distributions of adult barnacles. The physical processes which determine larval supply, including meteorological conditions and associated hydrodynamics over large spatial scales and fluid dynamics at small spatial scales (Shanks, 1986; Shanks & Wright, 1987; Farrell et al., 1991; Mullineaux & Butman, 1991; Roughgarden et al., 1991, 1994; Pineda, 1994a, 1994b; Alexander & Roughgarden, 1996) will primarily influence the demography of these populations.

At large spatial scales, hydrodynamics associated with larval transfer and movement of nutrient-rich water towards the coast differ geographically. For example, the formation of upwellings is different in south-eastern Australia and south-eastern United States (Cresswell, 1994). Roughgarden et al. (1991, 1994) have demonstrated that recruitment pulses of barnacles on the Californian coast are associated with the accumulation of larvae in fronts which are driven shorewards and deposited on the coast when winds relax. Other studies have shown a positive relationship with onshore winds (Hawkins & Hartnoll, 1982) or no relationship (Wethey, 1986a; Shanks, 1986).

At small spatial scales, Mullineaux and Butman (1991) indicated that hydrodynamic transport determined the arrival of cyprids of the barnacle *Balanus amphitrite*. Settlement was determined by larval behaviour in response to direction of flow and shear stress. By manipulating boundary-layer flows, Mullineaux and Garland (1993) showed that settlement responses were very species-specific: the same turbulence and shear stress always produced a similar pattern of settlement. Surface characteristics of the substratum and/or flow were responsible for these patterns of settlement although the degree of their influence, in isolation or in tandem, on settlement and recruitment is unknown (Mullineaux & Garland, 1993).

Turbulence in surf areas on rocky shores acts to mix relatively slowly-swimming larvae within the water column so that larvae are usually transported as passive particles. Soluble chemical cues which induce settlement may also be diluted by turbulence so that they only influence settlement over short distances (Crisp & Meadows, 1962; Denny & Shibata, 1989). Despite this, turbulence can transport and concentrate cyprid larvae in their normal habitat (Gaines et al., 1985; Denny & Shibata, 1989). Turbulence can also have a negative effect on settlement: boundary shear stresses in very fast currents may prevent attachment (Crisp, 1955; Bushek, 1988; Pawlik & Butman, 1993) or may cause settled larvae to detach (Eckman et al., 1990). Turbulence can be modified by topography of the substratum so that an association between roughness of the surface and slow water means that settlement is enhanced (Pawlik & Butman, 1993).

At small spatial scales, percentage mass lost from clod cards is considered to be a good index of water-flow or submergence (Doty, 1971; Caffey, 1983; Jokiel & Morrissey, 1993) and this technique has been used in the field to determine the relationship between larval supply of barnacles and water-flow (Otaiza, 1989) and between densities of settlers and water-flow (Caffey, 1983).

Larval supply, which is influenced by hydrodynamics, determines temporal variability within barnacle populations (Farrell et al., 1991; Roughgarden et al., 1991, 1994; Pineda, 1994a, 1994b) whereas spatial variability has been linked to larval behavioural responses and availability of substratum during settlement (Gaines & Roughgarden, 1985; Bushek, 1988; Minchinton & Scheibling, 1993; Pineda, 1994a). Most models in the literature emphasise free space as the main determinant of demography (Roughgarden et al., 1985, 1988; Possingham & Roughgarden, 1990). While this may be true for species with large numbers of larvae available and limited free space on the substratum, are similar processes operating in species that have abundant free space and relatively few larvae arrive?

Initial observations in 1989 at Cape Banks revealed that, contrary to previously described species, few larvae of the barnacle *Chamaesipho tasmanica* arrive and settle relative to the space available on the substratum, and great variations in densities occur within a small location. This barnacle often exists as continuous sheets of joined barnacles or in isolated groups of joined or separate individuals. In the more exposed areas at Cape Banks, a patchy distribution is prevalent whereas in sheltered areas cleared spaces may be scattered throughout aggregations of barnacles.

The main objective of this chapter was to propose models and test hypotheses devised from these initial field observations relevant to settlement and thus identify factors which determined spatial distributions of *Chamaesipho*. In particular, because previous studies have linked barnacle populations with larval supply (Grosberg, 1982; Hawkins & Hartnoll, 1982; Underwood & Denley, 1984; Gaines & Roughgarden, 1985), the influence of larval supply on demography of the barnacle was addressed. Attempts were also made to examine some physical processes affecting larval supply at large spatial scales (lunar cycles, wind direction, wind speed and wave height) and at small spatial scales (water-flow). Because cyprids of another intertidal barnacle *Tetraclitella purpurascens* (Wood) were at times caught in plankton traps with *Chamaesipho*, the issue of position in the water column as an influence on spatial distributions of different species of barnacles was also addressed.

Early in this study, when larval arrival was monitored from July to December, 1989, large numbers of cyprid larvae of *Chamaesipho* were recorded on the full moon in mid September and two days before the full moon in mid October. In 1988, however, when Otaiza (1989) secured plankton traps for 4 continuous days in February, March, July and September, very few cyprids were caught. This suggests that Otaiza (1989) may have missed major settlement peaks in his sampling. A more intensive sampling programme, incorporating lunar periods, was therefore necessary to test the hypothesis that larval supply would be associated with distributions of juveniles. In 1989, it was also observed that spatial variation in abundance exists at each site studied at Cape Banks with more barnacles on lower mid-littoral shores. It was therefore proposed that more cyprids arrive low on the shore than further up the shore to contribute to these patterns. It was predicted that, if traps were set to catch cyprids at different levels on the shore at one site, there would be more larvae caught in traps low on the shore than further up the shore.

During the pilot study in 1989, the major peak of larval arrival in September coincided with the presence of strong South-East winds and waves more than 1 metre in height. It was therefore proposed that, when high velocity Southerly winds and more than 1 metre waves are present, more cyprids will arrive. It was predicted that, if wind direction, wind speed and wave height were monitored for 24 hours over two tidal cycles during major peaks of arrival of larvae, more larvae should be caught in traps when high velocity Southerly winds and waves of more than 1 metre in height prevail.

It was also observed that different places submerge for different times than others because of waves, swash etc. and it was therefore proposed that more cyprids will be present where there is more water over the substratum, regardless of height. It was predicted that, if clod cards were secured within plankton traps and to the substratum, the % mass lost from each clod should be a measure of water-flow, and there should be a relationship between larval supply and water-flow: more cyprids should be caught where there is more water-flow. Because it was found that there was a positive relationship between numbers of larvae arriving and numbers settling on the substratum (see **3.3 Settlement on the Substratum**), it was proposed that this was because water-flow through traps and on the substratum next to them is similar. If clod cards were secured within plankton traps and to the substratum next to traps, % mass lost should be a measure of water-flow and should therefore be similar through traps and on the substratum next to them.

Earlier studies have indicated that more larvae may arrive on lower shores Because they settle first on lower shores, and later on upper shores (Roughgarden et al., 1988). In his study, Grosberg (1982) demonstrated that position in the water column is a major determinant of spatial distributions of barnacles. In this study, cyprids of another intertidal barnacle, *T. purpurascens* (Otaiza, 1989), were caught in traps with *Chamaesipho. Tetraclitella* is generally found in shaded areas on littoral shores from southern Queensland to Western Australia (Denley & Underwood, 1979; Bennett, 1992;Underwood & Chapman, 1993). Because each species of barnacle differs spatially, it was proposed that the numbers of larvae caught in traps reflect this spatial distribution and that the different position in the water column of each species is the main process involved. It was therefore predicted that, if numbers of cyprids of *Chamaesipho* and of *Tetraclitella* were counted from the same traps, and their numbers compared, larvae caught should be representative of their spatial distributions. Patterns of water-flow would also be expected to mirror these patterns of cyprid arrival.

Spatial variation in abundance of juvenile *Chamaesipho* was also observed, with more juveniles low on the shore than further up the shore. It was therefore proposed that numbers of arriving larvae cause the observed numbers of juveniles. It was predicted that, if numbers of cyprids arriving and numbers of settlers (lagged by one day) on the substratum were counted daily, there should be a positive correlation between them.

3.2 Larval Supply of *Chamaesipho tasmanica*

3.2.1 Experimental Method and Design

Plankton traps (Figs. 2.11, 2.12, 3.1) were secured to the substratum on Low and Mid/Upper heights at Site 4 (see **Chapter 2: Fig. 2.7**) in a nested design from late July generally to late December 1990 to 1993: duplicate sets each of three plankton traps were put at each of Low and Mid/Upper heights of *Chamaesipho's* distribution within the mid-shore level. (These sets of traps will be referred to hereafter as 1 Low, 2 Low, 1 Mid/Upper and 2 Mid/Upper). Sets of traps Low on the shore were 5 m apart and 1.02 m MLWS whereas trap sets at the Mid/Upper height were 3 m apart and 1.17 m MLWS. Sets of traps Low on the shore were 6 m away from Mid/Upper sets. Traps within these sets were approximately 30 cm apart. In 1990, traps were put on the rock platform every fortnight for 5 days leading up to the new and full moons to coincide with settlement. From 1991 to 1993 traps were also secured to the substratum one day after new and full moons. Plankton cups were collected and replaced daily and their contents examined under a binocular microscope; therefore, the numbers of cyprids captured during two tidal cycles were recorded.

Fig. 3.1

One set of plankton traps secured to the substratum at Site 4, Low on the shore.

3.2.2 Results

Larval Supply of *Chamaesipho tasmanica*

Each year from 1990 to 1993, larval supply was characterised by trickles of larvae, punctuated by one or two major pulses, from the end of July to mid December

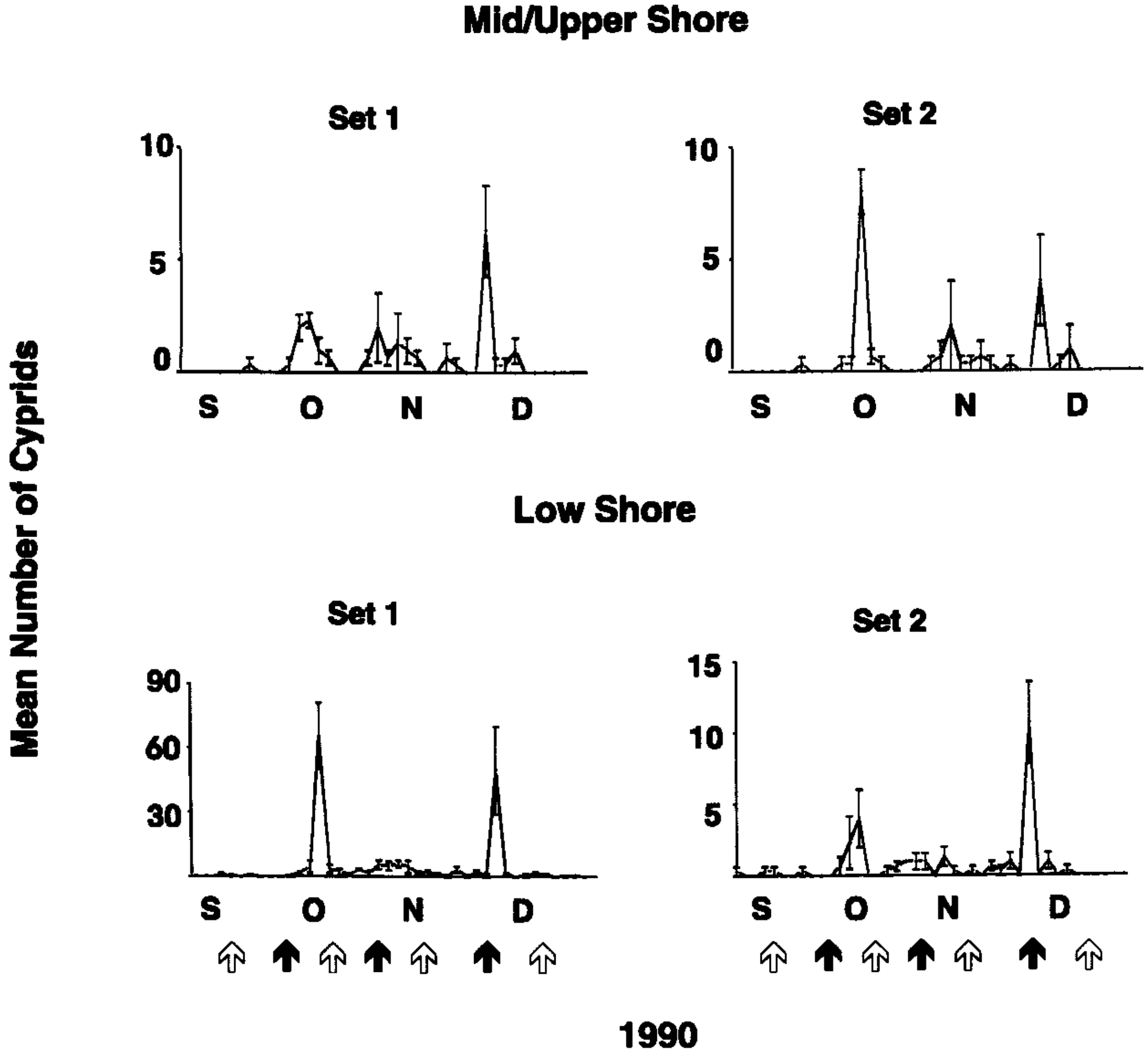

Fig. 3.2

Mean (± S.E.) numbers of cyprids in two sets of traps (n = 3) at two heights on the shore during new (⬆) and full moons (⇧), late July to late December, 1990. Note different scales on ordinate axes.

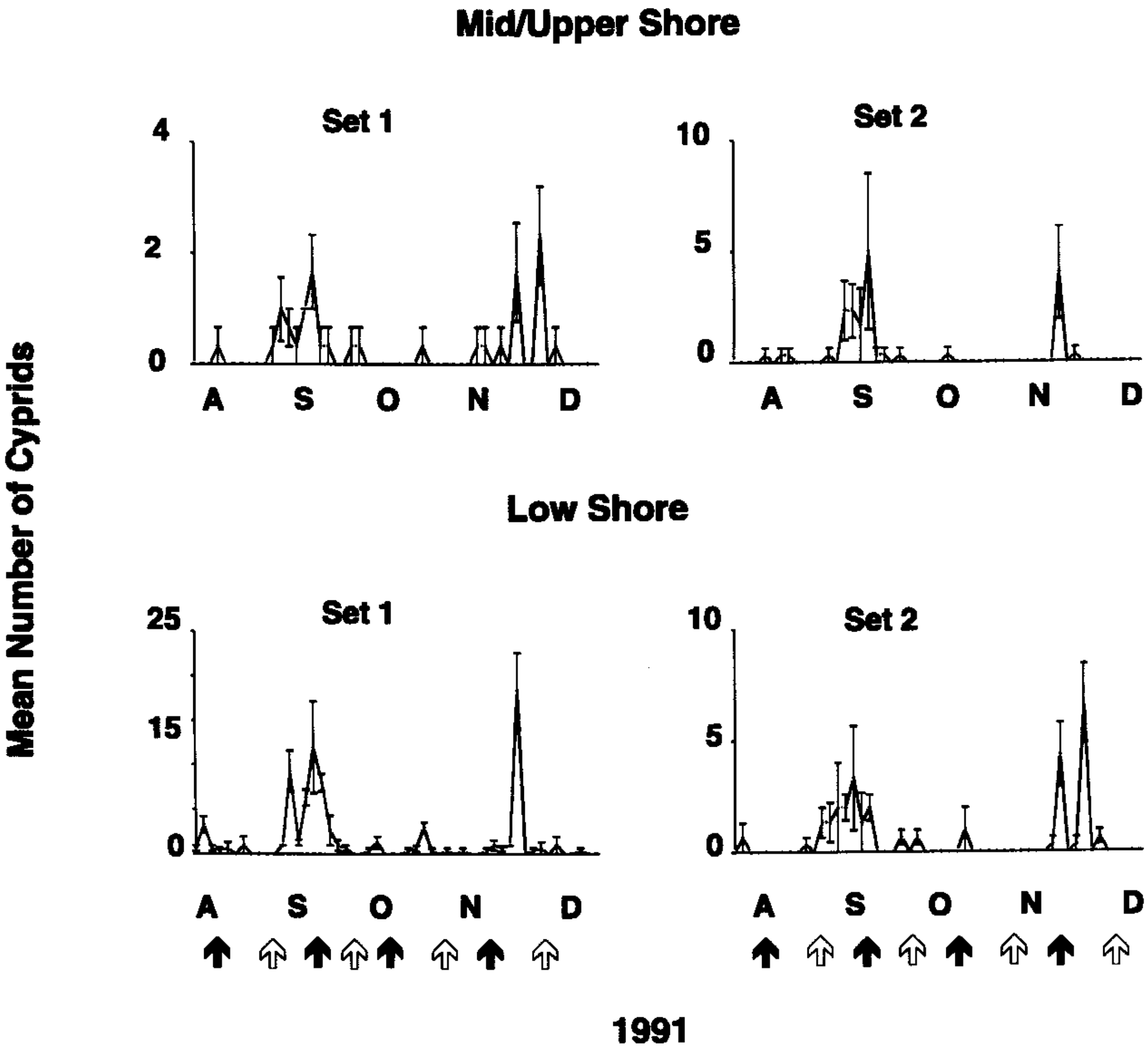

Fig. 3.3

Mean (± S.E.) numbers of cyprids in two sets of traps ($n = 3$) at two heights on the shore during new (⬆) and full moons (⇧), late July to early December, 1991. Note different scales on ordinate axes.

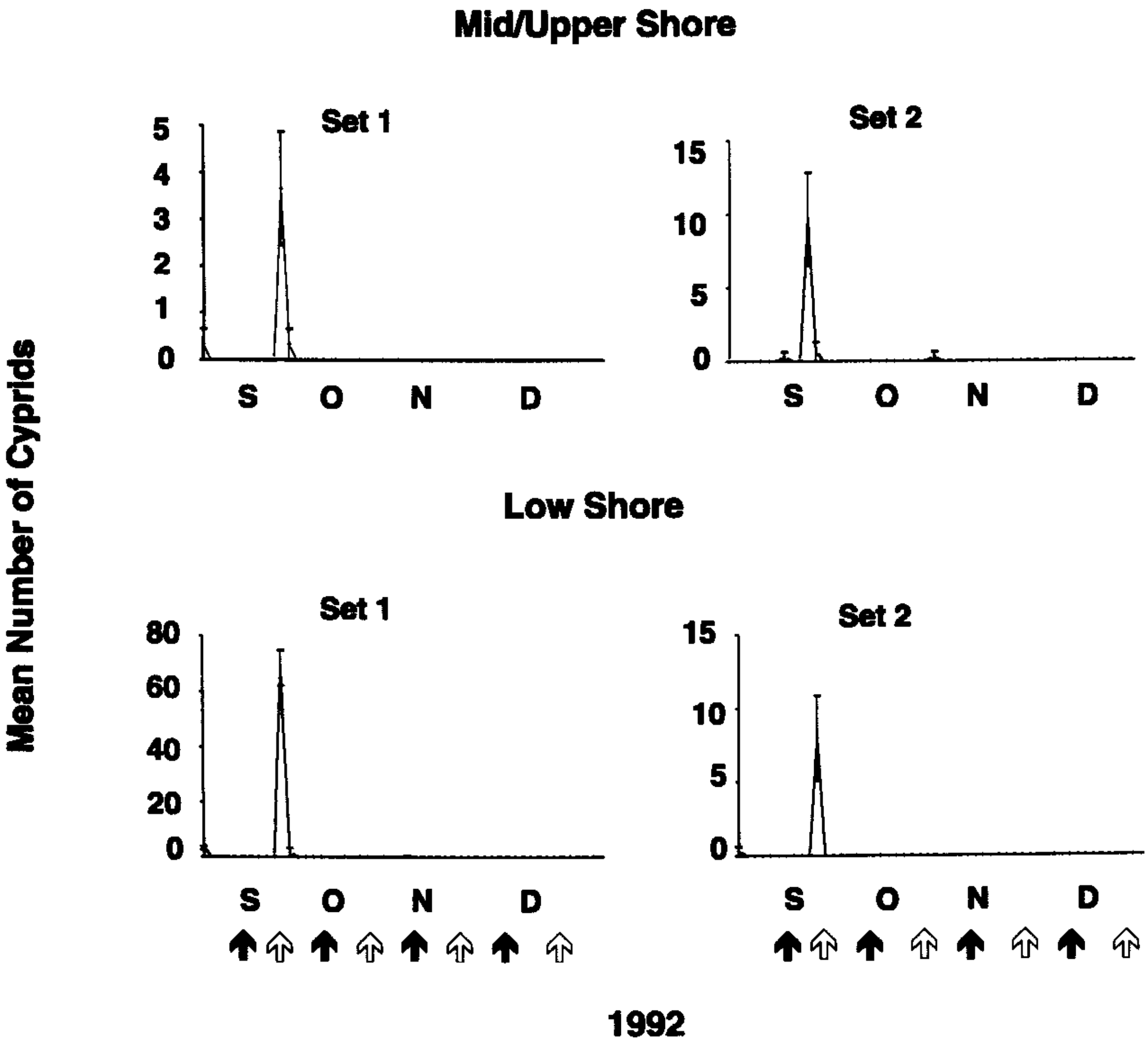

Fig. 3.4

Mean (± S.E.) numbers of cyprids in two sets of traps ($n = 3$) at two heights on the shore during new (⬆) and full moons (⇧), late July to late December, 1992. Note different scales on ordinate axes.

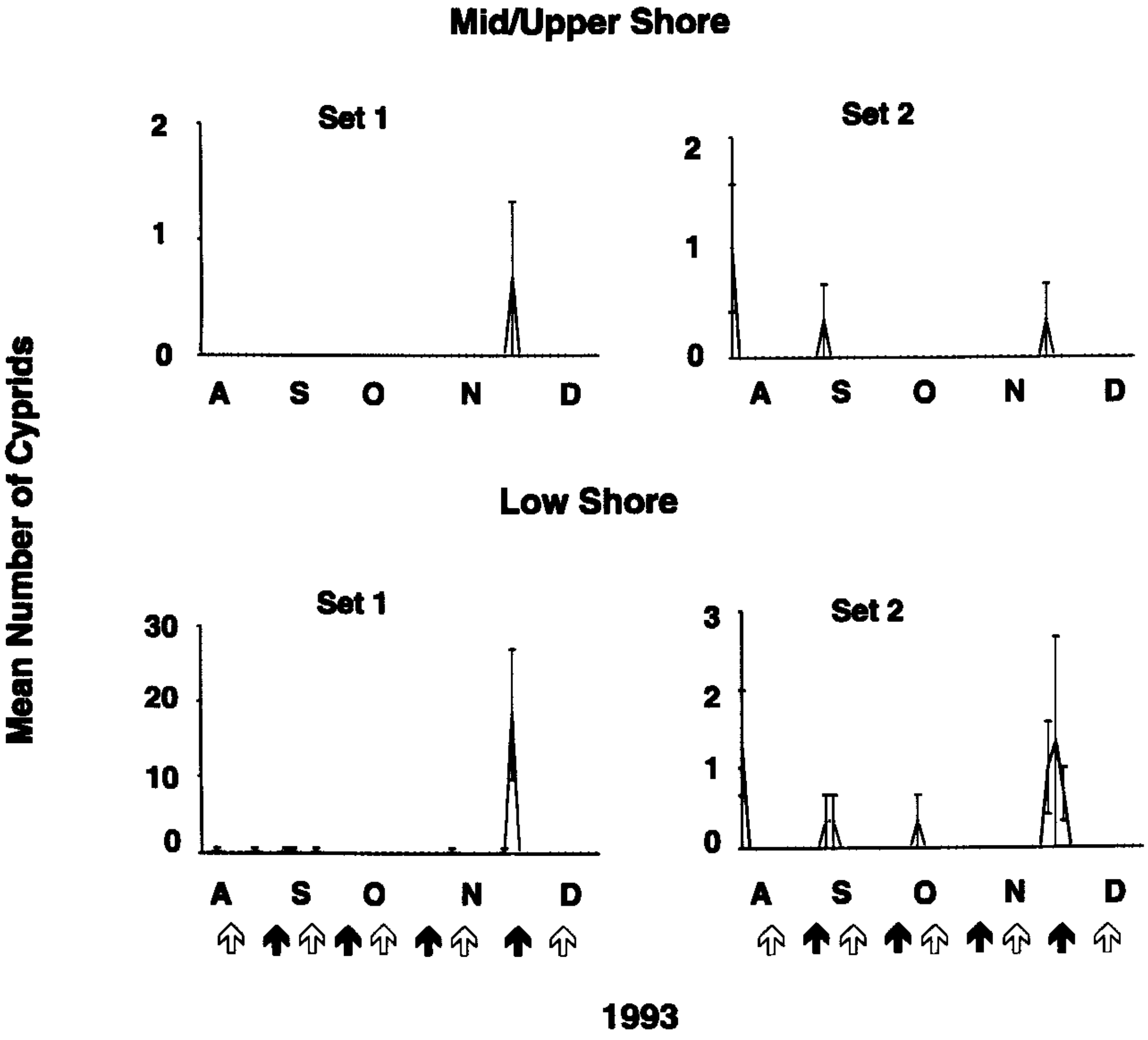

Fig. 3.5

Mean (± S.E.) numbers of cyprids in two sets of traps ($n = 3$) at two heights on the shore during new (🡅) and full moons (⇧), late July to mid December, 1993. Note different scales on ordinate axes.

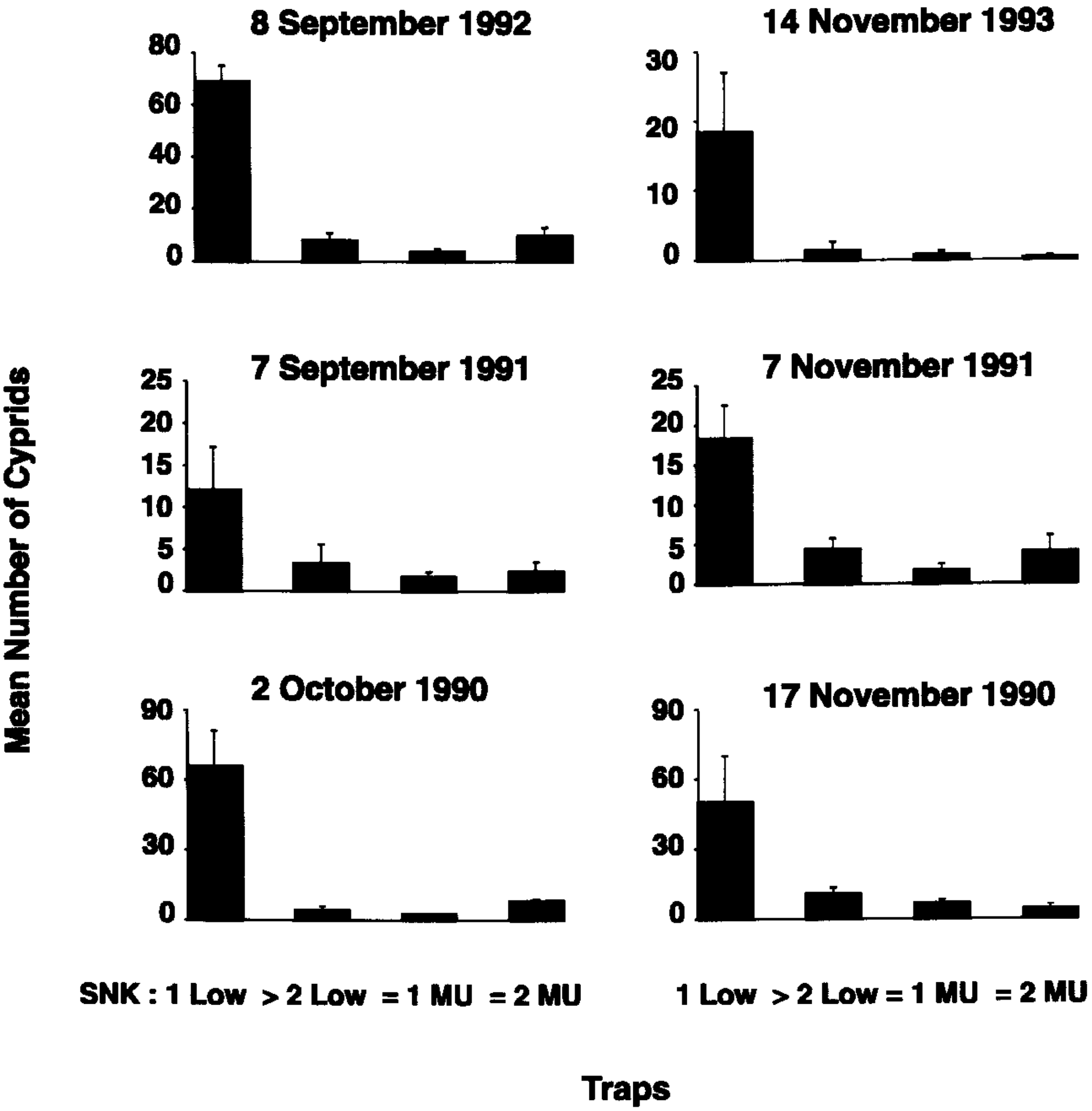

Fig. 3.6

Mean numbers of cyprids captured in sets of traps ($n = 3$) nested in Low and Mid/Upper heights of *Chamaesipho's* distribution; data are from peaks of arrival on 2nd October, 1990, 17th November, 1990, 7th September, 1991, 7th November, 1991, 8th September, 1992 and 14th November, 1993.

(Figs. 3.2 - 3.6). These major peaks of arrival of larvae over two tidal cycles and at two heights on the shore (Low and Mid/Upper) occurred two days before the full moon of 4th October, 1990, on the new moon of 17th November, 1990, one day before the new moon of 8th September, 1991, one day after the new moon of 6th November, 1991, four days before the full moon of 12th September, 1992 and on the new moon of 14th November, 1993 (Fig. 3.6). These main bursts of arrival were associated with prevailing Southerly winds (South, South-East, South-West and South-South-West).

There was temporal variation in numbers of cyprids available for settlement (Fig. 3.6; Table 3.1). There were, however, consistent spatial patterns in arrival of cyprid larvae of *Chamaesipho* within shore levels and among shore levels at these different times (Fig. 3.6). On lower mid-littoral shores, more *Chamaesipho* were always caught in 1 Low traps than 2 Low traps. Numbers of larvae arriving were always similar for 2 Low and 1 and 2 Mid/Upper traps (Fig. 3.6; Table 3.1). That is, patterns of larval supply varied consistently among places on the shore from 1990 to 1993: larval supply differed from Low to Mid/Upper heights among sets of traps and most larvae were caught in one set of Low shore traps.

Table 3.1

Analysis of mean numbers of cyprids in sets of plankton traps ($n = 3$) nested in Low and Mid/Upper levels of *Chamaesipho's* distribution on the shore at Site 4: data are from peaks of arrival on 2nd October, 1990, 17th November, 1990, 7th September, 1991, 7th November, 1991, 8th September, 1992 and 14th November, 1993. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $\text{Log}_e(x + 1)$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*P*
Time = T	5	4.94	9.84	**
Height = H	1	23.83	1.65	ns
Set (Height) = S(H)	2	14.44	32.81	***
T x H	5	0.12	0.23	ns
T x S(H)	10	0.50	1.14	ns
Residual	48	0.44		

3.3 Wind Direction, Wind Speed and Wave Height

3.3.1 Experimental Method and Design

Wind direction was recorded once daily at Site 4 (see **Chapter 2: Fig. 2.7**) when plankton traps were set. Additional average hourly wind data from July, 1989 to December, 1993 were obtained for La Perouse, close to Cape Banks, from Robert Hyde, School of Earth Sciences at Macquarie University. Wind data were only used for 6 peaks of larval arrival during 1990 to 1993 and each peak encompassed 24 hours of data from Low tide of one day to Low tide of the next to include two tidal cycles when cyprids would have been arriving.

Approximate wave heights were also recorded daily at Site 4 (see **Chapter 2: Fig. 2.7**) when plankton traps were set. Accurate wave data were provided by Bruce Hudson from the Maritime Services Board (Sydney Ports Authority) from offshore Waverider Buoys anchored in 73 m water depth just south of Cape Banks off Botany Bay (34^{0} 02'S, 151^{0} 15'E). Mean monthly wave heights from 1990 to 1993 (Waverider Buoys Numbers 1 and 4) and daily averages of highest third waves during six peaks of larval arrival from 1990 to 1993 (Waverider Buoy Number 4) were obtained.

3.3.2 Results

Wind Direction, Wind Speed and Wave Height

Winds from the south (South, South-East, South-West and South-South-West) prevailed during peaks of larval arrival 1990 to 1993, except on 7th September, 1991 when least cyprids were caught and North-East and North-West winds predominated: North-East winds were two to three times stronger than North-West winds and Southerly winds blew for one hour before Low tide on 8th September (Fig. 3.7).

There was a relationship between mean numbers of cyprids arriving at each larval peak and the average wind speed over 24 hours for that peak ($r = 0.76$; $p =$

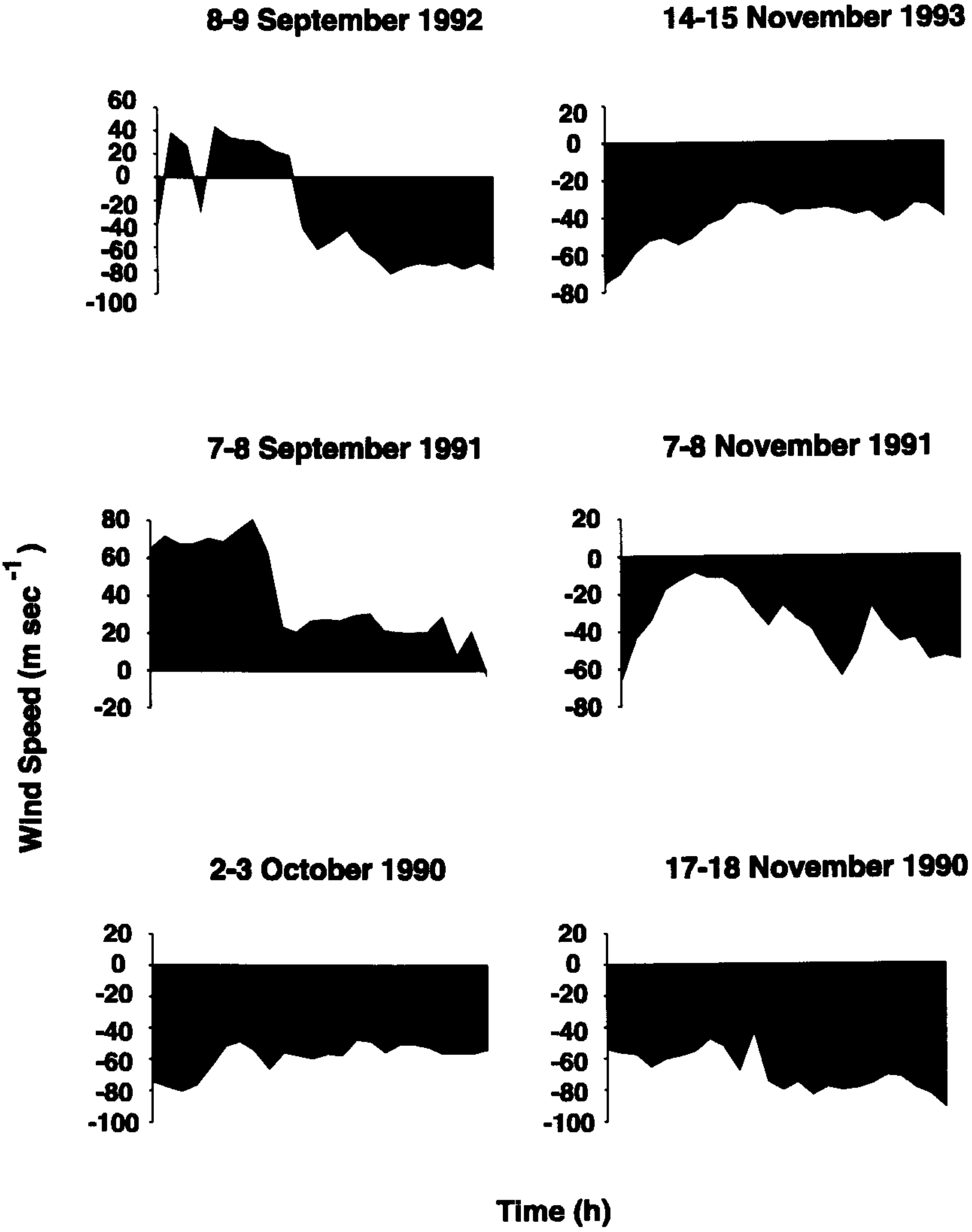

Fig. 3.7

Average hourly wind data for La Perouse near Cape Banks at six peaks of arrival 1990 to 1993. Data are for 24 hours from low tide of one day to low tide of the next and include two tidal cycles when cyprids would have been arriving. Positive values refer to Northerly winds (0^{o} - 90^{o}; 270^{o} - 360^{o}) and negative values to Southerly winds (90^{o} - 270^{o}).

0.08: Fig. 3.8). More cyprids arrived as wind velocities increased. At the two highest velocities within the range recorded, cyprid numbers were fewer than was expected: average 24 hour wind speeds ranged from 35.63 msec^{-1} to 68.08 msec^{-1} during these larval peaks (Fig. 3.8).

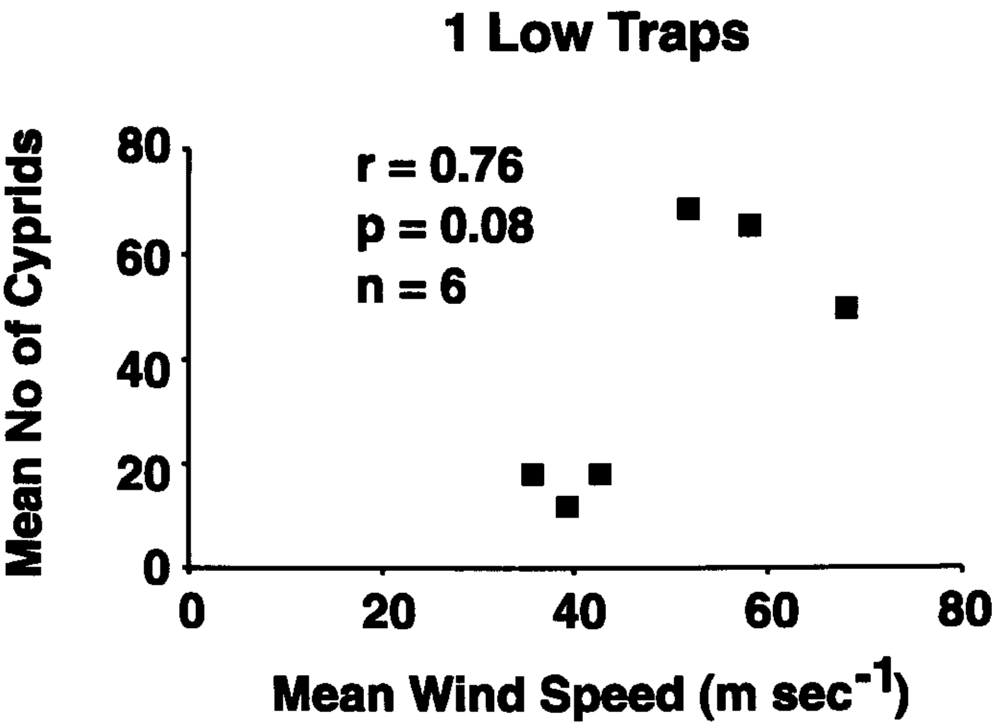

Fig. 3.8
Correlation of mean number of cyprids per 1 Low set of traps (*n* = 3) and mean wind speeds (msec^{-1}) over 24 hours of two tidal cycles for six peaks of arrival 1990 to 1993.

Data for mean monthly wave heights (Fig. 3.9) indicate that, at Cape Banks, highest waves predominated in February, March, June and October from 1990 to 1993 although large waves can occur at anytime. There was a strong correlation between mean numbers of cyprids arriving at each larval peak and mean daily height of waves during that peak ($r = 0.85$; $p < 0.05$: Fig. 3.10). More cyprids arrived when waves were high: average wave heights ranged from 1.2 m to 1.8 m during these larval peaks (Fig. 3.10).

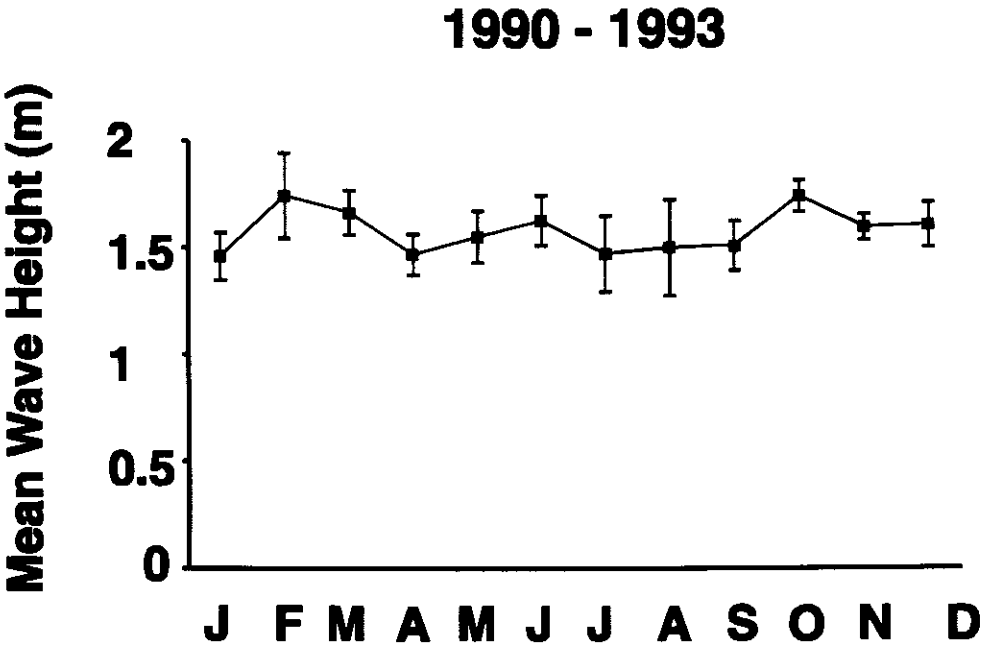

Fig. 3.9

Mean monthly wave height (m) 1990 to 1993 for Botany Bay Offshore Waverider Buoys Numbers 1 and 4.

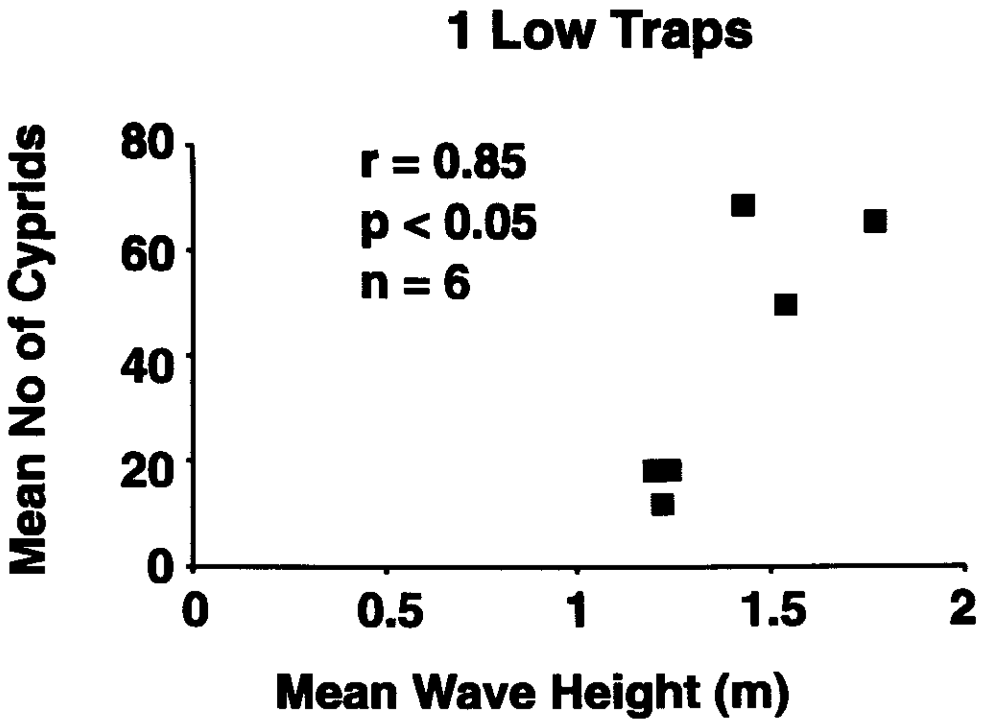

Fig. 3.10

Correlation of mean number of cyprids per 1 Low set of traps ($n = 3$) and mean highest third waves (m) for six peaks of larval arrival 1990 to 1993. Cyprids were sampled daily over two tidal cycles and wave data for daily peaks 1990 to 1993 were obtained from Botany Bay Offshore Waverider Buoy Number 4.

3.4 Water-Flow

3.4.1 Experimental Method and Design

Clod cards (Figs. 2.12, 2.13) were inserted in traps and on the substratum next to traps in a nested design in 1992 and 1993 at Low and Mid/Upper heights at Site 4 (see **Chapter 2: Fig. 2.7**) for 24 hours over two tides. The experimental design was the same as that used for testing the hypothesis about larval supply (see **3.2.1**). Clods on the substratum and in plankton traps were emplaced and removed concurrently except that problems with the battery operated drill meant that clods could not be fixed to the substratum on 8th September, 1992 (when a major peak of larval arrival occurred); clods in plankton traps were, however, utilised on this date.

All clod cards were replaced daily for five days up to, and one day after, each new and full moon (2 x 72 clod plates per lunar sampling period) from early September (8th September - plankton trap clods; 11th September - substratum clods) until mid December, 1992 and from late July until mid December, 1993.

3.4.2 Results

Water-Flow

On peaks of larval arrival at 8th September, 1992 and 14th November, 1993 there was no significant difference in percentage loss from clod cards, and therefore, water-flow, through all sets of traps at different places or across the substratum next to them at these places (Figs. 3.11, 3.12; Table 3.2). Water-flow could not therefore account for the large numbers of cyprids caught in 1 Low traps: water-flow does not explain the differences in larval supply of *Chamaesipho* from place to place.

Percentage mass lost from plankton trap clods and from substratum clods were positively correlated at each place where plankton traps and clod cards were secured in 1992 and 1993 (Figs. 3.13, 3.14).

Table 3.2

a) Analysis of mean % loss of plankton trap clods per set of traps (*n* = 3) on 8th September, 1992.

Analysis of Variance, data untransformed; Cochran's test, $p > 0.05$

Source	df	MS	*F*	*p*
Height	1	315.80	1.59	ns
Set(Height)	2	199.22	1.69	ns
Residual	8	117.54		

b) Analysis of mean % loss of substratum clods per set of traps (*n* = 3) on 14th November, 1993.

Analysis of Variance, data untransformed; Cochran's test, $p > 0.05$

Source	df	MS	*F*	*p*
Height	1	124.74	6.63	ns
Set(Height)	2	18.81	2.59	ns
Residual	8	7.28		

c) Analysis of mean % loss of plankton trap clods per set of traps (*n* = 3) on 14th November, 1993.

Analysis of Variance, data untransformed; Cochran's test, $p > 0.05$

Source	df	MS	*F*	*p*
Height	1	9.21	3.87	ns
Set(Height)	2	2.38	0.07	ns
Residual	8	32.35		

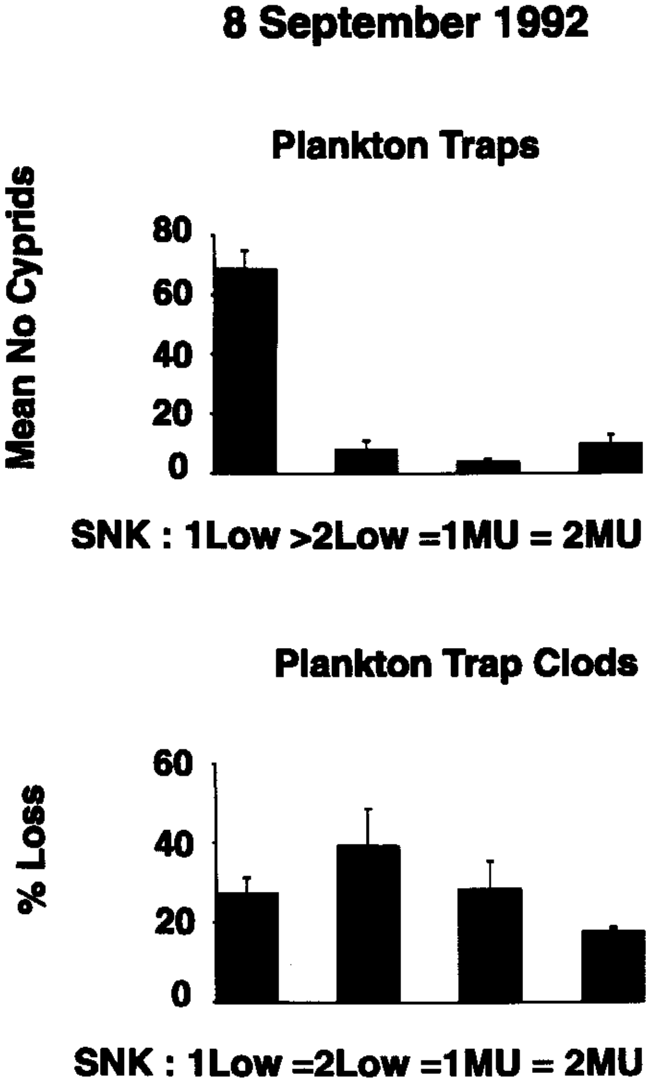

Fig. 3.11

Mean number of cyprids and mean % loss of plankton trap clods per set of traps (n = 3) on 8th September, 1992.

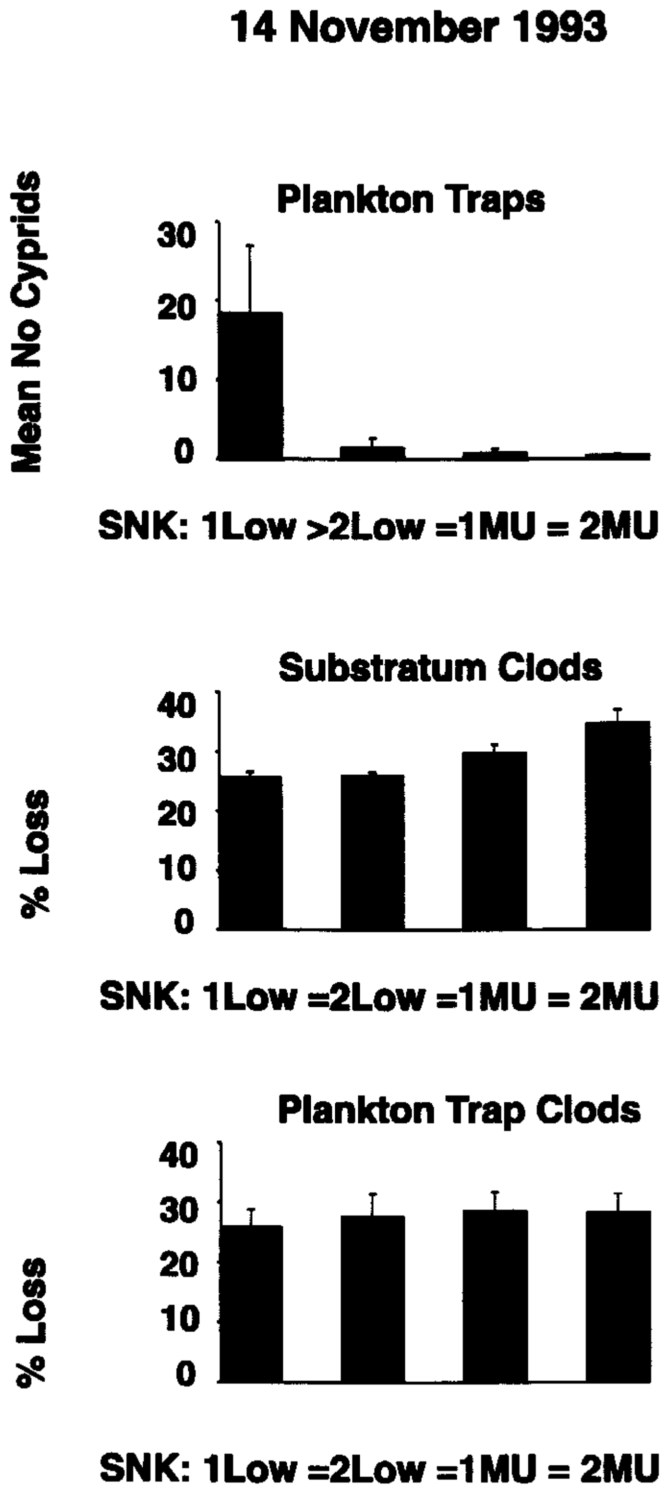

Fig. 3.12

Mean number of cyprids and mean % loss of substratum clods and plankton trap clods per set of traps (*n* = 3) on 14th November, 1993.

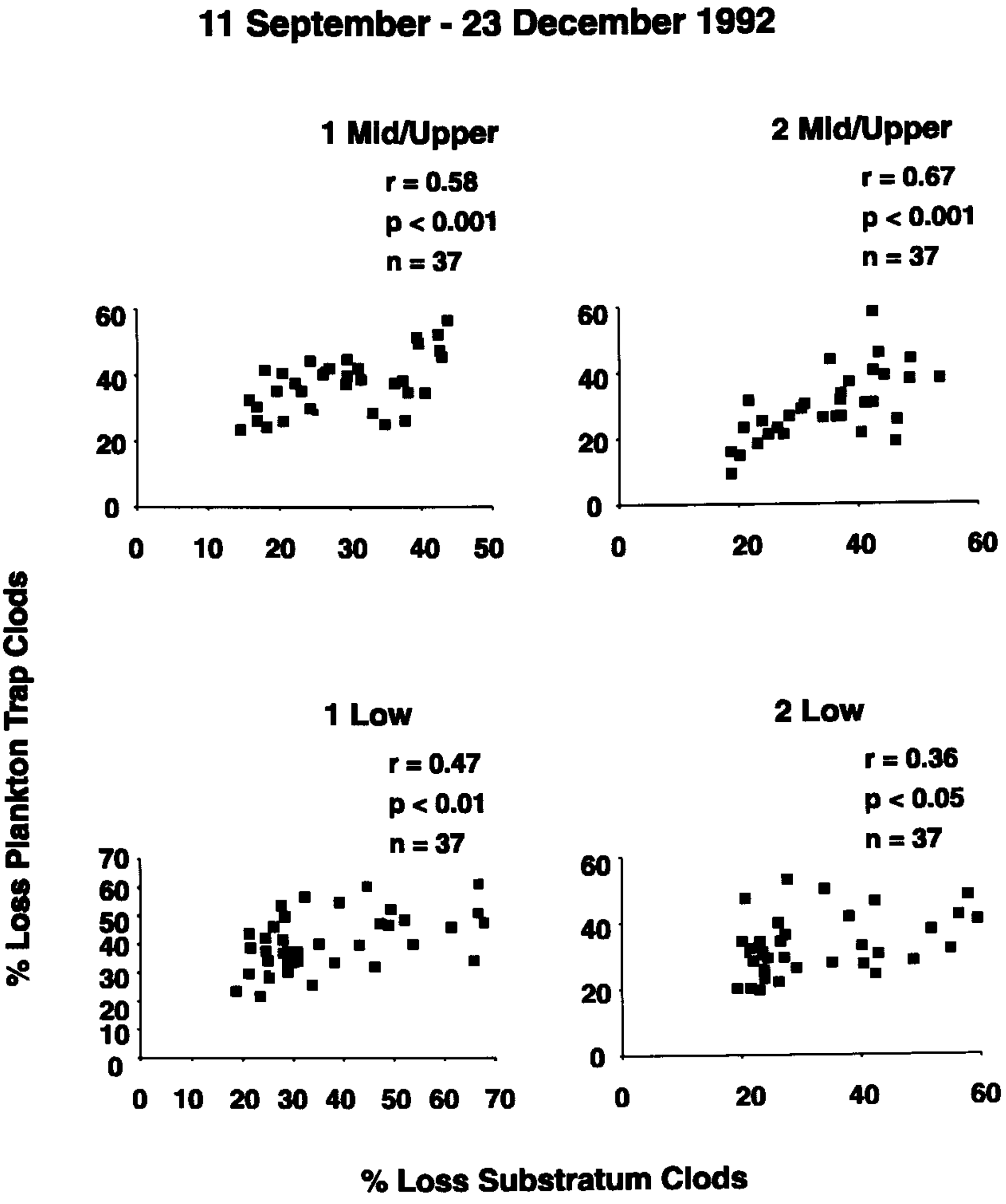

Fig. 3.13

The relationship between % loss plankton trap clods and % loss substratum clods for sets of traps nested in Low and Mid/Upper heights of distribution of *Chamaesipho* from mid September to late December 1992. Each point represents the mean daily % loss of three plankton trap clods and of three substratum clods.

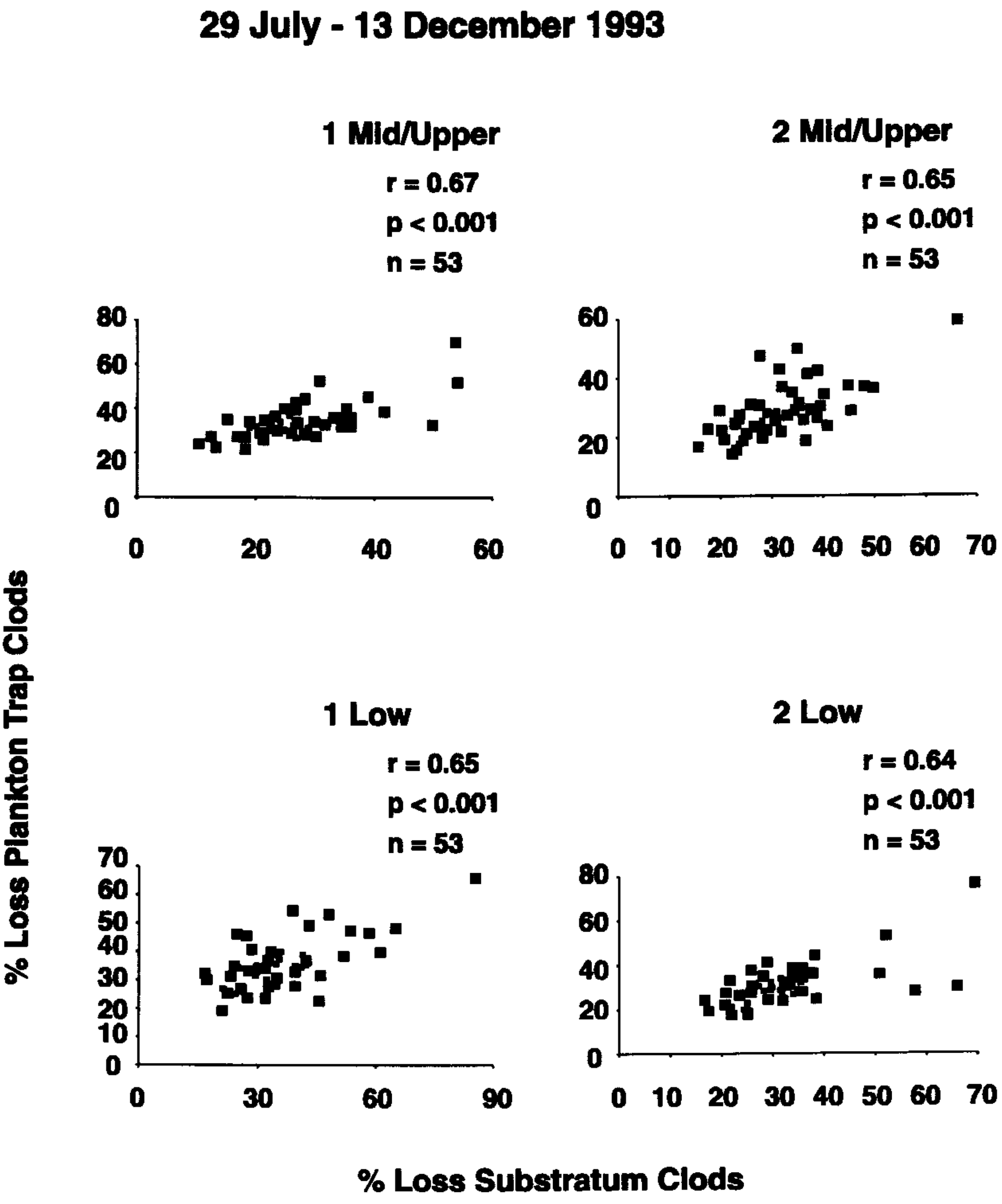

Fig. 3.14

The relationship between % loss plankton trap clods and % loss substratum clods for sets of traps nested in Low and Mid/Upper heights of distribution of *Chamaesipho* from late July to mid December 1993. Each point represents the mean daily % loss of three plankton trap clods and of three substratum clods.

3.5 Larval Supply of *Tetraclitella purpurascens*

3.5.1 Experimental Method and Design

Plankton traps were secured on the substratum in a nested design to entrap cyprids of *Chamaesipho.* Coincidental captures of cyprids of another closely associated barnacle, *T. purpurascens* (Otaiza, 1989) occurred. Clods were also secured to the substratum and within traps (for experimental methods and design see **3.2.1** and **3.4.1**).

3.5.2 Results

Larval Supply of *Tetraclitella purpurascens*

Coincidental captures of cyprids of *Chamaesipho* and *T. purpurascens* showed different patterns for major peaks of arrival on the mid-littoral shore. Many more cyprids of *Chamaesipho* were caught in one set of traps Low on the shore (Fig. 3.6; Table 3.1). There was, however, no significant difference in numbers of cyprids of *T. purpurascens* caught among sets of traps, although those traps on Mid/Upper heights caught marginally more larvae and one set of these Mid/Upper traps usually caught more than the other set (Figs. 3.15, 3.16; Tables 3.3, 3.4). When Times were pooled, there was also no significant difference in numbers of cyprids of *Tetraclitella* among Heights or among Sets of traps nested in Height (Table 3.3).

There was also no difference in percentage mass lost from each set of clods in plankton traps on 20th November, 1992 (Fig. 3.16; Table 3.4). That is, water-flow through traps was similar within and among shore levels. Because the mean number of cyprids caught in each set of traps, and percentage loss from each set of clods was similar, water-flow may be implicated in determining larval supply of *T. purpurascens*. Very few *T. purpurascens* cyprids were caught during this study from 1990 to 1992 and none were caught in 1993.

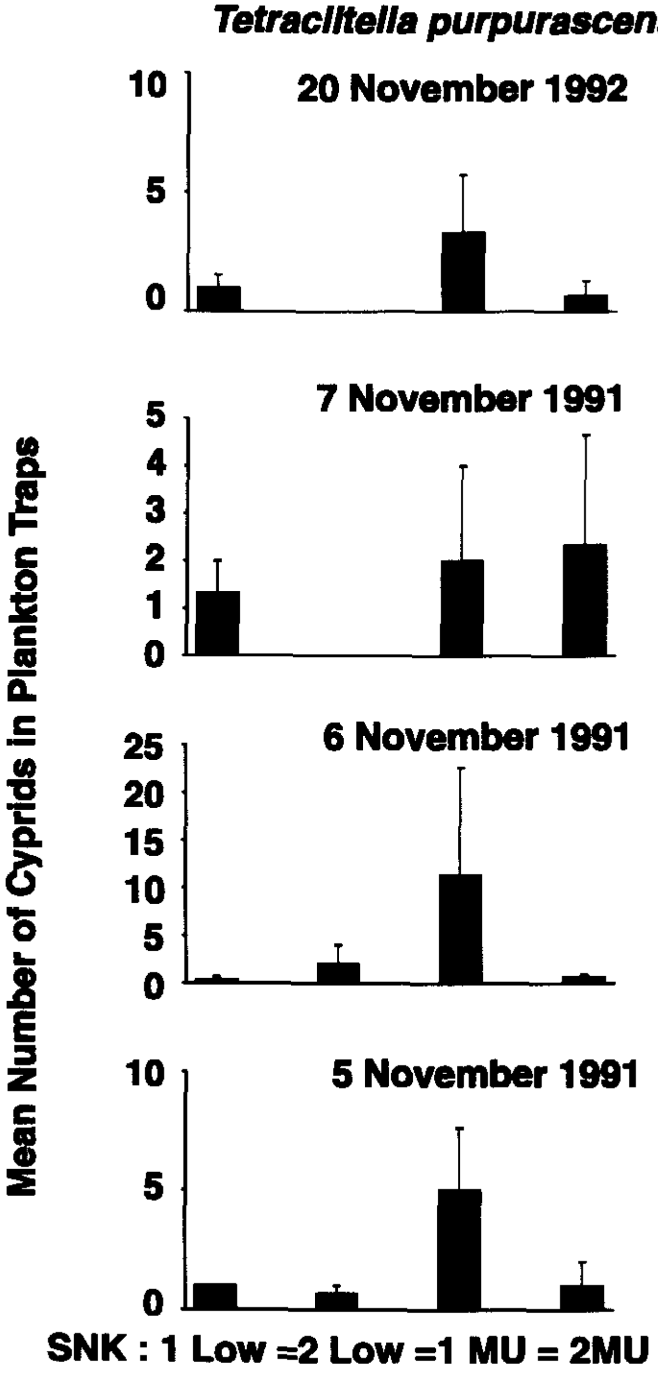

Fig. 3.15

Mean numbers of cyprids of *T. purpurascens* captured in sets of traps (*n* = 3) nested in Low and Mid/Upper heights of *Chamaesipho's* distribution on the shore at one site; data are from 5th to 7th November, 1991 and 20th November, 1992.

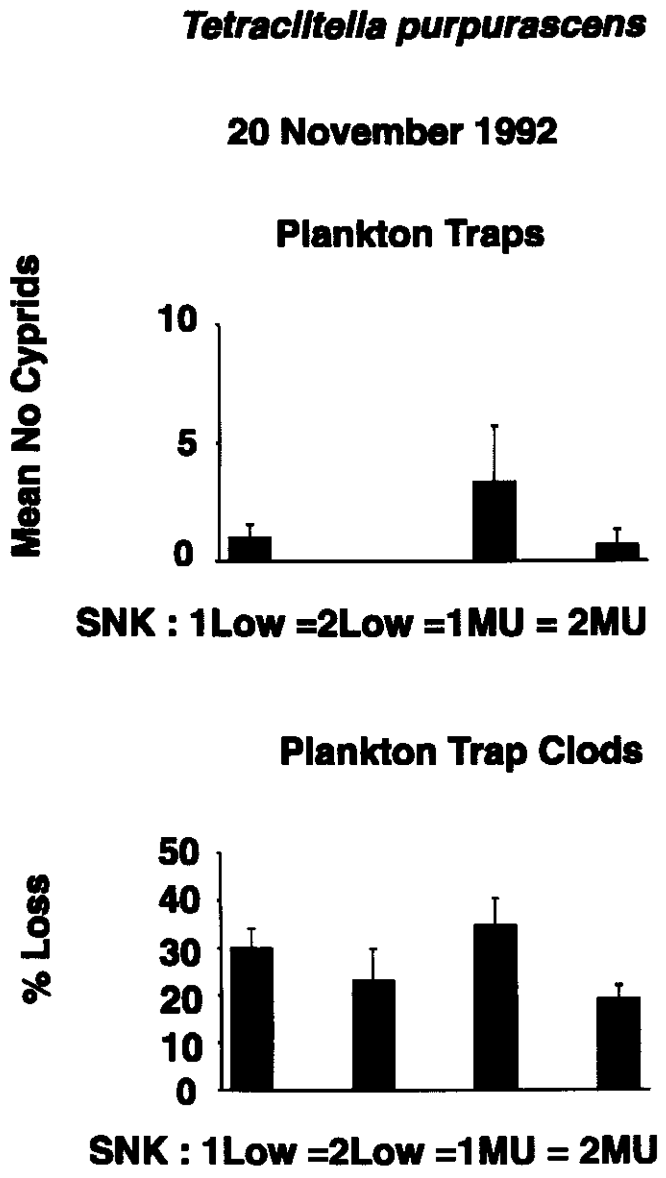

Fig. 3.16

Mean number of cyprids of *T. purpurascens* and mean % loss of plankton trap clods per set of traps ($n = 3$) on 20th November, 1992.

Table 3.3

Analysis of mean numbers of cyprids of ***Tetraclitella purpurascens*** in each set of plankton traps ($n = 3$) nested in Low and Mid/Upper heights of ***Chamaesipho's*** distribution on the shore at Site 4: data are from 5th to 7th November, 1991 and 20th November, 1992. Transformation could not stabilise the variances for pooled data. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

a) Analysis of Variance, data transformed $\mathrm{Log_e}(x + 1)$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	3	0.16	0.46	ns
Height = H	1	1.65	1.28	ns
Set (Height) = S(H)	2	1.29	1.57	ns
T x H	3	0.01	0.03	ns
T x S(H)	6	0.34	0.42	ns
Residual	32	0.82		

b) Analysis of Variance, Times pooled, data untransformed; Cochran's test, $p < 0.01$

Source	df	MS	*F*	*p*
Height	1	75.00	1.38	ns
Set (Height)	2	54.38	2.15	ns
Residual	44	25.28		

Table 3.4

a) Analysis of mean numbers of cyprids of *Tetraclitella purpurascens* in each set of plankton traps (n = 3) nested in Low and Mid/Upper heights of *Chamaesipho's* distribution on the shore at Site 4 on 20th November, 1992.

Analysis of Variance, data transformed $(x + 1)^{0.5}$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Height	1	0.45	1.01	ns
Set(Height)	2	0.44	1.32	ns
Residual	8	0.33		

b)Analysis of mean % loss of plankton trap clods per set of traps (n = 3) on 20th November, 1992.

Analysis of Variance, data untransformed; Cochran's test, $p > 0.05$

Source	df	MS	*F*	*p*
Height	1	0.57	0.00	ns
Set(Height)	2	216.77	2.76	ns
Residual	8	78.5		

3.6 Settlement on the Substratum

3.6.1 Experimental Method and Design

In July in each year from 1991 to 1993, a 6 cm diameter patch was cleared within aggregations of barnacles next to each plankton trap (n = 3) secured in two sets (1 Low, 2 Low, 1 Mid/Upper, 2 Mid/Upper) at each height (Low and Mid/Upper) of the distribution of *Chamaesipho* at Site 4 (see **Chapter 2: Fig. 2.7**). A hammer and cold chisel were used to remove any remnants of adults in the rocky substratum. Each replicate was washed after preparation to remove any fine particles of sand.
Generally from late July to late December, cyprids and settlers were counted and

removed daily during the lunar sampling period with a dissecting needle from these patches concurrent with the removal of samples from plankton traps.

Time constraints meant that numbers of settlers could not be recorded on 9th September, 1992 after two tidal cycles when a major peak of arrival occurred; plankton samples were, however, collected on that day.

3.6.2 Results

Settlement on the Substratum

From late July to late December in each year from 1991 to 1993, the daily mean numbers of cyprids caught in plankton traps were generally positively correlated with daily mean numbers of settlers (lagged by one day) on the substratum next to these traps at Low and Mid/Upper heights within *Chamaesipho's* distribution (Fig. 3.17; Table 3.5). This generally consistent positive relationship occurred even though very different numbers of larvae and settlers were recorded for different sets of traps and on cleared patches next to them (Fig. 3.18). The numbers of cyprids arriving were directly related to the numbers of larvae settling; that is, the distribution of juvenile *C. tasmanica* is strongly correlated with larval supply.

Table 3.5

Summary of analyses of relationship between daily mean numbers of cyprids caught in plankton traps and daily mean numbers of new settlers (lagged by one day) at two heights (Low and Mid/Upper) on the shore within *Chamaesipho's* distribution at Site 4. Data are generally from late July to late December 1991 to 1993.

	1991			1992			1993		
	df	*r*	*p*	df	*r*	*p*	df	*r*	*p*
1 Low	41	0.57	< 0.001	31	0.41	< 0.05	47	0.65	< 0.001
2 Low	41	0.44	< 0.01	31	0.17	ns	47	0.65	< 0.001
1 MU	41	0.46	< 0.01	31	0.90	< 0.001	47	0.97	< 0.001
2 MU	41	0.44	< 0.01	31	0.89	< 0.001	47	0.08	ns

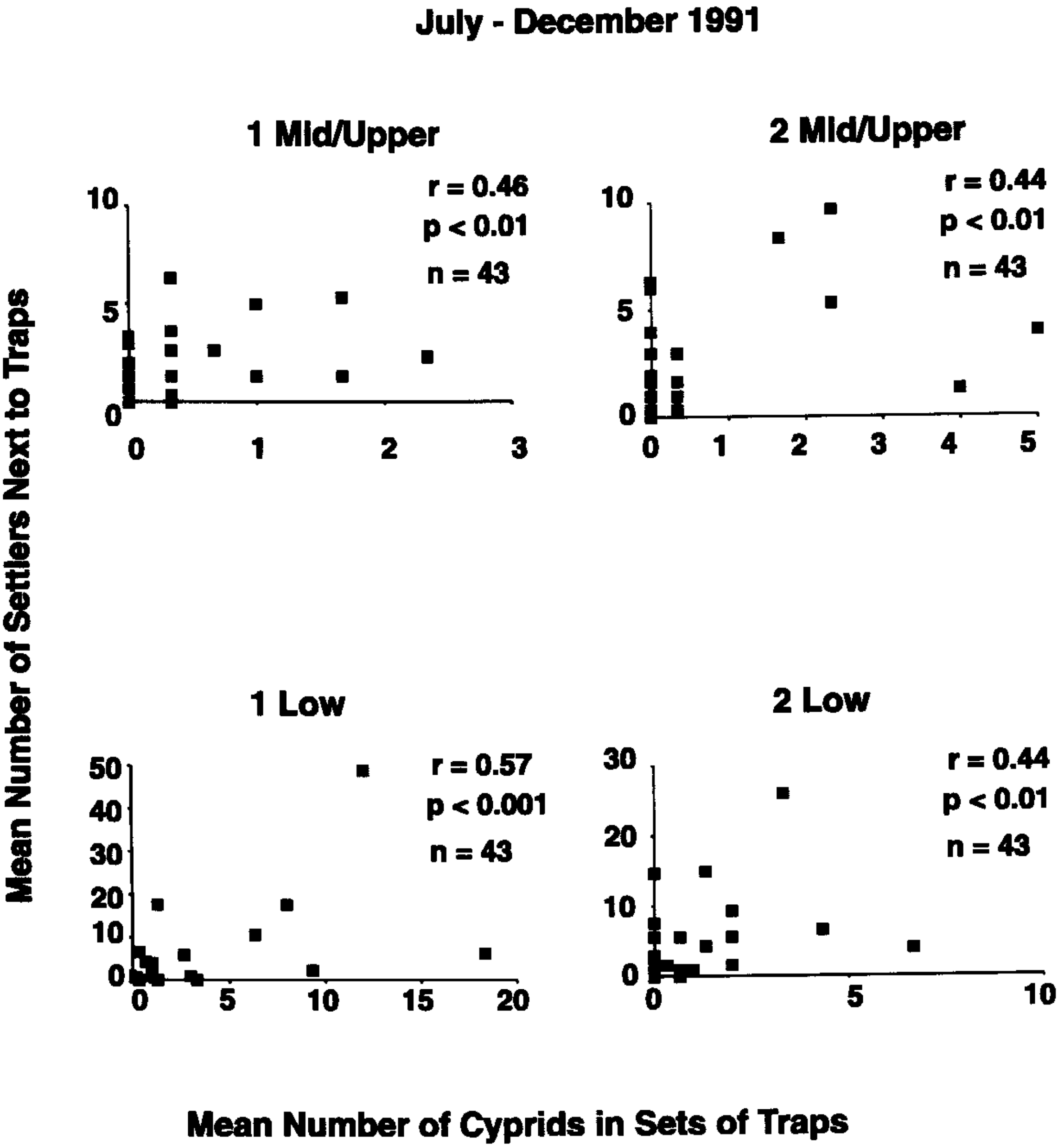

Fig. 3.17

The relationship between daily mean numbers of cyprids and daily mean numbers of new settlers (lagged by one day) from late July to early December 1991. Each point represents the mean daily capture of cyprids in three traps and the mean daily settlement in three patches on the substratum next to these traps for each area on the shore sampled. Note different scales on axes.

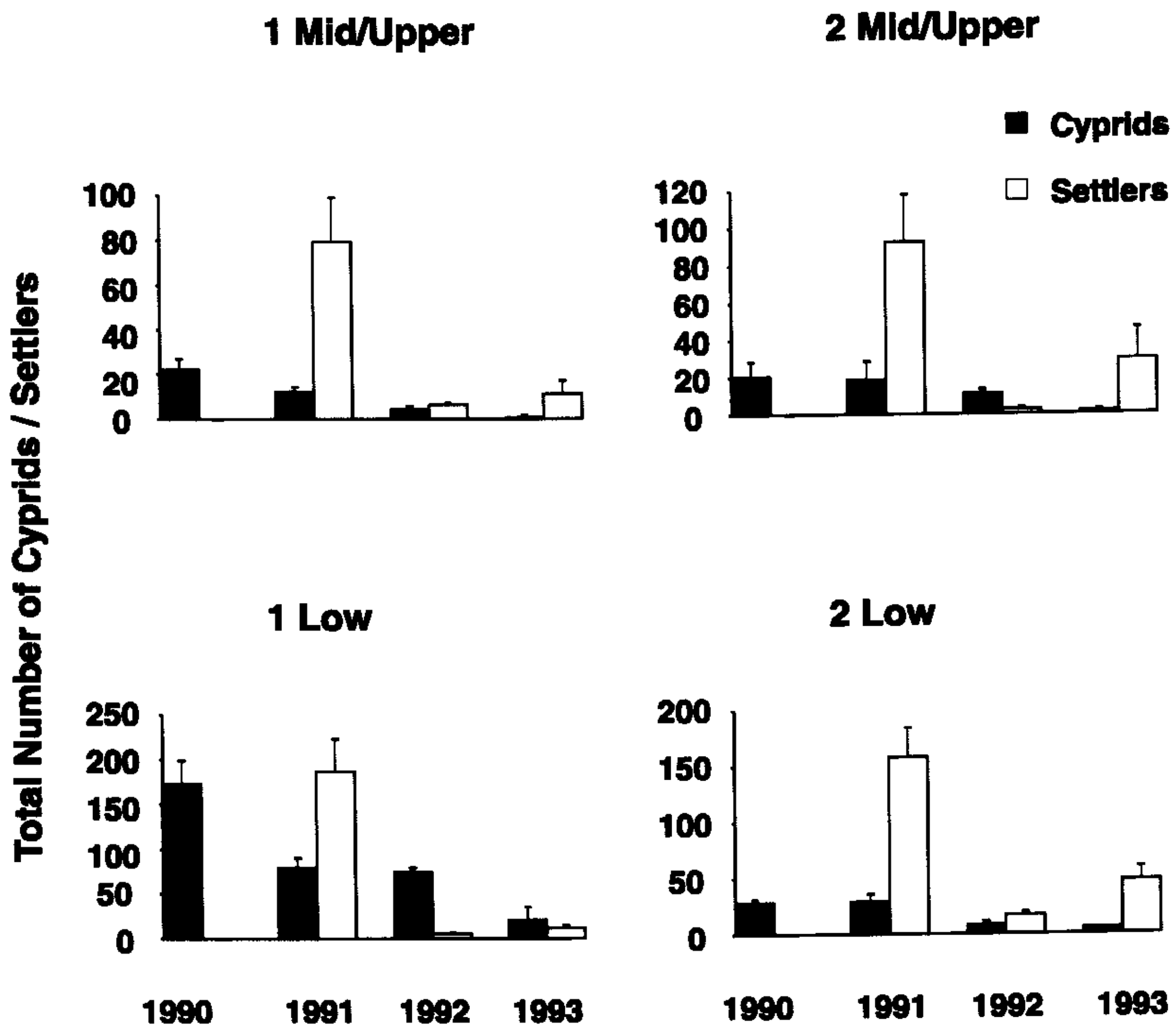

Fig. 3.18

Annual total numbers of cyprids caught in sets of plankton traps ■ and total numbers of settlers in sets of cleared patches on the substratum □ (*n* = 3) 1990 to 1993. Settlers were not recorded in 1990 nor on 9th September, 1992 (settlement lagged by one day after the peak of arrival on 8th September, 1992).

Total Numbers of Cyprids and Settlers

In 1990, numbers settling were not recorded and in 1992, the numbers settling were not recorded on the one day that they settled in relatively large numbers (Fig. 3.18). There were generally more settlers on the substratum than cyprids caught in traps (Fig. 3.18; Table 3.6) which could reflect efficiency of traps rather than true larval availability. Despite this discrepancy, there were strong correlations between daily numbers of cyprids arriving and daily numbers settling on the substratum (Fig. 3.17; Table 3.5) which indicates that the recorded data were "reliable".

Table 3.6

Analysis of total numbers of cyprids caught in sets of plankton traps and total numbers of settlers in sets of cleared patches on the substratum ($n = 3$) at two heights (Low and Mid/Upper) on the shore within *Chamaesipho's* distribution at Site 4. Experiments were renewed each year and data are totals from December in 1991 and 1993. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $(x + 1)^{0.5}$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	1	273.87	38.7	*
Height = H	1	79.98	21.49	*
Set(Height) = S(H)	2	3.72	1.40	ns
Cyprids versus Settlers =CSe	1	181.11	15.79	0.058
T x H	1	12.54	1.77	ns
T x S(H)	2	7.08	2.65	ns
T x CSe	1	34.84	20.40	*
H x CSe	1	0.08	0.01	ns
CSe x S(H)	2	11.47	4.30	*
T x H x CSe	1	1.82	1.07	ns
CSe x T x S(H)	2	1.71	0.64	ns
Residual	32	2.67		

Greater numbers of settlers and cyprids were recorded in 1991 than 1993 and Low shore levels received more cyprid larvae and settlers than did Mid/Upper heights (Fig. 3.18; Table 3.6). In 1991, more total settlers were recorded than total cyprids whereas numbers were similar for 1993 when relatively few cyprids arrived and settled. In 1991 and 1993, more settlers than cyprids were recorded from 2 Low and 1 and 2 Mid/Upper sets of traps and from cleared patches on the substratum next to these traps. In 1 Low sets of traps and cleared patches, total numbers of cyprids and settlers did not differ, because there were few cyprids and settlers in 1993. 1 Low sets of traps received more cyprids than 2 Low traps although similar numbers of larvae settled on cleared patches next to each set of Low shore traps. Both Mid/Upper sets of traps caught similar numbers of cyprids although more larvae settled on one set of cleared patches at this height (Fig. 3.18; Table 3.6).

There was a strong correlation between numbers of larvae arriving and numbers settling from 1991 to 1993 (Fig. 3.17; Table 3.5) and a decline in total numbers of larvae arriving from 1990 to 1993 (Fig. 3.19).

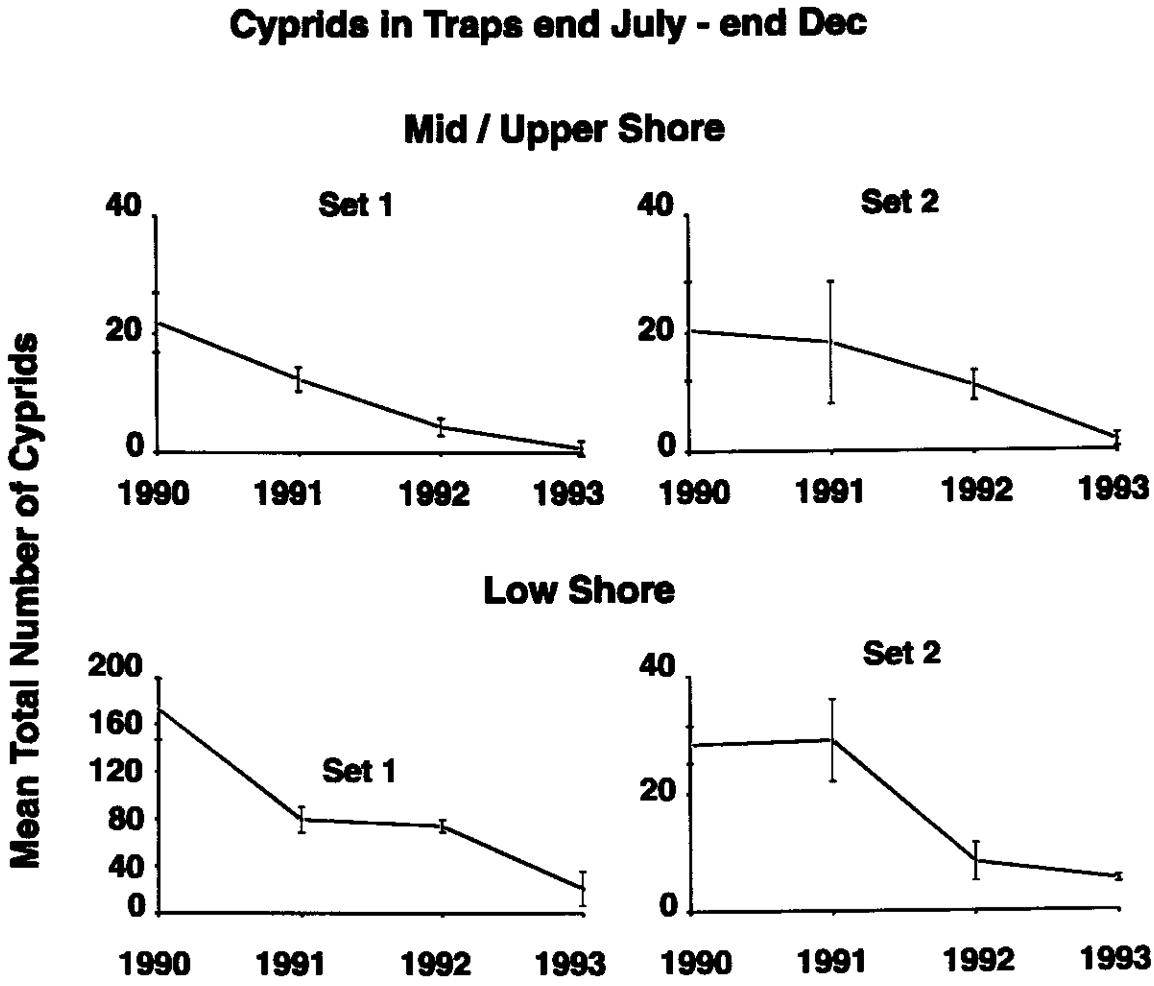

Fig. 3.19
Mean annual total numbers of cyprids captured in sets of traps ($n = 3$) nested in Low and Mid/Upper heights of *Chamaesipho's* distribution from 1990 to 1993.

3.7 Discussion

Earlier studies have suggested that more larvae settle on lower shores because larvae may arrive and settle first on lower shores, leaving fewer to settle on upper heights (Roughgarden et al., 1988). The greater numbers on lower shores could also be a function of longer periods of submersion (Denley & Underwood, 1979; Underwood & Denley, 1984), aggregations of cyprids in the plankton (de Wolf, 1973; Gaines et al., 1985; Roughgarden et al., 1987, 1988), or the position of larvae in the water column (Grosberg, 1982; Gaines et al., 1985).

These statements may not explain the distributions of all species of barnacles. For example, in this study, during major peaks of arrival, coincidental captures of *Chamaesipho* and *T. purpurascens* showed different patterns of larval distributions. *Chamaesipho* larvae were consistently caught in one set of Low shore traps whereas *T. purpurascens* larvae were evenly distributed across the mid-littoral shore with marginally more larvae caught at Mid/Upper heights rather than Low on the shore. Adult distributions of *T. purpurascens* are consistent with these larval distributions (Denley & Underwood, 1979; Bennett, 1992; Underwood & Chapman, 1993). Obviously *T. purpurascens* larvae do not arrive and settle on Low shores first, leaving fewer for Mid/Upper shores because Low and Mid/Upper traps caught similar numbers of cyprids, and one set of Mid/Upper traps usually caught slightly more larvae than all other sets of traps. *Chamaesipho* cyprids, however, were always concentrated on Low shores although not in all places. From 1990 to 1993, one set of Low shore traps always caught more cyprids than the other set which caught similar numbers of cyprids to Mid/Upper shore traps. Obviously, because patterns of larval supply were spatially consistent, the roles of patchy distribution of larvae in the plankton and the possibility that more cyprids arrive first to settle on lower shores, can be discounted in determining patterns of larval arrival in both species.

Periods of submersion may also be unimportant in determining the distribution of some species of barnacles. Duplicated sets of traps Low on the shore caught consistently different numbers of *Chamaesipho* larvae during major peaks of arrival, even though traps were submerged for the same period. One set of Low shore traps caught similar numbers to those at Mid/Upper heights. Numbers of *T. purpurascens* larvae were also similar for Low and Mid/Upper heights, when submersion times would be expected to be different. Aggregations of cyprid larvae in the plankton can also be discounted in determining patterns of larval supply: larval aggregations would be expected to be random and reflect patterns of capture whereas patterns of captures of *Chamaesipho* cyprids recurred within and among shore levels at all times.

It was also found that water-flow does not determine the distribution of arrival of cyprids of *Chamaesipho* at different places and heights. During major peaks of arrival from 1990 to 1993, many more cyprids arrived consistently at one place, Low on the shore even though water-flow, indicated by percentage loss from plankton trap clods and substratum clods, was similar for all places and heights. Direction of flow may be implicated, but was not measured.

When cyprids arrive to settle, because spatial patterns of arrival recurred from 1990 to 1993, I suspect that small-scale hydrodynamics, as a function of topography of the substratum, interact with the position of larvae in the water column to concentrate larvae in specific patterns in different areas. For example, turbulence can transport and concentrate cyprid larvae in their normal habitat (Gaines et al., 1985; Denny & Shibata, 1989). Turbulence can also be modified by topography of the substratum so that an association between roughness of the surface and slow water means that settlement is enhanced (Pawlik & Butman, 1993). Further to this, Grosberg (1982) showed that stratification of larvae in the water column was an important mechanism for determining larval supply of two species of barnacles *Balanus glandula* and *Balanus crenatus*.

The different numbers of cyprids in different places cannot be explained by cyprids arriving first on lower shores, the longer periods of submersion at lower levels, nor aggregations of larvae in the plankton. Other processes must influence the distributions of larval *Chamaesipho* and *T. purpurascens*. Because spatial patterns of larval arrival were consistent, they may be influenced by position of larvae in the water column and site-specific characteristics of fluid dynamics at small spatial scales. Peaks of arrival of *Chamaesipho* coincided with processes such as lunar periodicity and specific wind speeds, wind direction and wave heights. Nevertheless, variations in larval supply were found to be responsible for the variations in distributions of juveniles on the substratum.

CHAPTER FOUR

LARVAL CHOICE

4.1 Introduction

Once cyprid larvae have arrived at a shore, their behavioural responses at settlement can influence the numbers that settle and, hence, the abundance of local populations. Gregarious larvae will settle near members of their own species, be they other cyprids, newly-metamorphosed individuals, older juveniles, or adults (Meadows & Campbell, 1972; Crisp, 1974, 1984; Burke, 1986; Pawlik, 1992). Being gregarious is believed to convey an advantage for adults because most barnacles are hermaphroditic and cross-fertilization is often necessary. The degree of exposure to adult conspecifics, rather than the amount of space available, determines settlement of gregarious larvae (Raimondi, 1990). In different-shaped patches of equal area, more larvae would be expected to settle in patches with longer perimeters of adult barnacles (Raimondi, 1990).

Only some barnacles are gregarious (Crisp, 1984; Wethey, 1984, 1986a; Raimondi, 1988b, 1990, 1991). Many barnacles will not readily settle on the shells of adults of their own species (Moyse & Hui, 1981; Gaines & Roughgarden,1985; Chabot & Bourget, 1988). Gaines & Roughgarden (1985) found that *Balanus glandula* cyprids would generally only metamorphose on adults when there was very little other space available. The conflict between lack of settlement on conspecific barnacles and the induction of gregarious larval behaviour by the presence of adults (Moyse & Hui, 1981), indicates that different processes are operating. Although cyprids of *Semibalanus balanoides* avoid settling on adults, the presence of conspecifics enhanced settlement of larvae (Chabot & Bourget, 1988). There was, however, a reduction in settlement of *S. balanoides* proportional to a decrease in available free space (Chabot & Bourget, 1988; Bertness et al., 1992). Larvae of *S. balanoides* have been shown to settle on the basal scars of recently removed adults, rather than on the shells of adults (Knight-Jones, 1953; Wethey, 1984), suggesting different chemical and physical cues for settlement on the outside versus the bases of barnacles (Moyse & Hui, 1981).

Although gregariousness of newly-arriving larvae to adult barnacles has been studied, very little is known about the effect of the presence of newly-metamorphosed juveniles on inducing settlement. Kendall et al. (1985) and Minchinton and Scheibling (1991) found that new settlers inhibited further settlement of *S. balanoides*, as also found by Raimondi (1990) for *Chthamalus anisopoma*. Wethey (1984), however, found that cyprids of *S. balanoides* settled closer to other larvae but further away from metamorphs. Thus, the presence of newly-settled barnacles is strongly implicated as an important process influencing gregariousness during settlement. Cyprids are often aggregated in the plankton (De Wolf, 1973; Gaines et al., 1985; Roughgarden et al., 1987, 1988) which may influence patterns during settlement.

The honeycomb barnacle *Chamaesipho tasmanica* settles gregariously in response to the presence of adults (Otaiza, 1989). Early in this study, *Chamaesipho* cyprids were seen to settle and metamorphose close to adults and near newly-settled juveniles around the perimeter of cleared patches. Hydrodynamic edge-effects were not the cause because the same peripheral pattern was recorded regardless of whether patches were bordered by a few tiny, flat individuals or by abundant large, tall barnacles. It is assumed that chemicals released from older recruits and adult barnacles facilitate settlement (Meadows & Campbell, 1972; Crisp, 1974, 1984, 1985; Burke, 1986; Gabbott & Larman, 1987; Pawlik, 1992). In areas of abundant free space, cyprid larvae of *Chamaesipho* were initially observed close to, but never on, adults, whereas later arrivals were more evenly scattered. Larvae were sometimes in bare patches on basal scars recently vacated by adults and on the substratum within empty tests.

From these initial observations at Cape Banks, it was thought that, similar to previously reported information on other barnacles (Knight-Jones, 1953; Wethey, 1984, 1986a; Gaines & Roughgarden, 1985; Chabot & Bourget, 1988; Raimondi, 1988a, 1988b, 1990, 1991), behavioural cues may influence settlement of *Chamaesipho*. Chapter 3 has already shown that larval supply is integral in determining the numbers of cyprids of *Chamaesipho* that arrive and settle at Cape Banks. I proposed that larval choice at settlement, in response to environmental cues, also has a primary role in influencing densities of cyprids that settle, and thus the spatial distributions of *Chamaesipho*. In particular, gregariousness (with respect to adults and also to the presence of new settlers and recruits) is an important determinant of patterns of settlement.

Because *Chamaesipho* is gregarious (Otaiza, 1989) it was predicted that there would be a relationship between the numbers of larvae settling and the numbers of adults already occupying the substratum. It was also predicted that, if newly-settled barnacles were counted at varying distances from adults, there would be more settlement in those areas closer to adults. If settlers were removed daily from different-sized plots (large, 6 cm; medium, 3 cm; small, 1.5 cm) half of which were painted with adult barnacle extract, there should be more settlement in painted plots, and in the smallest painted plots which were closer to adults, than in large and medium-sized plots. If settlers were not removed daily from large 6 cm patches, half of which were painted with adult barnacle extract, it was predicted that there would be more settlement in painted patches. If barnacle extract was also painted on some 2 cm patches outside the normal distribution of *Chamaesipho* on upper shores, there should also be increased settlement in these painted patches. Because *Chamaesipho* cyprids were initially perceived to settle in greater quantities near other newly-settled juveniles, it was predicted that there would be reduced settlement where new settlers were removed daily from some plots.

The degree of exposure to adults along perimeters of patches and the presence of already newly-settled barnacles may interact to influence settlement of cyprids. It was therefore predicted that, in different-sized plots (large, 6 cm; medium, 3 cm; small, 1.5 cm) half of which had been cleared daily of newly-settled barnacles and the rest of which remained uncleared, there would be most settlement in smallest plots with greatest relative exposure to adults along perimeters and where juveniles had not been picked off.

4.2 Gregariousness

4.2.1 Experimental Method and Design

Gregarious Response to Adults

From late July to late December in each year from 1989 to 1993, numbers of larvae settling and densities of adults were recorded in 6 cm diameter replicates already inhabited by established adult *Chamaesipho.*

Distance from Adults

In 1993, three 6 cm diameter patches were cleared within aggregations of barnacles at each of Low, Mid and Upper heights within *Chamaesipho's* distribution at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**). In November, during new and full moons, newly-settled barnacles were counted daily within each patch at varying distances from adults at the edge of these patches. At each time of sampling, new settlers in three randomly selected quadrats, each 0.75 cm x 0.75 cm, were recorded in each patch at distances ranging from 0 - 0.75 cm, 0.75 - 1.5 cm, 1.5 - 2.25 cm and 2.25 - 3 cm from adults.

Barnacle Extract

Barnacle Extract and Settlers Removed Daily

In July 1991 and 1992, six 6 cm, 3 cm and 1.5 cm diameter patches were cleared on the substratum within aggregations of barnacles at each of Low, Mid and Upper heights within *Chamaesipho's* distribution at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**). In July 1993, six 6 cm patches only were cleared at each height. Daily during the sampling period, half of these patches were painted with barnacle extract (whole barnacles blended in sea water) and settlers were removed concurrently from all patches until December 1991, 1992 and 1993. Numbers per cm^2 of settlers were compared in these different-sized patches in each experiment in 1991 and 1992. Because the degree of exposure to adults at the edge of these patches may also have been influencing settlement, numbers of settlers were multiplied by Perimeter/Surface Area ratios for each size of patch.

Barnacle Extract and Settlers Not Removed

In 1991 and 1992, six 6 cm diameter patches were prepared at different places within aggregations of adult barnacles Low on the shore at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**). Half of these patches were painted with barnacle extract (*n* = 3). Each day, during each lunar sampling period, from September 1991 and July 1992, numbers of new settlers were recorded on each set of patches until mid and late December, respectively. Settlers were not removed daily.

Barnacle Extract Above the Distribution of *Chamaesipho tasmanica*

In July 1991 and 1992, six 2 cm diameter patches were cleared on the substratum above *Chamaesipho's* upper limit of distribution at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**). Half of these were painted daily with barnacle extract (*n* = 3) for six consecutive days during each sampling period over new and full moons. Settlers were removed, when present, from every patch until December of each year.

New Settlers/New Recruits

Each year, six randomly-scattered 2.5 cm diameter patches were cleared with a hammer and cold chisel at each of Low, Mid and Upper shore levels of the distribution of *Chamaesipho* at each of two sheltered sites, Sites 3 and 4, (see **Chapter 2: Fig. 2.7**). Heights ranged from 0.08 m above MLWS for 3 Low replicates to 1.37 m above MLWS for 4 Upper replicates.

Cyprids and settlers were removed daily during the sampling period from three Removal replicates. Three replicate Controls were monitored concurrently at each height and site. The new and previous settlers and recruits in each treatment were counted and mapped on acetate sheets for 7-8 successive days every two weeks during new and full moons from the end of October to late December 1990, from late July to early December 1991 and from August to the end of December 1992 to coincide with expected major peaks of settlement. After settlement, the surviving recruits were counted each month from January to July for each year. For successive experiments in 1991 and 1992, all replicates were cleared and new experimental plots prepared on different areas of the substratum at the end of July.

4.2.2 Results

Gregarious Response to Adults

There was a positive relationship between annual total numbers of settlers and annual total numbers of adults at six sites and three heights (Low, Mid, Upper) from 1989 to 1993 (Fig. 4.1). More cyprids settled in areas where adults were dense (Fig. 4.1).

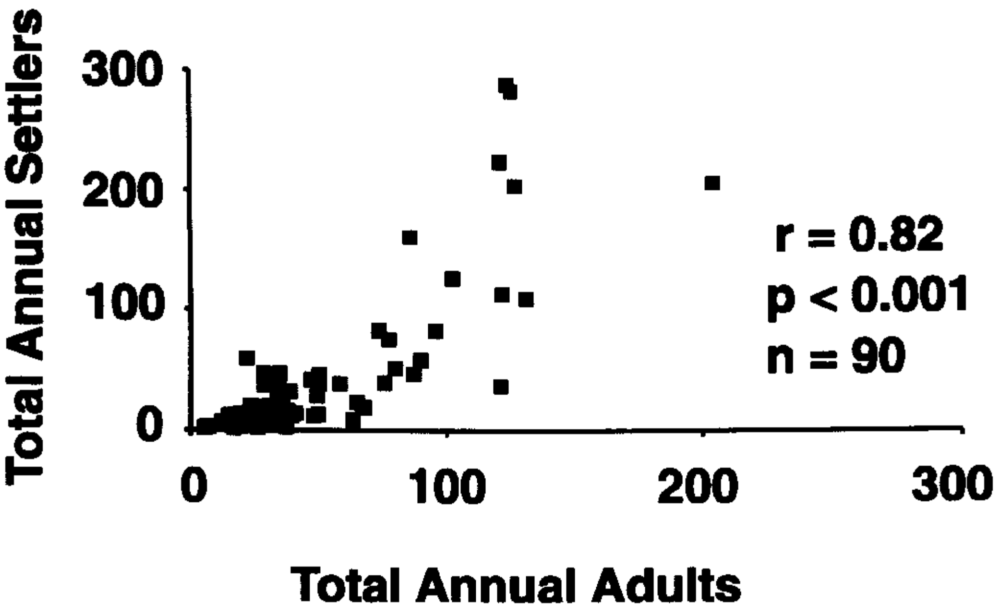

Fig. 4.1

Relationship between annual total numbers of settlers and annual total numbers of adults ($n = 3$). Each point represents the mean total number of larvae settling in three 6 cm replicates and the mean total number of adult barnacles already populating these replicates at six sites and three heights (Low, Mid, Upper) of *Chamaesipho's* distribution from 1989 to 1993.

Distance from Adults

During a major settlement on 15th November, 1993 at Sites 3 and 4, more settlers were always within 0.75 cm of adults, than at any other distance in every set of replicates (Fig. 4.2; Table 4.1). At further distances away from adults (1.5, 2.25 and 3 cm), there were fewer larvae and the numbers were not different among heights (Fig. 4.2; Table 4.1). *Chamaesipho* larvae settle gregariously in response to the presence of adults and in decreasing numbers with increasing distance from adults.

Table 4.1

Analysis of numbers of new settlers in each 0.75 cm x 0.75 cm quadrat at varying distances from adults (0.75 cm, 1.5 cm, 2.25 cm, 3 cm) in three sets of 6 cm cleared patches each on Low, Mid and Upper Heights at Sites 3 and 4 on 15th November, 1993 ($n = 3$). Transformation could not stabilise the variances; Cochran's test, C = 0.32, $p < 0.01$. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data untransformed, Cochran's test, $p < 0.01$.

Source	df	MS	*F*	*p*
Site = S	1	0.17	0.25	ns
Height = H	2	7.76	186.33	**
Set(SxH) = Se(SxH)	12	0.66	3.74	***
Distance = D	3	9.29	28.40	*
SxH	2	0.04	0.06	ns
SxD	3	0.33	1.01	ns
HxD	6	4.72	43.08	***
DxSe(SxH)	36	0.32	1.84	**
SxHxD	6	0.11	0.34	ns
Residual	144	0.18		

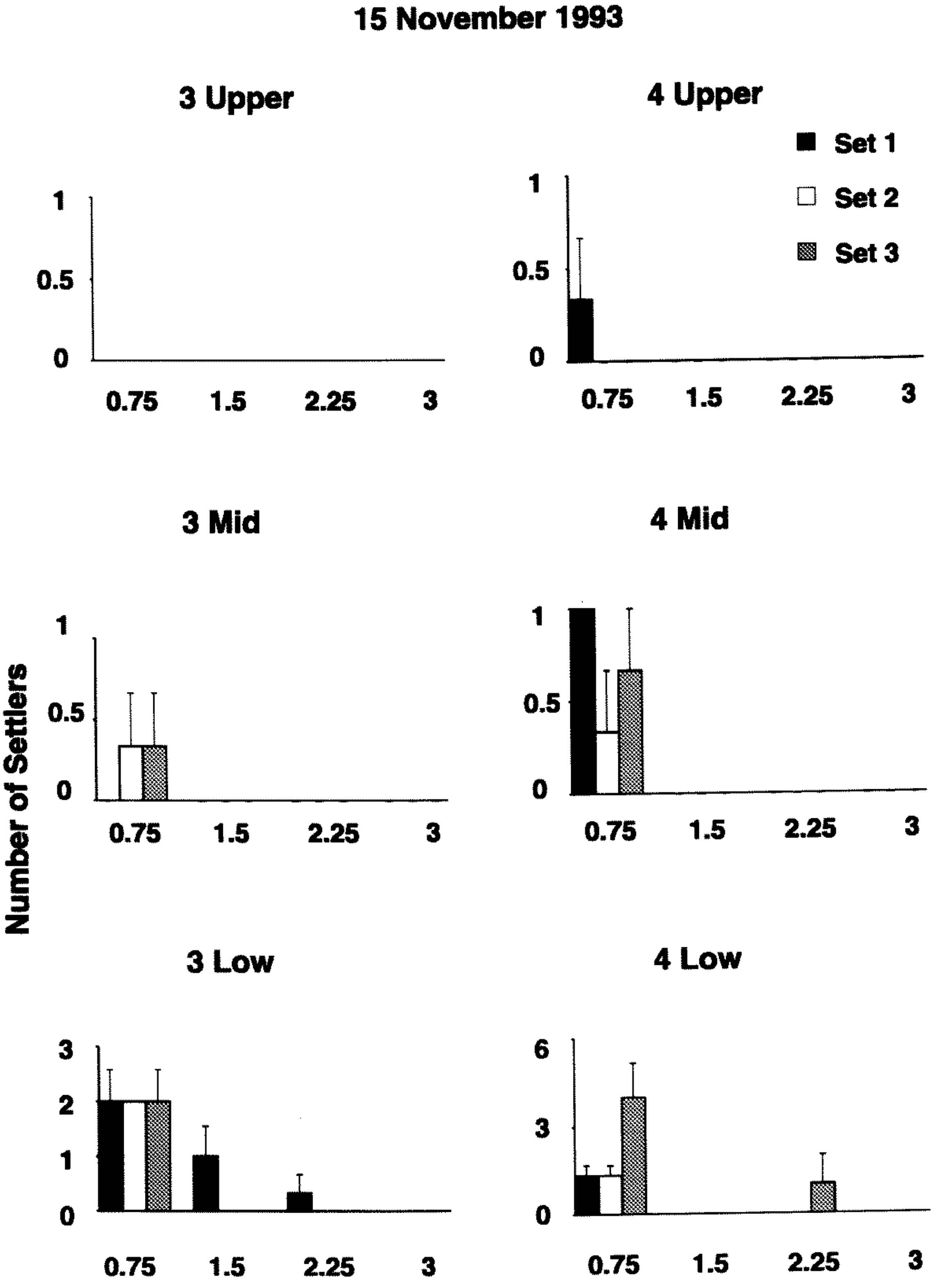

Fig. 4.2

Mean numbers of new settlers in each 0.75 cm x 0.75 cm quadrat (n = 3) at varying distances from adults (0.75 cm, 1.5 cm, 2.25 cm, 3 cm) in three sets of 6 cm cleared patches each on Low, Mid and Upper Heights at Sites 3 and 4 on 15th November, 1993 after a major settlement. No settlement was recorded at Site 3 Upper.

Barnacle Extract

Barnacle Extract and Settlers Removed Daily

In 1991 and 1992, more settlers were recorded in 6 cm than 3 cm than 1.5 cm patches (Figs. 4.3 - 4.5). From 1991 to 1993, there was no obvious induction of settlement of larvae due to extract of adults in 6 cm patches within *Chamaesipho's* distribution. Although many sets of 6 cm patches (9 of 18) painted with extract in separate experiments from 1991 to 1993 had more mean total settlers, these numbers were not significantly different from mean total numbers of larvae settled on unpainted patches (Table 4.2). Only two sets of 6 cm patches (1991, Site 4 Upper; 1993, Site 4 Low) had significantly greater numbers of settled barnacles on painted than unpainted patches (Fig. 4.3; Table 4.2). Barnacle extract did not appear to influence settlement when total settlers were divided by the area of patch (Fig. 4.6; Table 4.3).

Total settlers in patches of different diameters (6 cm, 3 cm, 1.5 cm) each year were multiplied by Perimeter/Surface Area ratios. Despite various interactions (Table 4.4), there were generally more settlers in 1991 than in 1992 in the smallest patches Low on the shore. Barnacle extract had some effect on settlement in these different-sized patches, especially in the smallest (1.5 cm) patches (Fig. 4.7; Table 4.4).

Barnacle Extract and Settlers Not Removed

When barnacle extract was applied to 6 cm patches Low on the shore at Sites 3 and 4 in 1991 and 1992 and settlers were not removed daily, there were mixed results. In 1991, more total settlers were recorded on patches minus extract at Site 3 Low. In contrast, there was no effect of the presence or absence of extract on settlement in Site 4 Low. In 1992, only at Site 4, Low on the shore, was there a positive influence of the barnacle extract: more total settlers were recorded on painted than on unpainted patches. Even though there was no significant difference between numbers of barnacles in painted and unpainted patches at Site 4 Low in 1991 and Site 3 Low in 1992, more settlers were recorded on painted patches (Table 4.5).

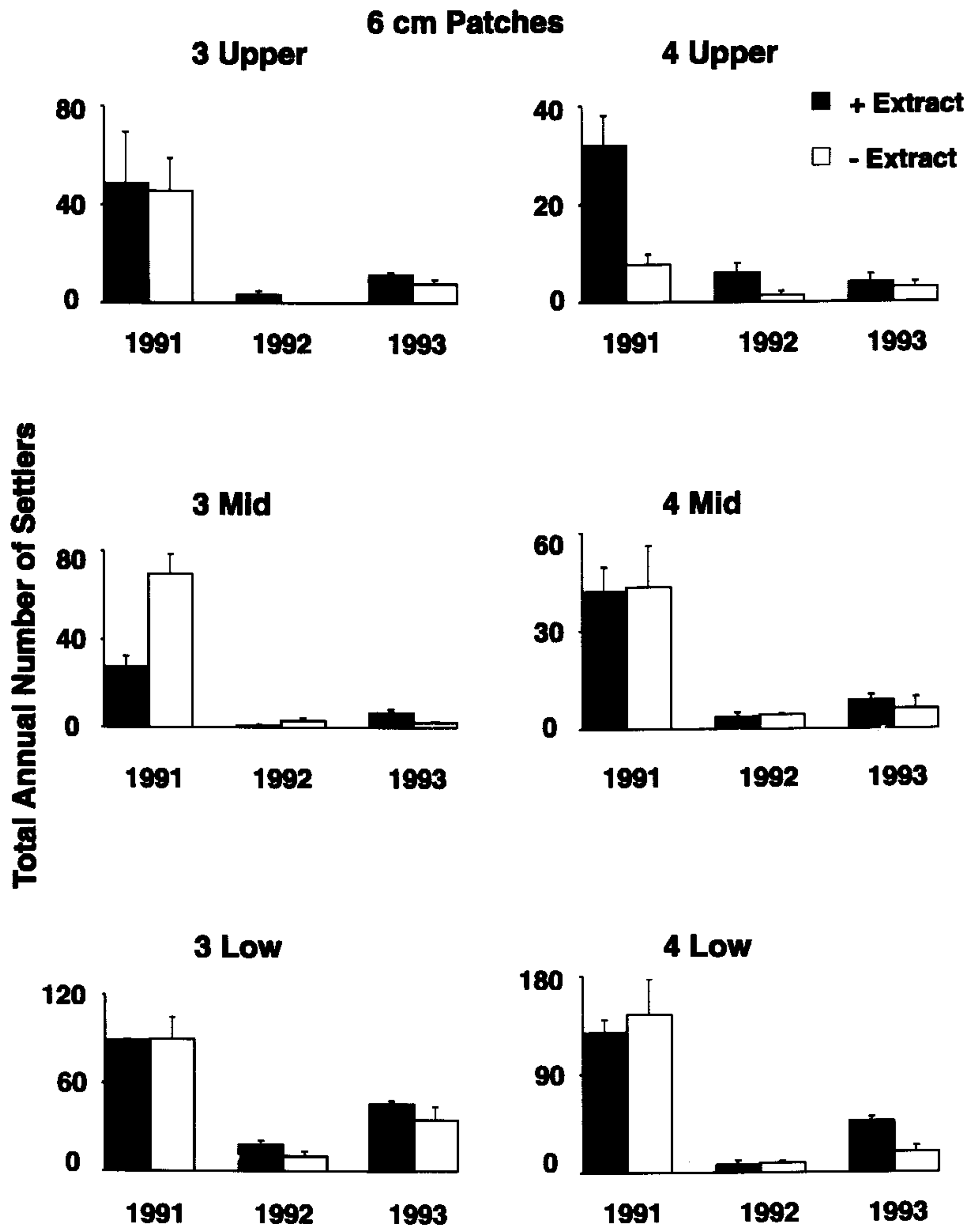

Fig. 4.3

Mean total annual numbers of settlers in 6 cm patches painted with barnacle extract ■ and in patches left unpainted □ ($n = 3$) at Sites 3 and 4 and Low, Mid and Upper heights of *Chamaesipho's* distribution. Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991, 1992 and 1993.

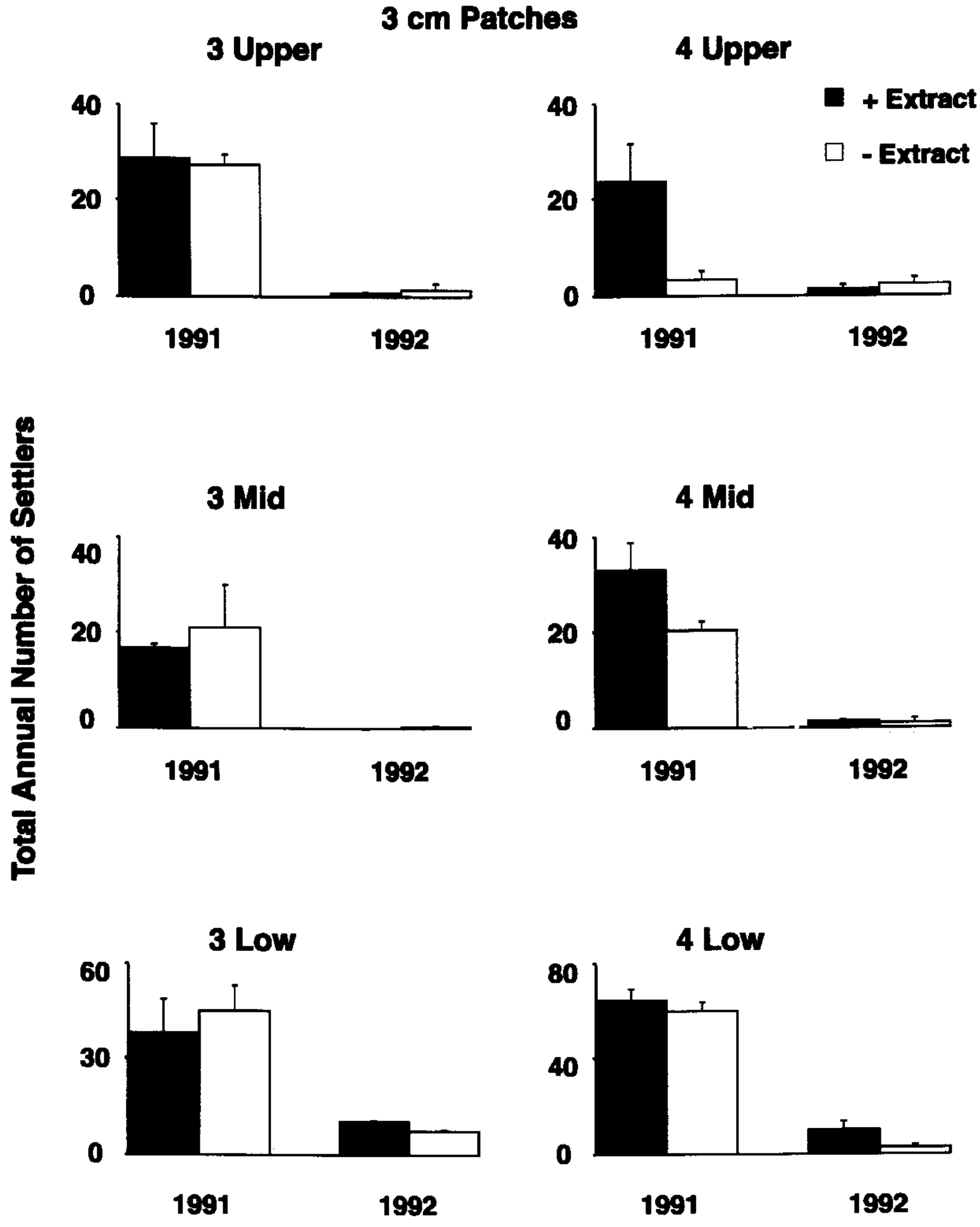

Fig. 4.4

Mean total annual numbers of settlers in 3 cm patches painted with barnacle extract ■ and in patches left unpainted □ ($n = 3$) at Sites 3 and 4 and Low, Mid and Upper heights of *Chamaesipho's* distribution. Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991 and 1992.

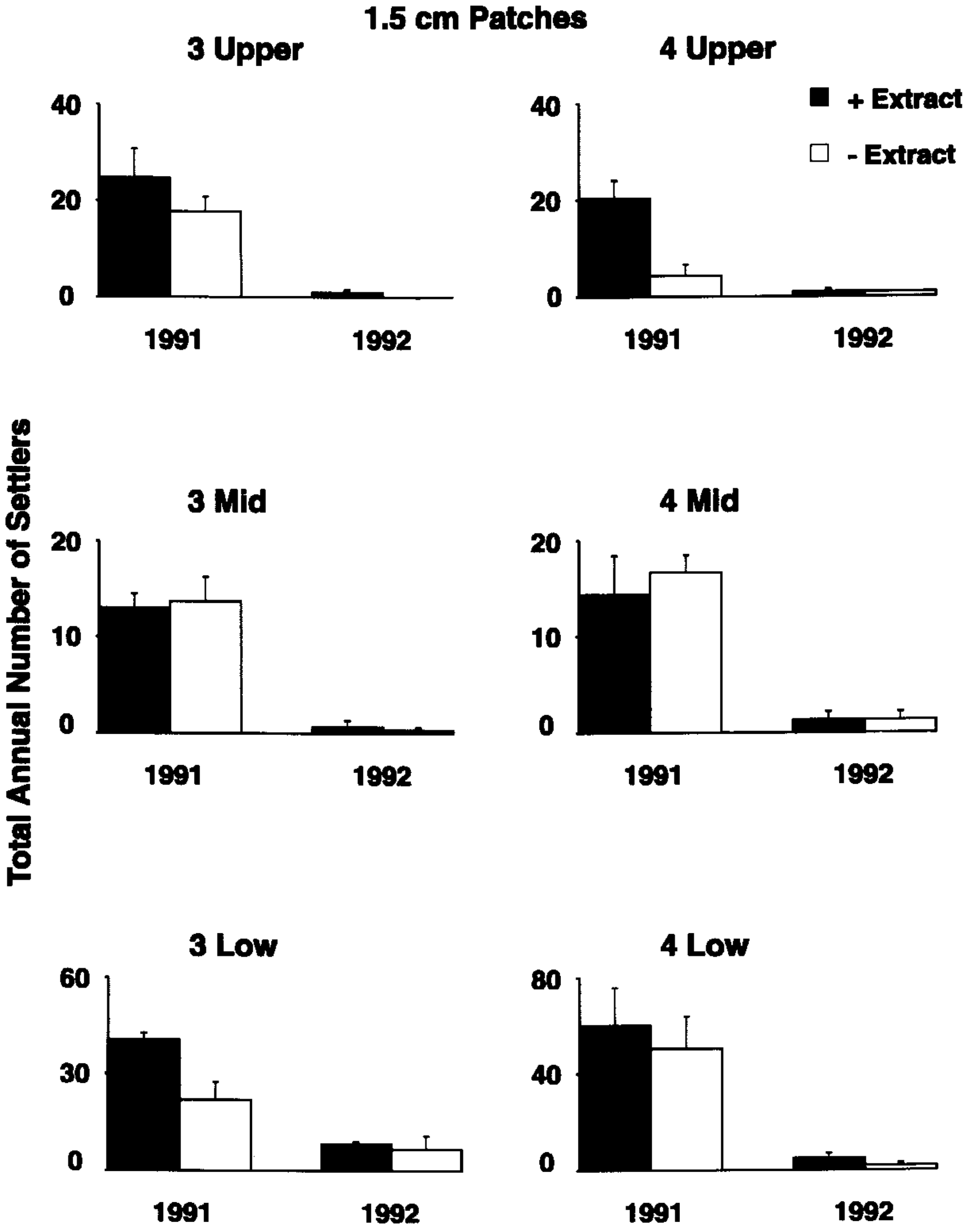

Fig. 4.5

Mean total annual numbers of settlers in 1.5 cm patches painted with barnacle extract ■ and in patches left unpainted □ ($n = 3$) at Sites 3 and 4 and Low, Mid and Upper heights of *Chamaesipho's* distribution. Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991 and 1992.

Table 4.2

χ^2 Analysis of total annual numbers of settlers in cleared 6 cm patches painted with barnacle extract (+) and in cleared unpainted patches (–) ($n = 3$) at three heights (Low, Mid, Upper) of *Chamaesipho's* distribution at Sites 3 and 4. Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991, 1992 and 1993.

	1991				1992				1993			
	+	–	χ^2(1df)	p	+	–	χ^2(1df)	p	+	–	χ^2(1df)	p
3 Low	89.00	89.67	0.003	> 0.95 ns	17.67	10.00	2.120	> 0.1 ns	45.33	35.00	1.330	> 0.1 ns
3 Mid	27.67	69.67	18.120	< 0.005 *	1.00	3.00	1.000	> 0.25 ns	6.67	2.33	2.090	> 0.1 ns
3 Upper	48.67	45.67	0.130	> 0.5 ns	3.33	0.00	3.360	> 0.05 ns	11.33	7.67	0.710	> 0.25 ns
4 Low	128.00	144.67	1.020	> 0.25 ns	7.00	8.67	0.179	> 0.5 ns	46.67	18.33	12.360	< 0.005 *
4 Mid	42.00	43.33	0.020	> 0.9 ns	3.67	4.33	0.054	> 0.75 ns	8.67	6.00	0.490	> 0.25 ns
4 Upper	32.00	7.67	14.940	< 0.005 *	6.00	1.33	2.960	> 0.05 ns	4.00	3.00	0.140	> 0.5 ns

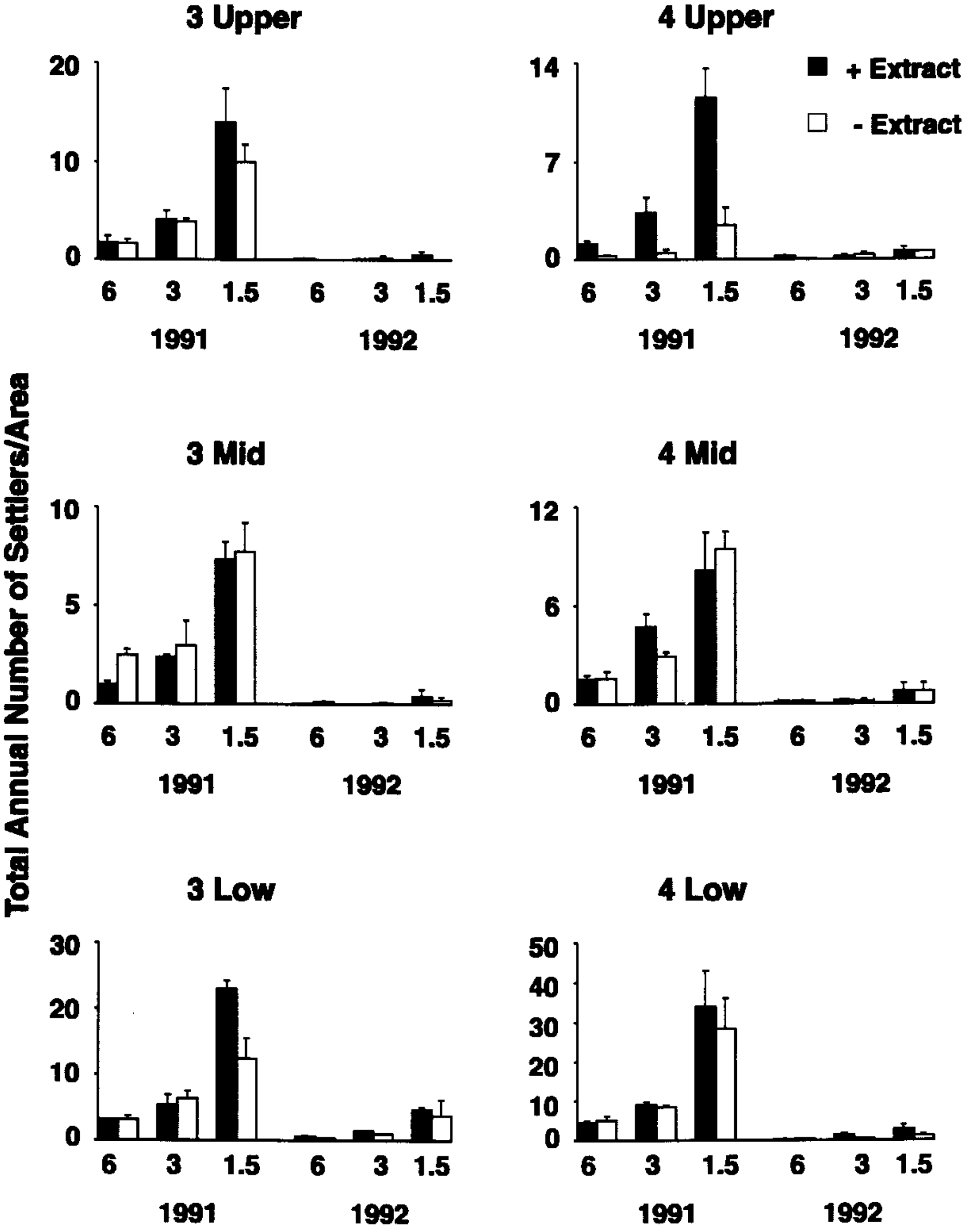

Fig. 4.6

Mean Total Numbers of Settlers/Surface Area of Patch in different-sized patches (6 cm, 3 cm, 1.5 cm) painted with barnacle extract or left unpainted ($n = 3$) at Sites 3 and 4 on Low, Mid and Upper heights of *Chamaesipho's* distribution. Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991 and 1992.

Table 4.3

Analysis of Mean Total Numbers of Settlers/Surface Area of Patch in different-sized patches (6 cm, 3 cm, 1.5 cm) painted with barnacle extract or left unpainted ($n = 3$). Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991 and 1992. Transformation could not stabilise the variances. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data untransformed; Cochran's test, C = 0.40, $p < 0.01$

Source	df	MS	*F*	*p*
Time = T	1	2118.53	66.46	ns
Site = S	1	18.31	2.17	ns
Height = H	2	462.75	7.12	ns
Patch = P	2	847.50	98.66	*
Extract = E	1	51.37	20.00	ns
TxS	1	31.88	3.79	ns
TxH	2	231.88	2.08	ns
TxP	2	574.30	34.42	*
TxE	1	26.18	12.81	ns
SxH	2	64.96	7.72	***
SxP	2	8.59	1.02	ns
SxE	1	2.57	0.31	ns
HxP	4	139.73	6.71	*
HxE	2	17.59	4.70	ns
PxE	2	35.10	15.14	ns
TxSxH	2	111.58	13.25	***
TxSxP	2	16.69	1.98	ns
TxSxE	1	2.04	0.24	ns
TxHxP	4	71.57	1.81	ns
TxHxE	2	11.34	1.80	ns
TxPxE	2	23.39	14.96	ns
SxHxP	4	20.83	2.47	*
SxHxE	2	3.75	0.44	ns
SxPxE	2	2.32	0.28	ns
HxPxE	4	12.43	5.66	ns
TxSxHxP	4	39.45	4.69	**
TxSxHxE	2	6.29	0.75	ns
TxSxPxE	2	1.56	0.19	ns
TxHxPxE	4	9.53	2.84	ns
SxHxPxE	4	2.19	0.26	ns
TxSxHxPxE	4	3.36	0.40	ns
Residual	144	8.42		

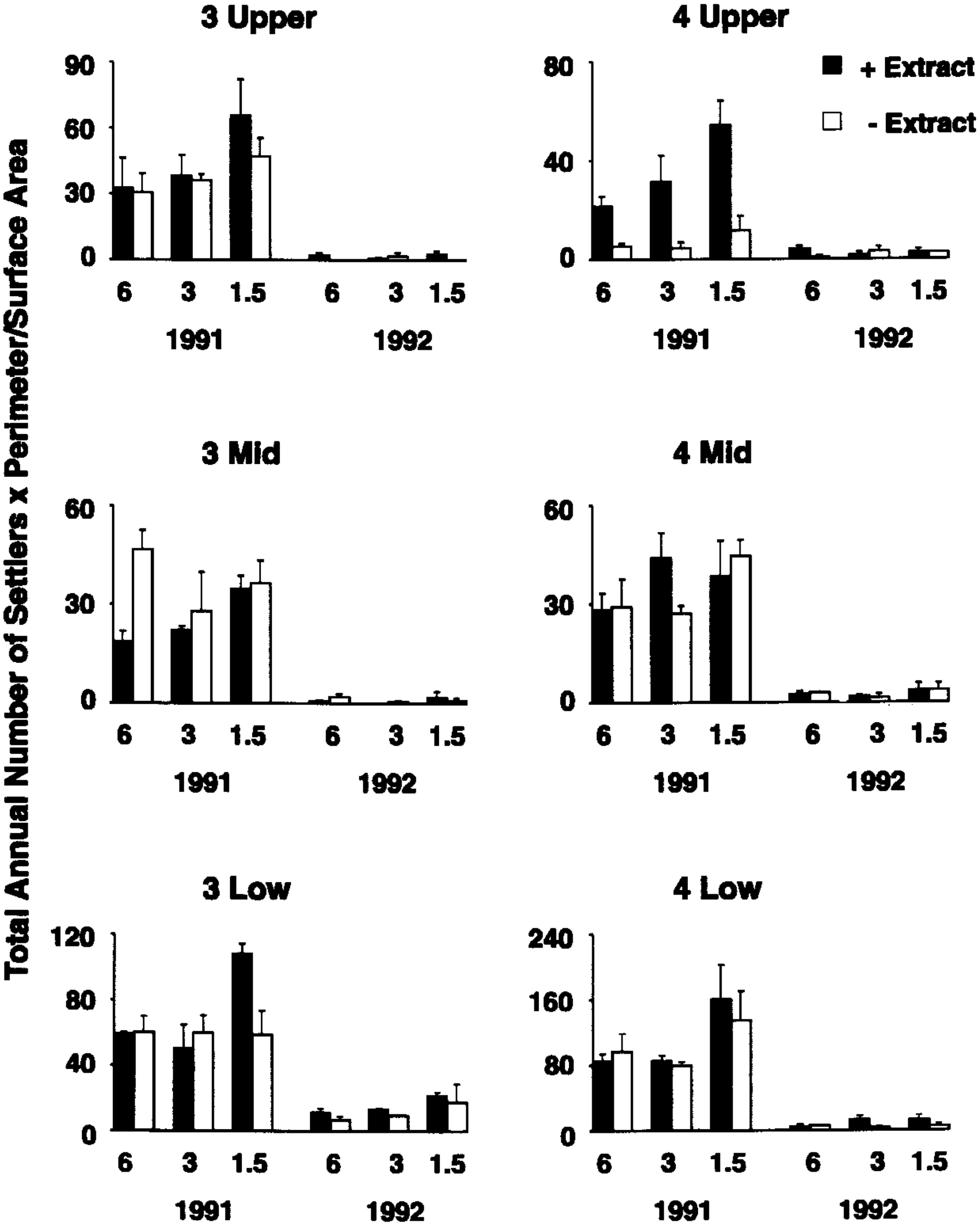

Fig. 4.7

Mean Total Numbers of Settlers x Perimeter/Surface Area ratio for different-sized patches (6 cm, 3 cm, 1.5 cm) painted with barnacle extract or left unpainted ($n = 3$) at Sites 3 and 4 on Low, Mid and Upper heights of *Chamaesipho's* distribution. Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991 and 1992.

Table 4.4

Analysis of Mean Total Numbers of Settlers x Perimeter/Surface Area ratio for different-sized patches (6 cm, 3 cm, 1.5 cm) painted with barnacle extract or left unpainted ($n = 3$). Settlers were removed daily. Experiments were renewed each year and data are totals in December in 1991 and 1992. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $(x + 1)^{0.5}$; Cochran's test, $p > 0.05$

Source	df	MS	*F*	*p*
Time = T	1	1140.04	3238.66	*
Site = S	1	0.16	0.14	ns
Height = H	2	167.17	14.16	ns
Patch = P	2	19.06	100.06	**
Extract = E	1	14.46	3.01	ns
TxS	1	0.35	0.31	ns
TxH	2	24.33	0.68	ns
TxP	2	7.92	14.47	ns
TxE	1	1.30	0.26	ns
SxH	2	11.80	10.23	***
SxP	2	0.19	0.17	ns
SxE	1	4.80	4.16	*
HxP	4	1.95	5.84	ns
HxE	2	7.55	3.46	ns
PxE	2	3.61	2.28	ns
TxSxH	2	35.58	30.84	***
TxSxP	2	0.55	0.47	ns
TxSxE	1	4.89	4.24	*
TxHxP	4	1.27	1.35	ns
TxHxE	2	5.09	1.29	ns
TxPxE	2	1.86	3.81	ns
SxHxP	4	0.33	0.29	ns
SxHxE	2	2.18	1.89	ns
SxPxE	2	1.58	1.37	ns
HxPxE	4	1.33	1.92	ns
TxSxHxP	4	0.93	0.81	ns
TxSxHxE	2	3.95	3.42	*
TxSxPxE	2	0.49	0.42	ns
TxHxPxE	4	1.21	1.80	ns
SxHxPxE	4	0.69	0.60	ns
TxSxHxPxE	4	0.67	0.58	ns
Residual	144	1.15		

Table 4.5

Analysis of mean total numbers of settlers in 6 cm patches painted with barnacle extract (+) and in unpainted patches (–) ($n = 3$). Settlers were not removed daily. Experiments were renewed each year and data are annual totals in December in 1991 and 1992.

	1991				1992			
	+	–	χ^2 (1df)	*p*	+	–	χ^2 (1df)	*p*
3 Low	22.67	57.00	14.80	< 0.005 *	11.67	4.00	3.77	> 0.05 ns
4 Low	17.00	14.67	0.17	> 0.5 ns	12.00	3.00	5.40	< 0.025 *

Barnacle Extract Above the Distribution of *Chamaesipho tasmanica*

The total numbers of settlers recorded for six consecutive days during new and full moons from July to December were pooled from separate experiments in 1991 and 1992. Data are mean total numbers of settlers recorded in each 2 cm diameter patch ($n = 3$) painted or unpainted with barnacle extract above the limit of distribution of *Chamaesipho* at Sites 3 and 4 over two years. No settlers were recorded on unpainted patches at either site in 1991 and 1992 and there were more settlers in patches painted with barnacle extract at Site 3 than at Site 4. Very few larvae settled above the distribution of adult *Chamaesipho* (Fig. 4.8).

New Settlers/New Recruits

Peaks of Settlement

Numbers of settlers were recorded daily from two tidal cycles. Daily records of settlement over 7-8 day periods during new and full moons from late October to late December 1990, from late July to early December 1991 and from August to the end of December 1992 demonstrated that there was typically a series of minor settlements followed by a major peak (Fig. 4.9). Few barnacles arrived each day on experimental plots until major settlement occurred near new and full moons. These peaks of settlement were recorded on 3rd, 12th, and 18th November, 1990, 8th September and 8th November, 1991 and on 10th September, 1992 (Figs. 4.9, 4.10).

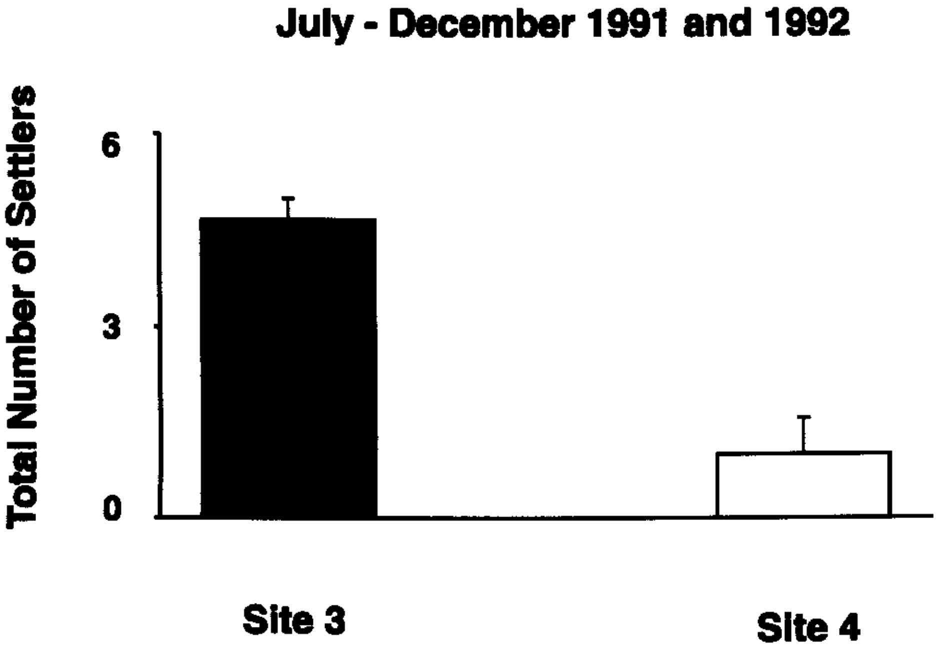

Fig. 4.8

Mean total numbers of settlers from July to December, 1991 and 1992, in each 2 cm patch ($n = 3$) painted with barnacle extract above the Upper limit of distribution of *Chamaesipho* at Sites 3 and 4. No settlers were recorded in unpainted patches.

During peaks of settlement, numbers of barnacles settling on 2.5 cm plots where previous settlers were removed (Removals) did not differ from plots where previous arrivals were present (Controls). The presence of new settlers and recruits did not influence settlement of cyprid larvae (Fig. 4.10; Table 4.6).

Total Annual Settlement

Analysis of peaks of settlement showed that there was no difference in the numbers of settlers on Removal or Control treatments, that is, new settlers and recruits did not enhance further settlement of larvae (Fig. 4.10; Table 4.6). Different results were obtained when total numbers of settlers on Removals and Controls in each experiment in each year from 1990 to 1992 were compared. Generally, total

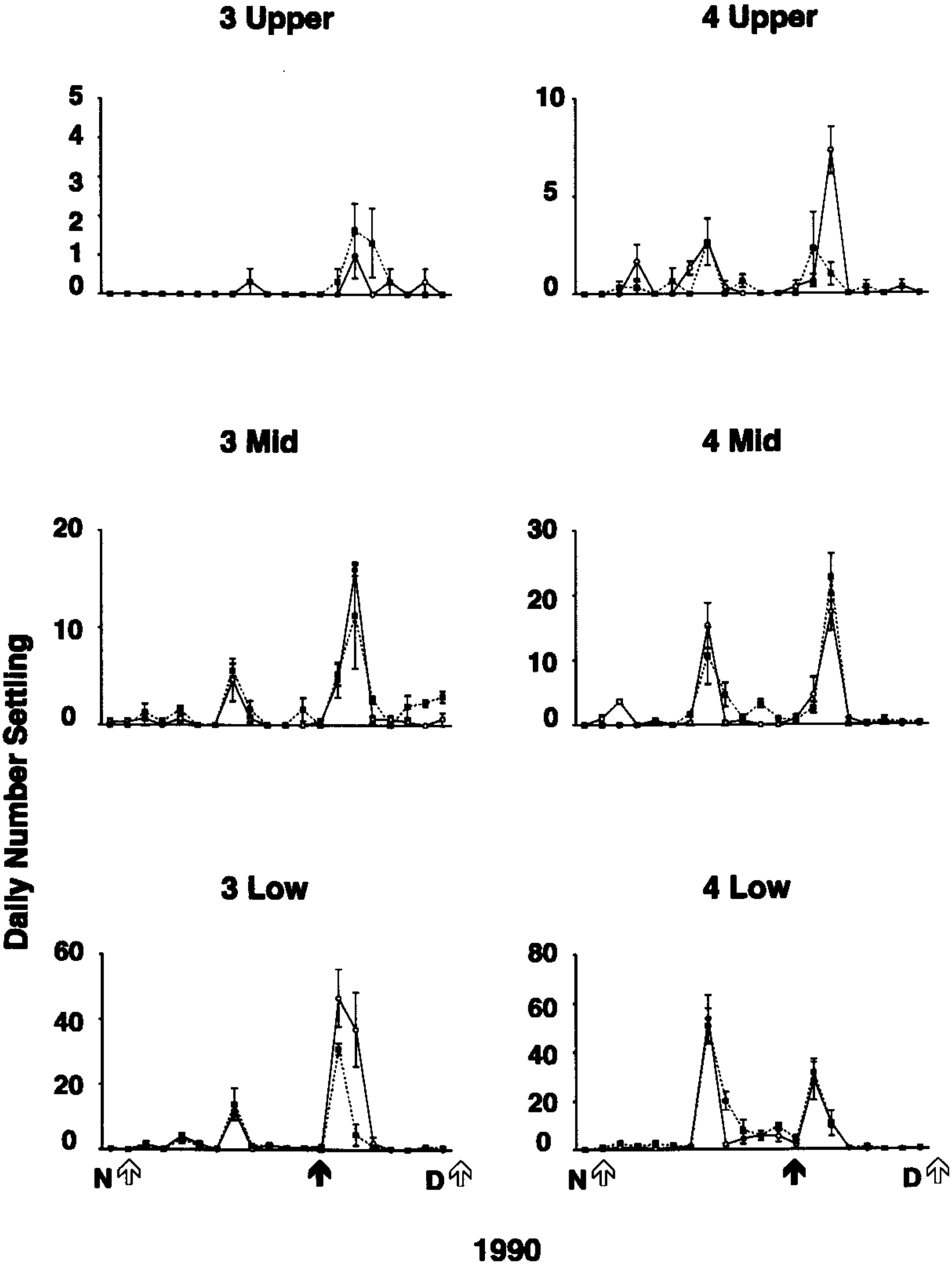

Fig. 4.9

Daily record of mean numbers of new settlers on Removal and Control treatments (n = 3) from late October to early December, 1990 during new (⬆) and full (⇧) moons. —: numbers of new settlers on Removals; – –: numbers of new settlers on Controls.

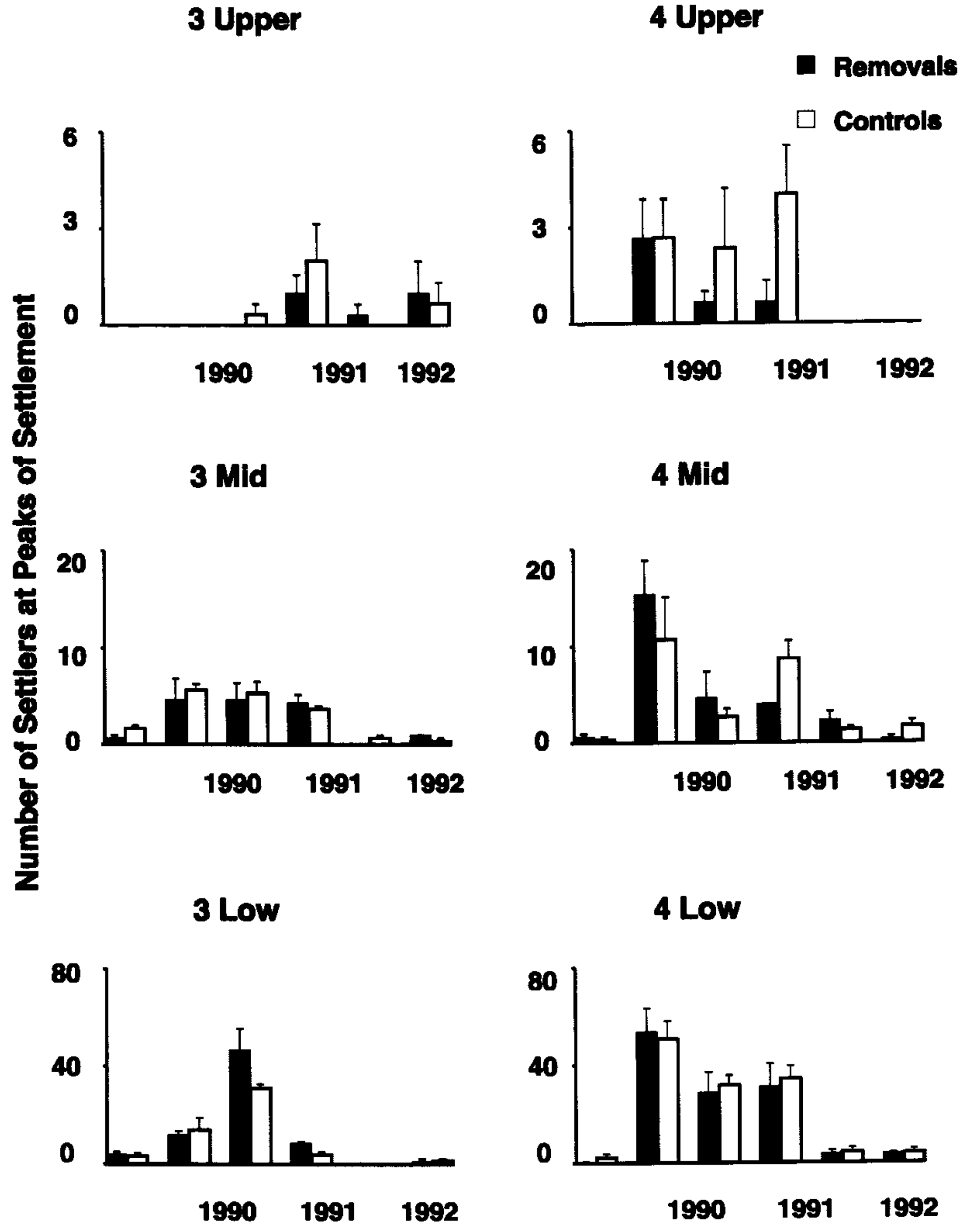

Fig. 4.10

Mean numbers of barnacles settling in ■ Removal versus □ Control 2.5 cm patches ($n = 3$) at Sites 3 and 4 and Low, Mid and Upper heights of the distribution of *Chamaesipho* during peaks of settlement on 3rd, 12th and 18th November, 1990, 8th September and 8th November, 1991, and 10th September, 1992.

Table 4.6

Analysis of numbers of barnacles settling in peaks in 2.5 cm Removal/Control patches ($n = 3$) at two randomly chosen sites (Sites 3 and 4) and three heights on the shore within *Chamaesipho's* distribution. Experiments were renewed each year and data are from peaks on 3rd, 12th and 18th November, 1990, 8th September and 8th November, 1991 and 10th September, 1992. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $\text{Log}_e(x + 1)$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	5	19.15	6.98	*
Height = H	2	51.71	62.50	*
Site = S	1	6.73	34.28	***
Removal versus Control = RC	1	0.21	0.72	ns
T x H	10	3.39	4.01	*
T x S	5	2.74	13.98	***
T x RC	5	0.13	0.37	ns
H x S	2	0.83	4.22	*
H x RC	2	0.22	0.87	ns
S x RC	1	0.30	1.52	ns
T x H x S	10	0.85	4.32	***
T x H x RC	10	0.19	0.71	ns
T x S x RC	5	0.35	1.76	ns
H x S x RC	2	0.25	1.29	ns
T x H x S x RC	10	0.27	1.36	ns
Residual	144	0.20		

numbers of settlers were greater on Controls than Removals. This indicates that there was a gregarious response to previously settled older barnacles (Fig. 4.11; Table 4.7).

4.3 Interaction between Exposure to Adults and Presence of Juveniles

4.3.1 Experimental Method and Design

Exposure to Adults and Presence of Juveniles

In July 1991, 1992 and 1993, 6 cm diameter patches were cleared on the substratum at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**) at each Low, Mid and Upper height of *Chamaesipho's* distribution. 3 cm and 1.5 cm patches were also cleared, but only in July 1991 and 1992. In half of these patches settlers were removed daily during the lunar sampling period, and settlers were not removed in the remaining patches (Removal versus Control Treatments). Numbers of barnacles that settled in all of these patches were recorded until December of each year of the experiment.

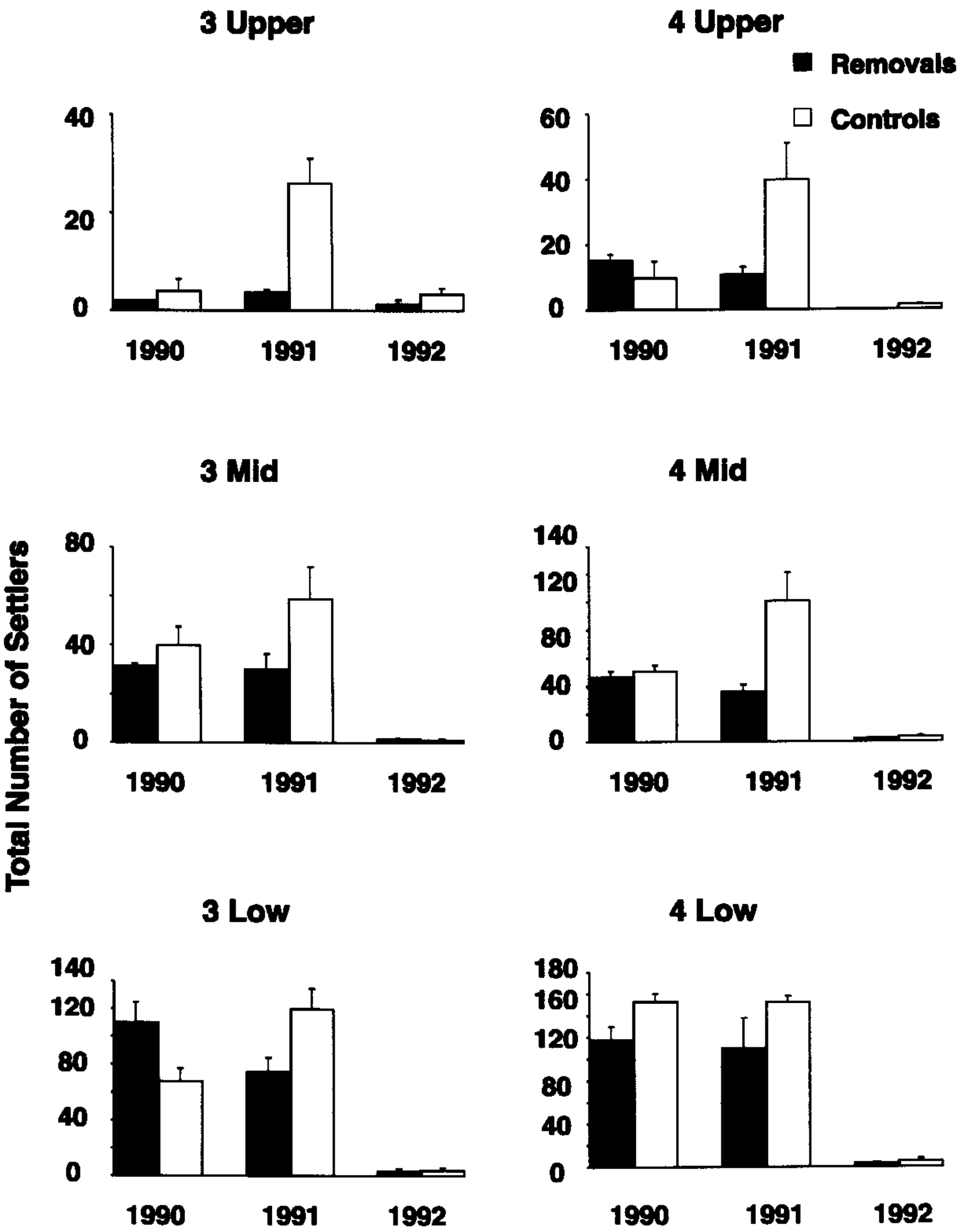

Fig. 4.11

Mean total numbers of barnacles settling in ■ Removal versus □ Control 2.5 cm patches ($n = 3$) at two randomly chosen sites (Sites 3 and 4) and three heights on the shore within *Chamaesipho's* distribution in December, 1990 to 1992. No settlement was recorded in 4 Upper Removal replicates in 1992.

Table 4.7

Analysis of total numbers of barnacles settling in 2.5 cm Removal/Control patches ($n = 3$) at two randomly chosen sites (Sites 3 and 4) and three heights on the shore within *Chamaesipho's* distribution. Experiments were renewed each year and data are totals in December in 1990, 1991 and 1992. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $(x + 1)^{0.5}$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	2	336.04	50.25	*
Height = H	2	216.85	386.17	**
Site = S	1	28.10	33.90	***
Removal versus Control = RC	1	26.21	14.01	ns
T x H	4	43.06	69.96	***
T x S	2	6.69	8.07	***
T x RC	2	20.15	319.29	**
H x S	2	0.56	0.68	ns
H x RC	2	0.51	0.30	ns
S x RC	1	1.87	2.26	ns
T x H x S	4	0.62	0.74	ns
T x H x RC	4	0.43	0.19	ns
T x S x RC	2	0.06	0.08	ns
H x S x RC	2	1.72	2.07	ns
T x H x S x RC	4	2.31	2.78	*
Residual	72	0.83		

Total numbers of settlers in these different-sized patches (Patch Treatments) in each experiment in 1991 and 1992 were compared. To account for a possible gregarious response to adults along the edges of different-sized patches when settling, data were standardised by multiplying numbers of settlers by Perimeter/Surface Area ratios.

4.3.2 Results

Exposure to Adults and Presence of Juveniles

Total Annual Settlement

Settlers were removed from patches of different diameter (6 cm, 3 cm, 1.5 cm) and total numbers of settlers in December for each year were compared (Fig. 4.12; Table 4.8). Mixed results were obtained for Removal/Control treatments. In 1991 Low on the shore at Site 3 and at Upper heights in Site 4, more settlers were recorded on Controls than on Removals in all patches. In contrast, in 1992 there were more settlers on Removals at Site 3 Low in all patches. At all other times, sites and heights, numbers settling on all Removal and Control patches were similar. Overall, there was generally a decreased gradient in numbers of settlers as patch size decreased (6 cm > 3 cm > 1.5 cm). When numbers of settlers from different-sized patches were compared, generally, more settlers were recorded on Removal patches than on Control patches. That is, while the presence of juveniles did not enhance settlement (Fig. 4.10; Table 4.6), older recruits also did not appear to induce settlement in different-sized patches in this experiment in 1991 and 1992 (Fig. 4.12; Table 4.8).

χ^2 analysis of 6 cm Removal and Control patches in 1991, 1992 and 1993 also showed mixed results. In 1991 and 1992, more settlers were again recorded on Removals than on Controls. In contrast, in 1993, only on Control patches at Site 4 on Low and Mid heights on the shore were greater numbers of barnacles recorded settling (Table 4.9).

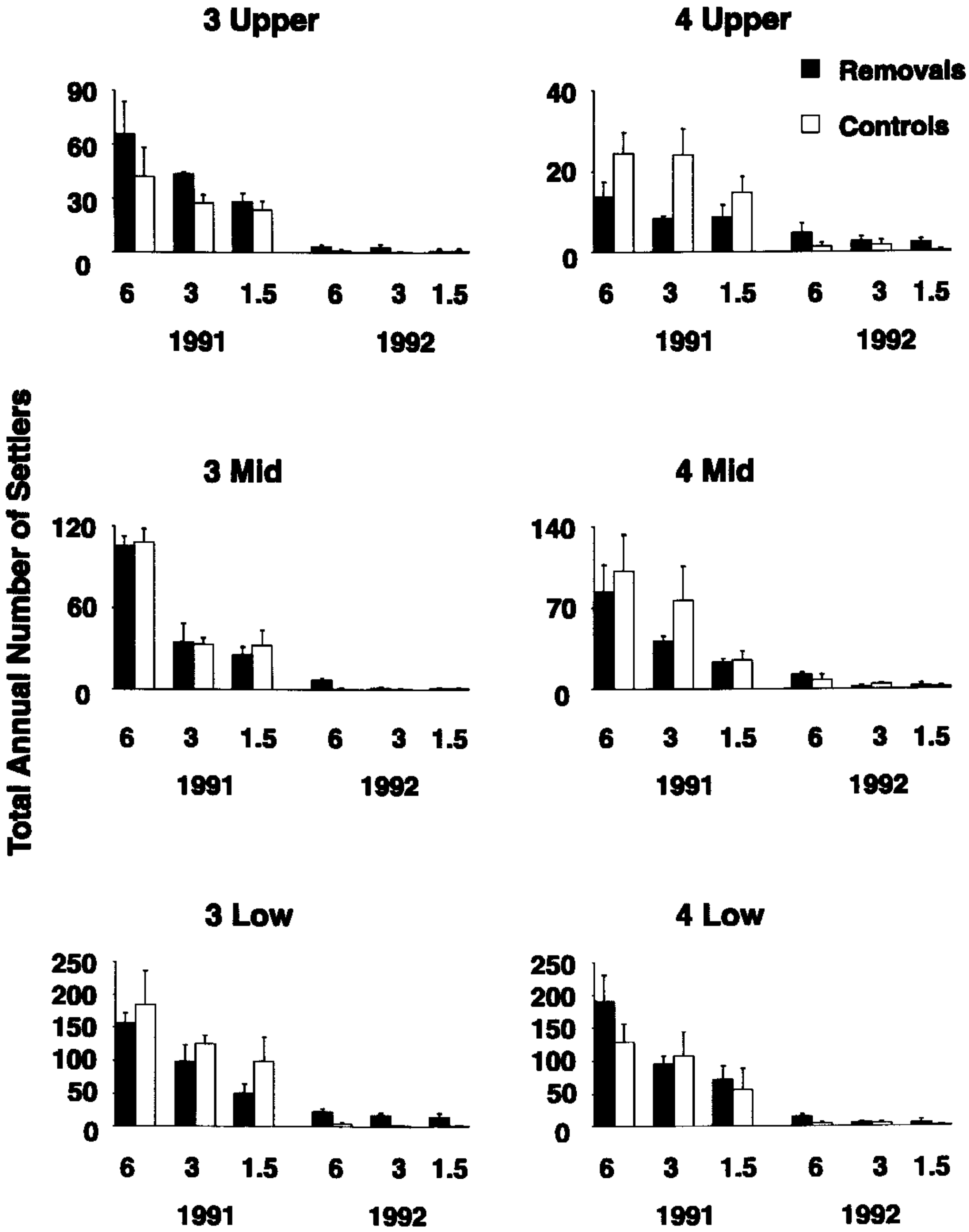

Fig. 4.12

Mean total annual numbers of barnacles settling in ■ Removal versus □ Control patches ($n = 3$) of different size (6 cm, 3 cm, 1.5 cm) at Sites 3 and 4 on Low, Mid and Upper heights of *Chamaesipho's* distribution in December, 1991 and 1992.

Table 4.8

Analysis of total annual numbers of barnacles settling in different-sized patches (6 cm, 3 cm, 1.5 cm) on which settlers were removed (Removals) or not removed (Controls) ($n = 3$) at Sites 3 and 4 on Low, Mid and Upper heights of *Chamaesipho's* distribution. Experiments were renewed each year and data are totals in December in 1991 and 1992. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $(x + 1)^{0.5}$; Cochran's test, $p > 0.05$

Source	df	MS	*F*	*p*
Time = T	1	1581.61	124.34	ns
Site = S	1	8.50	4.35	*
Height = H	2	192.71	20.69	*
Patch = P	2	89.36	79.29	*
Removal/Control = RC	1	4.34	1.88	ns
TxS	1	12.72	6.51	*
TxH	2	75.67	11.47	ns
TxP	2	36.55	20.08	*
TxRC	1	17.79	18.59	ns
SxH	2	9.31	4.77	**
SxP	2	1.13	0.58	ns
SxRC	1	2.31	1.18	ns
HxP	4	8.13	8.32	*
HxRC	2	3.48	1.02	ns
PxRC	2	3.50	1.16	ns
TxSxH	2	6.60	3.38	*
TxSxP	2	1.82	0.93	ns
TxSxRC	1	0.96	0.49	ns
TxHxP	4	3.48	2.51	ns
TxHxRC	2	1.92	0.14	ns
TxPxRC	2	0.12	0.21	ns
SxHxP	4	0.98	0.50	ns
SxHxRC	2	3.42	1.75	ns
SxPxRC	2	3.01	1.54	ns
HxPxRC	4	0.41	1.53	ns
TxSxHxP	4	1.39	0.71	ns
TxSxHxRC	2	13.97	7.15	**
TxSxPxRC	2	0.56	0.29	ns
TxHxPxRC	4	0.45	6.93	*
SxHxPxRC	4	0.26	0.14	ns
TxSxHxPxRC	4	0.06	0.03	ns
Residual	144	1.95		

Table 4.9

χ^2 Analysis of mean total annual numbers of settlers in 6 cm patches on which new settlers have been removed (Removals) or not removed (Controls) ($n = 3$) at three heights (Low, Mid, Upper) of *Chamaesipho's* distribution at Sites 3 and 4. Experiments were renewed each year and data are totals in December in 1991, 1992 and 1993.

	1991				1992				1993			
	R	C	χ^2(1df)	p	R	C	χ^2(1df)	p	R	C	χ^2(1df)	p
3 Low	156.33	185.00	2.41	> 0.1 ns	23.33	4.67	12.44	< 0.005 *	49.33	44.33	0.27	> 0.75 ns
3 Mid	105.67	108.33	0.03	> 0.75 ns	7.00	0.66	5.25	< 0.025 *	3.33	7.33	1.50	> 0.1 ns
3 Upper	66.00	42.33	5.18	< 0.025 *	3.33	1.00	1.27	> 0.25 ns	10.00	1.33	6.64	< 0.01 *
4 Low	191.00	128.67	12.16	< 0.005 *	14.67	4.33	5.63	< 0.025 *	26.00	50.33	7.76	< 0.01 *
4 Mid	83.67	101.33	1.69	> 0.1 ns	12.33	8.00	0.93	> 0.25 ns	11.00	24.00	4.83	< 0.05 *
4 Upper	13.67	24.33	2.99	> 0.05 ns	4.67	1.33	1.86	> 0.1 ns	4.33	4.66	0.01	> 0.9 ns

Total Annual Settlers x Perimeter/Surface Area

Total settlers in 1991 and 1992 were multiplied by Perimeter/Surface Area ratios to account for the influence on settlement of different relative exposure to adults along perimeters. At Mid and Upper heights, where fewer settlers were recorded, numbers that settled on different-sized patches were similar. At Low heights, however, there was a decreasing gradient in abundance of settlers with increasing patch size (1.5 cm > 3 cm > 6 cm). Even though data were standardised, most settlers were recorded in the smallest patches. This suggests that bordering adults may provide cues for settlement because the smallest patches had the greatest relative exposure to adults along their perimeters. Inconclusive results were again obtained for Removal/Control treatments and only patches at Site 3 Low had more settlers on Control patches. The presence of older recruits did not appear to induce settlement in different-sized patches in this experiment (Table 4.10).

4.4 Discussion

Once larvae arrive, larval choice will modify the numbers that settle in response to particular environmental cues (Crisp & Meadows, 1962, 1963; Wethey, 1984, 1986a, 1986b; Raimondi, 1988a, 1988b, 1990, 1991; Dineen & Hines, 1992, 1994a, 1994b; Keough & Raimondi, 1995). Gregariousness is implicated in determining distributions of juvenile *Chamaesipho* because a strong relationship was found between annual total settlers and annual total adults from the end of 1989 to the end of 1993. In fact, most settlement occurred close to adults. Settlement was not induced by the presence of other new settlers, but, as these settlers aged, settlement was enhanced. Barnacle extract painted on the substratum above the distribution of adults also elicited a response by settlers. Also, when numbers of settlers from different-sized patches were standardised to account for exposure to adults along perimeters, generally, most barnacles settled in the smallest patches.

Sousa (1985) emphasised that the ratio of perimeters to surface areas of patches varied with different patch sizes and that smaller patches have greater ratios of perimeters to areas. Raimondi (1990) also stated that perimeters of adults are important in determining settlement of gregarious larvae. When different-sized

Table 4.10

Analysis of total annual settlers x Perimeter/Surface Area ratios in different-sized patches (6 cm, 3 cm, 1.5 cm) on which settlers were removed (Removals) or not removed (Controls) ($n = 3$) at Sites 3 and 4 on Low, Mid and Upper heights of *Chamaesipho's* distribution. Experiments were renewed each year and data are totals x Perimeter/Surface Area per patch in December in 1991 and 1992. Transformation could not stabilise the variances, Cochrans test, C = 0.11. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data untransformed; Cochran's test, $p < 0.05$

Source	df	MS	*F*	*p*
Time = T	1	322537.35	125.49	ns
Site = S	1	3192.12	2.34	ns
Height = H	2	68511.84	42.66	*
Patch = P	2	7046.22	8.38	ns
Removal/Control = RC	1	296.29	1.74	ns
TxS	1	2570.25	1.88	ns
TxH	2	48850.63	49.71	*
TxP	2	4743.78	7.30	ns
TxRC	1	3833.12	3.52	ns
SxH	2	1606.13	1.18	ns
SxP	2	841.07	0.62	ns
SxRC	1	169.92	0.12	ns
HxP	4	2596.01	8.59	*
HxRC	2	268.40	0.09	ns
PxRC	2	546.12	0.31	ns
TxSxH	2	982.80	0.72	ns
TxSxP	2	650.27	0.48	ns
TxSxRC	1	1088.29	0.80	ns
TxHxP	4	1519.67	5.12	ns
TxHxRC	2	1221.34	0.21	ns
TxPxRC	2	808.43	0.52	ns
SxHxP	4	302.06	0.22	ns
SxHxRC	2	3062.79	2.24	ns
SxPxRC	2	1759.20	1.29	ns
HxPxRC	4	189.66	0.47	ns
TxSxHxP	4	296.97	0.22	ns
TxSxHxRC	2	5754.91	4.22	*
TxSxPxRC	2	1544.17	1.13	ns
TxHxPxRC	4	532.76	0.78	ns
SxHxPxRC	4	401.69	0.29	ns
TxSxHxPxRC	4	682.26	0.50	ns
Residual	144	1365.25		

patches (6 cm, 3 cm, 1.5 cm) were painted with barnacle extract and settlers were removed daily, the greatest colonisation was always recorded in the smallest patches when data were standardised by dividing by patch Area and by multiplying by Perimeter/Surface Area ratios. Only when data were standardised by incorporating

Perimeter in the formula was barnacle extract seen to induce settlement. The degree of exposure to other barnacles along perimeters of patches, rather than the amount of space available, should therefore determine settlement of larvae in different-shaped patches and may also have influenced settlement in this study when patches were painted with extract.

Some inconsistent results were obtained with respect to settlement in different-sized patches (6 cm, 3 cm, 1.5 cm) when data were standardised by multiplying by appropriate Perimeter/Surface Area ratios. When barnacle extract was painted on the substratum, as patch size decreased, greatest colonisation of settlers occurred in smallest patches which had the largest relative perimeters exposed to adults. That is, cues from adults on perimeters of plots seemed to override cues from the barnacle extract. When barnacles were removed or not removed from different-sized unpainted patches and data were again standardised by including perimeter in the formula, in areas of greatest settlement, Low on the shore, most settlers were recorded in smallest 1.5 cm patches and least numbers in largest 6 cm patches. At Mid and Upper heights, where there were fewer barnacles, there was no difference in settlement among patch sizes. These disparate results for settlement in different patch sizes suggest that, while adults on the fringe of patches induce settlement, in some areas Low on the shore, and at Mid and Upper heights, these influences may be reduced in more sparsely populated areas due to a decreased availability of chemical cues.

While Chapter 3 has shown that larval supply and the associated processes determine larval availability of *Chamaesipho* at settlement, this chapter has shown that the numbers of barnacles settling are density-dependent and more larvae will settle where there are more adults or older recruits. That is, in this study, *Chamaesipho* cyprids settled gregariously and in decreasing numbers with increasing distance from adults. Otaiza (1989) also found a gregarious response by *Chamaesipho* to the presence of adults when settling. This study therefore corroborates his findings and emphasises that larval supply, enhanced by the gregarious response of larvae to adult conspecifics, determines distributions of juvenile populations of *Chamaesipho* at Cape Banks. While new settlers and recruits were shown not to induce settlement, a gregarious response developed with increasing time. That is, larval availability determined the numbers that settled when young barnacles occupied the substratum but, as these settlers aged, they elicited a gregarious response in settling cyprids. That is, cyprids do not act as passive particles at settlement but will actively select the habitat on which they settle. Larval choice will therefore modify the numbers of larvae that arrive and settle in response to various physical and biological cues, and, in conjunction with larval supply, larval choice is considered to have a major role in determining the abundance and distribution of *Chamaesipho*.

CHAPTER FIVE

ABUNDANCE AND DISTRIBUTION

5.1 Introduction

As discussed in Chapter 1, there are conflicting views in the literature on the relative influences of *initial settlement* (larval supply and larval choice and their associated processes) and *post-settlement mortality* on the distributions of adult barnacles. Observations of adult barnacles in 1989 indicated that there is spatial variation in abundance and distribution of *Chamaesipho tasmanica* at Cape Banks. Underwood and Denley (1984) found that patterns of distribution could be determined primarily by recruitment. Chapters 3 and 4 have shown that larval supply can cause the observed patterns of distribution of juvenile *Chamaesipho*, but the numbers settling may be modified by larval choice in response to cues when cyprids arrive to settle. For example, the presence of older recruits or adults will enhance settlement of this gregarious barnacle. Otaiza (1989) also found that more *Chamaesipho* recruited to areas where adults were abundant. In fact, in this study, a significant positive correlation was found between total annual numbers of settlers and total annual numbers of adults from 1989 to 1993 (see **Chapter 4**).

Because larval supply determines distributions of juveniles (see **Chapter 3**), it was assumed that increased larval availability would also be associated with increased ultimate abundancesof adults. That is, it was predicted that, if newly-settled barnacles were monitored similar spatial patterns would be maintained through time while barnacles grew to adulthood, despite the effects of mortality. It was also predicted that if adults and total numbers of new settlers were counted each year at six sites at Cape Banks, similar spatial patterns of abundance of settlers and subsequent adults at these sites would confirm that larval supply dictated distribution and abundance of adult *Chamaesipho* at Cape Banks. Alternatively, distributions may be determined by processes acting after cyprids settle and metamorphose. In this case, one can hypothesise that post-settlement mortality will influence these adult distributions. This chapter will therefore concentrate on those aspects which affect patterns of distributions of adults.

Although Otaiza (1989) found a relationship between patterns of settlement and recruitment when he monitored newly-settled cyprids which later metamorphosed into barnacles, he stated that larval supply did not determine adult patterns of distribution of *Chamaesipho* because adult patterns of abundance did not match patterns of arrival of cyprid larvae. His plankton traps were, however, only secured for 4 continuous days in February, March, July and September in 1988 and very few cyprids were caught. Early in this study, when larval arrival was monitored from July to December, 1989, large numbers of cyprid larvae of *Chamaesipho* were recorded on the full moon in mid September and two days before the full moon in mid October. This suggested that Otaiza (1989) may have missed major settlement peaks in his sampling. Patterns of arrival of cyprids that he obtained should not therefore have been extrapolated to adult patterns of abundance. A more intensive sampling programme was therefore necessary to test the hypotheses that larval supply would be associated with distributions of juveniles, and with the ultimate distributions of adults. Hence, in this study, plankton traps were secured for 5-6 successive days during lunar periods, generally from July to mid December from 1990 to 1993 at Site 4 (see **Chapter 3**) and settlement was recorded concurrently.

It is uncertain to what degree, if at all, post-settlement mortality of juveniles and/or adult mortality affects the abundance and distribution of populations of adult *Chamaesipho*. It was therefore necessary to examine the models that post-settlement mortality determines juvenile, in addition to adult, spatial distributions at Cape Banks. In this study, larval supply was positively correlated with distributions of juveniles (see **Chapter 3**). Results in this chapter further illustrate that initial settlement influences distributions of adult *Chamaesipho* because spatial patterns of settlers and adults were similar (see **5.3.2**). Mortality of adults already on the substratum also needed to be studied to test the hypothesis that increased adult mortality would be associated with a decrease in densities of established populations of barnacles. Fewer barnacles were observed on upper and more exposed shores at Cape Banks and it was considered that differences in post-settlement mortality, and in adult mortality, in these areas may contribute to these patterns. It was therefore predicted that if numbers of juvenile and adult *Chamaesipho* surviving over time were counted, greater mortality of barnacles on exposed and upper shores would result in fewer barnacles in these areas. That is, it was predicted that differential mortality of juvenile and adult barnacles would be measured which would reflect the spatial distribution and abundance of juvenile and adult populations at Cape Banks.

Early in this study, the limpet *Cellana tramoserica* was observed in greater numbers on lower mid-shores within distributions of *Chamaesipho* at the sheltered Sites 3 and 4 (see **Chapter 2: Fig. 2.7**) than at Site 5 which was semi-exposed. At the exposed Sites 6, 2 and 1, *Cellana* occupied areas of the substratum below *Chamaesipho*. Whenever patches were cleared within aggregations of *Chamaesipho* at Sites 3 and 4, *Cellana* was seen to immigrate almost immediately to these spaces. Also, whenever limpets were added to cleared patches containing randomly scattered new settlers of *Chamaesipho*, juvenile barnacles were soon only distributed around the edges of these patches and there were fewer newly-settled barnacles in these patches than in those without *Cellana*.

Cellana can crush or bulldoze newly-settled *Tesseropora rosea* (Denley & Underwood, 1979; Underwood et al., 1983), a barnacle which is often found in the same areas as *Chamaesipho*. Because *Cellana* also occurs among *Chamaesipho*, it was proposed that the limpet may also be contributing to adult patterns of distribution of *Chamaesipho* by killing new settlers. That is, the presence of *Cellana* would influence juvenile mortality and hence, the distributions of adults. If new settlers of *Chamaesipho* were exposed to *Cellana* there should be a significantly reduced survival of these barnacles compared to barnacles in areas without limpets. The null hypothesis was that there will be no difference in survival of newly-settled barnacles when *Cellana* is present or absent, or there will be less mortality in plots with *Cellana*.

5.2 Abundance and Distribution

5.2.1 Sampling Design

In August 1989, 6 cm diameter replicates ($n = 3$) of mixed cohorts of barnacles were marked with an inscribed metal tag cemented into the substratum at six sites (see **Chapter 2: Fig. 2.7**) and three heights (Low, Mid, Upper) of *Chamaesipho's* distribution on mid-shore levels at Cape Banks. These replicates were photographed in the field and processed black and white negatives were mounted on an Image Analyser: Tracor Northern TN8502/B computer with binocular microscope and camera attachments. The image of each field of view of the binocular microscope at power x 2.5 and equivalent to the size of the computer screen was 2.66 mm. A black and white negative of a grid (100 squares) was then prepared so that each grid square, when projected through the microscope, matched the computer screen exactly. This numbered grid was superimposed over the field negative so that the metal tag images on the negative and grid were matched up. Both were then sandwiched between two glass slides and mounted on the microscope stage. This ensured that the same individual barnacle could be recorded and measured over time. Populations of barnacles were mapped with this procedure so that at the end of each year, new or missing barnacles could be recorded.

Numbers of barnacles (settlers, recruits, adults) were counted from August 1989 until December 1993. Percent cover of these resident barnacles was also determined. To do this, a Hanimex Hanimette 35 mm colour slide projector with film strip attachment was used to project negatives of replicates onto a large screen, divided into 100 intersecting points. Percent cover was estimated from the number of these points in contact with barnacles.

5.2.2 Results

Spatial and temporal variations in numbers of mixed cohorts of adults occurred from 1989 to 1993 at Cape Banks (Fig. 5.1; Table 5.1). There were significant differences among Times and among Sites and there were interactions among Times and Sites and among Sites and Heights (Table 5.1). Greatest densities

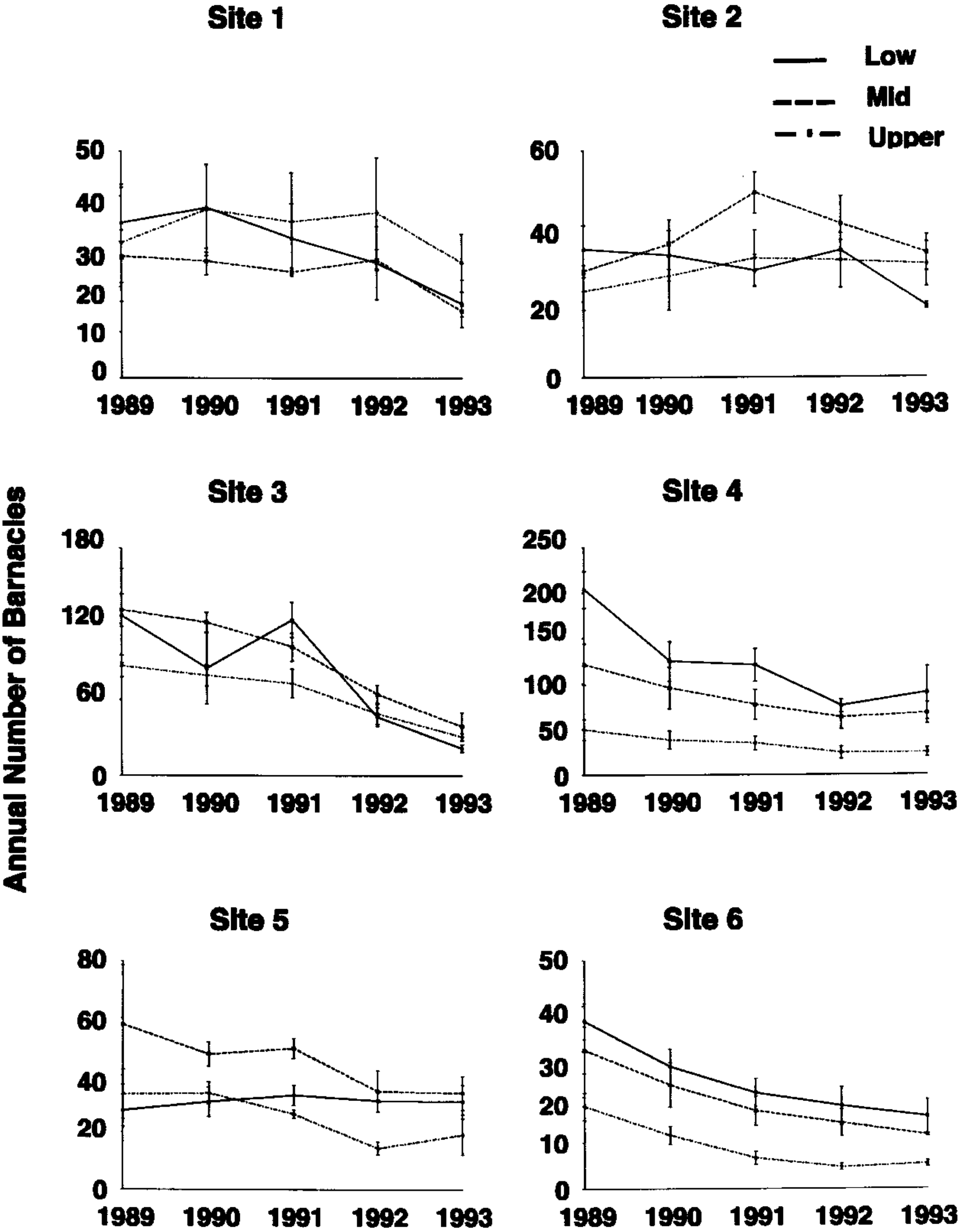

Fig. 5.1

Total density of barnacles ($n = 3$) at — Low, – – Mid and – · – Upper heights of *Chamaesipho's* distribution at six sites from the end of 1989 to the end of 1993.

Table 5.1

Analysis of numbers of mixed cohorts of adult barnacles ($n = 3$) at Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: data are from the end of each year from 1989 to 1993. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $(x + 1)^{0.5}$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	4	37.98	5.75	**
Site = S	5	152.78	115.67	***
Height = H	2	50.58	2.96	ns
T x S	20	6.61	5.00	***
T x H	8	1.12	1.30	ns
S x H	10	17.11	12.95	***
T x S x H	40	0.86	0.65	ns
Residual	180	1.32		

were recorded at sheltered Sites 3 and 4 and least at exposed Site 6 (Fig. 5.1). Generally most adults were counted in 1989. Sites with least abundance of barnacles had no significant differences in numbers of barnacles recorded each year from 1989 to 1993. At Site 6, however, there were some differences among years, but only between 1989 and 1991, 1992 and 1993 in that order. Most adults generally occurred Low on the shore and least adults on Upper shores, although there were some differences among Heights (Fig. 5.1; Table 5.1). When data for percent cover were analysed, similar results were obtained (Fig. 5.2; Table 5.2) although there were some differences which indicated that growth-rate, mortality-rate or size of barnacles may have varied in some areas. There was a significant correlation between percent cover and numbers of barnacles recorded at six Sites and three Heights from 1989 to 1993 (Fig. 5.3). Recruitment each year was not sufficient to maintain densities of *Chamaesipho* so that populations at Cape Banks were observed to decrease at all Sites and Heights from 1989 to 1993 (Figs. 5.1, 5.4).

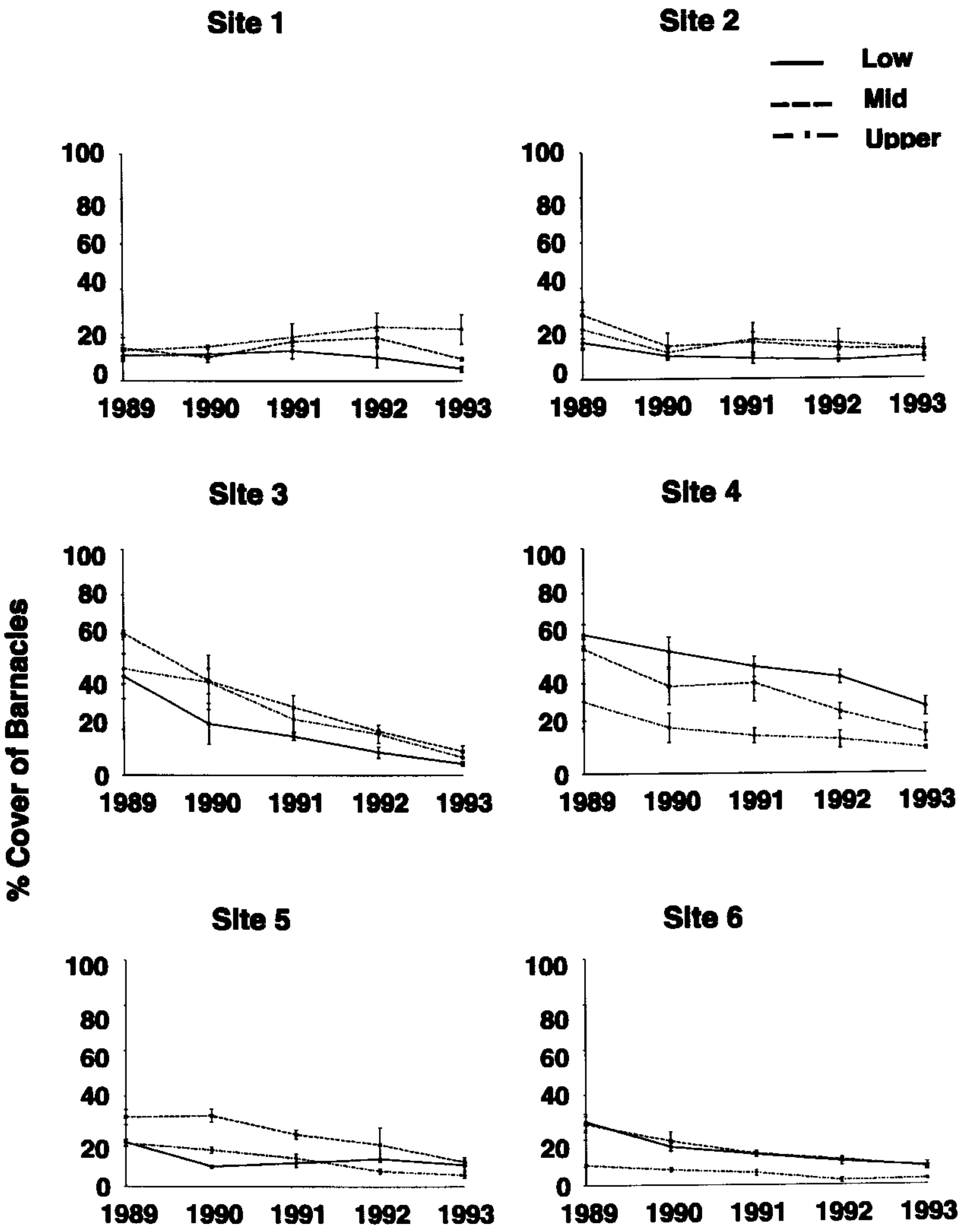

Fig. 5.2

Percent cover of barnacles ($n = 3$) at — Low, – – Mid and – · – Upper heights of *Chamaesipho's* distribution at six sites from the end of 1989 to the end of 1993.

Table 5.2

Analysis of percent cover of mixed cohorts of adult barnacles ($n = 3$) at Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: data are from the end of each year from 1989 to 1993. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed arc sine (%); Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	4	1426.28	8.99	***
Site = S	5	1645.03	62.88	***
Height = H	2	606.27	1.42	ns
T x S	20	158.69	6.07	***
T x H	8	27.03	1.63	ns
S x H	10	427.96	16.36	***
T x S x H	40	16.61	0.63	ns
Residual	180	26.16		

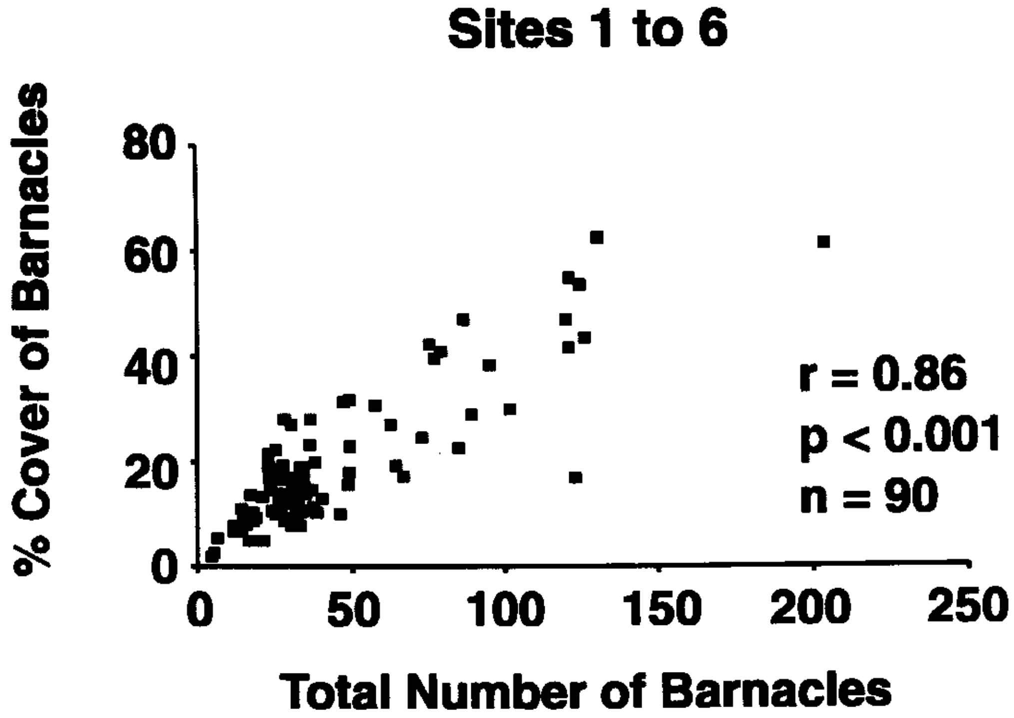

Fig. 5.3

Relationship between percent cover and total number of barnacles at Low, Mid and Upper heights of *Chamaesipho's* distribution at six sites from the end of 1989 to the end of 1993. Each point represents the mean ($n = 3$) for each variable. There are 90 data points in each correlation.

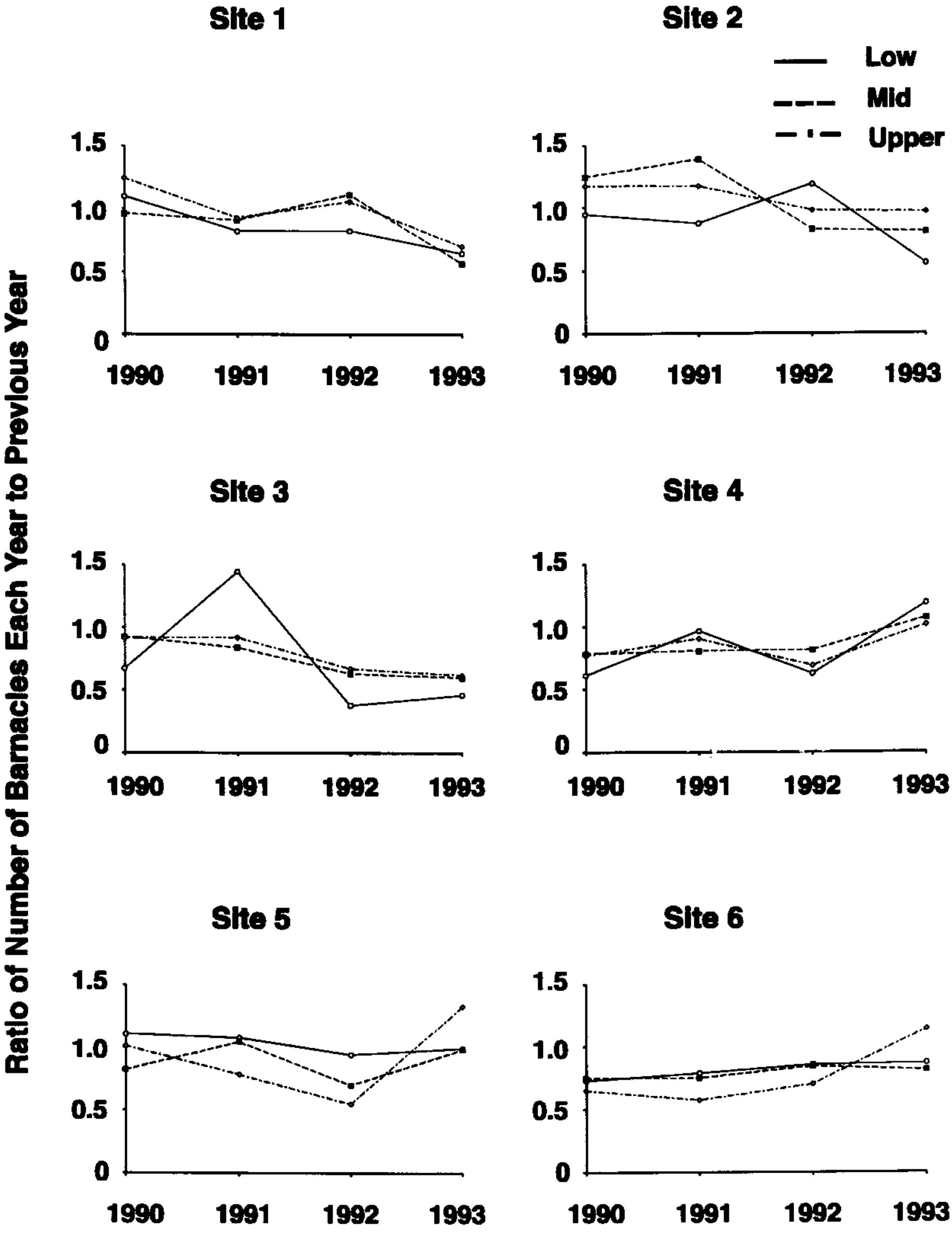

Fig. 5.4

Renewal of barnacles at — Low, – – Mid and – · – Upper heights of *Chamaesipho's* distribution at six sites each year from the end of 1989 to the end of 1993: numbers of barnacles recorded one year divided by the numbers of barnacles recorded in the previous year.

5.3 Initial Settlement and Adult Distribution

5.3.1 Experimental Method and Design

Distributions of Settlers and Adults at Six Sites

From July to December in each year from 1989 to 1993, numbers of new settlers among mixed cohorts of adults on the substratum in replicates (*n* = 3) labelled with an inscribed metal tag (see **5.2.1**) were counted on consecutive days, weather, tide and time permitting, at six sites (see **Chapter 2 : Fig. 2.7**) and three heights of *Chamaesipho's* distribution every fortnight during new and full moons. In the field, new settlers were identified by their dark-blue centres (terga and scuta) and translucent, shining quality of the yet uncalcified shell. In the laboratory, 6 plates and sutures were easily seen on 2-3 day old settlers under a microscope. Older individuals had 4 plates (see **Chapter 2: Fig. 2.2**). Numbers recorded at each height and site were totalled for each year and these data were analysed to determine spatial patterns of settlement. These patterns were compared with adult spatial patterns at six sites and three heights from 1989 to 1993 (see Figs. 5.1, 5.5; Tables 5.1, 5.3).

Distributions of Juveniles and Adults at One Site

At Site 4 (see **Chapter 2: Fig. 2.7**) numbers of newly-settled barnacles (< 1day old) on the substratum were recorded in November 1993 from two places nested in each of two heights (Low, Mid/Upper). These were monitored and the patterns obtained through time were compared with adult patterns. To do this, numbers of 1993 recruits, that is, with aperture lengths < 1 mm, were randomly counted in 1994 from 6 cm uncleared patches (*n* = 3) on the substratum. At the same time, numbers of mixed cohorts were counted from 6 cm patches (*n* = 3) in other areas. Settler, older recruit and adult patterns were then compared.

5.3.2 Results

Distributions of Settlers and Adults at Six Sites

Spatial and temporal variation in total numbers of settlers occurred from 1989 to 1993 at six Sites and three Heights (Low, Mid, Upper) of *Chamaesipho's* distribution studied at Cape Banks (Fig. 5.5; Table 5.3). Interactions occurred among Time and Sites and among Sites and Heights (Table 5.3). Generally barnacles settled in greatest densities in 1989 and in least numbers in 1993. Most barnacles always settled at Sites 3 and 4 and the smallest numbers generally settled at Site 6 (Fig. 5.5; Table 5.3). That is, most settlement was recorded on sheltered shores and least on exposed shores. At sheltered Sites 3 and 4, most barnacles settled Low on the shore whereas at the more exposed Sites 1, 2, 5 and 6, there was no real difference among Heights although at Sites 2 and 6, total numbers of settlers were similar at Low and Mid Heights which were greater than numbers that settled at Upper Heights (Fig. 5.5; Table 5.3). Spatial patterns of juveniles (Site 3 = 4 > 5 = 2 > 1 > 6) (Fig. 5.5; Table 5.3) that settled among mixed cohorts of adults were similar to spatial patterns of these adults (Site 3 = 4 > 5 = 2 = 1 > 6) (Fig. 5.1; Table 5.1) that were already established on the substratum.

Table 5.3

Analysis of total numbers of settlers ($n = 3$) each year at Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: data are from the end of each year from 1989 to 1993. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data transformed $\mathrm{Log}_e(x + 1)$; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	4	17.58	12.33	***
Site = S	5	30.33	123.31	***
Height = H	2	11.09	4.34	*
T x S	20	1.42	5.79	***
T x H	8	0.12	0.35	ns
S x H	10	2.56	10.40	***
T x S x H	40	0.33	1.35	ns
Residual	180	0.25		

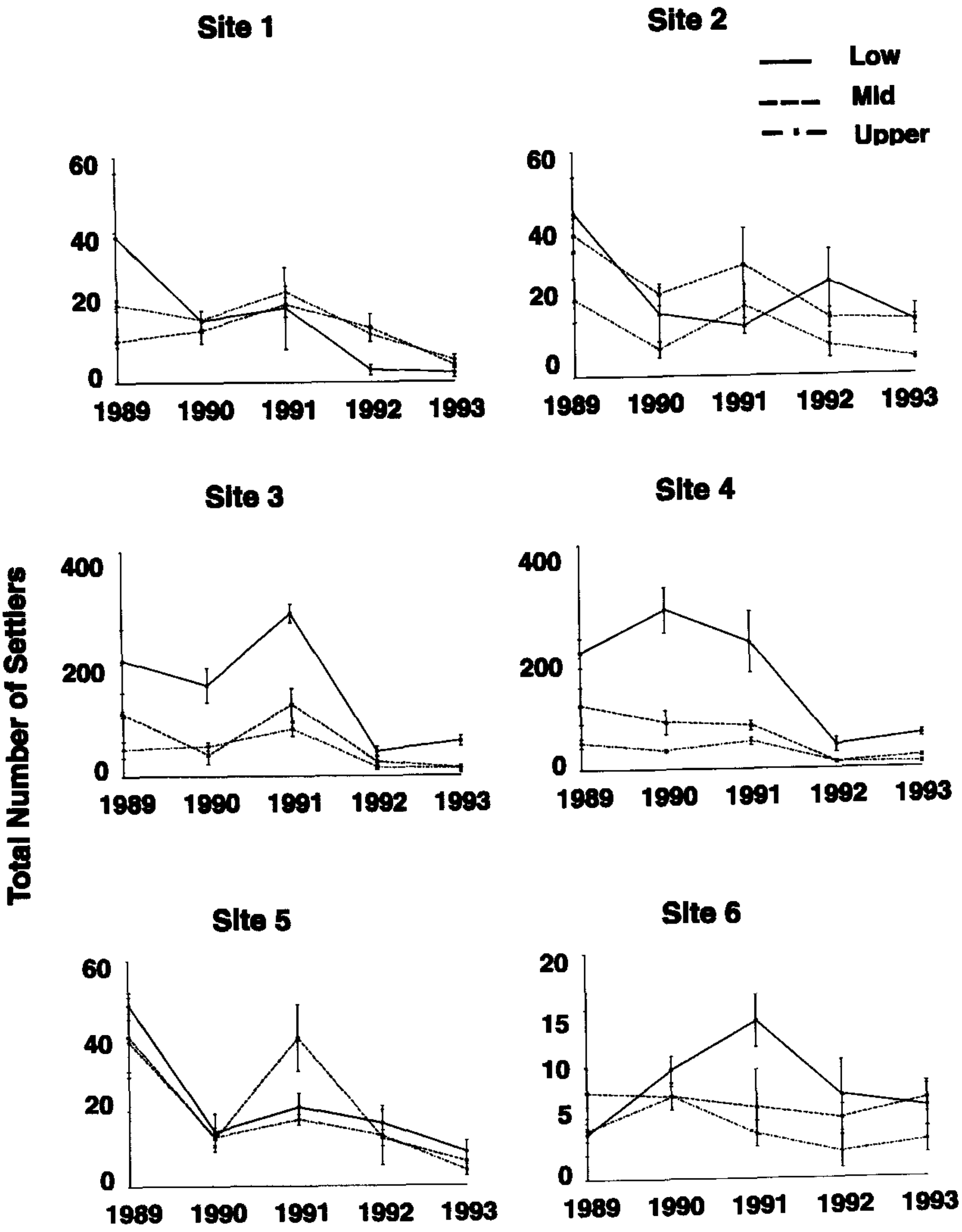

Fig. 5.5

Total number of settlers ($n = 3$) each year at — Low, – – Mid and – · – Upper heights of *Chamaesipho's* distribution at six sites from 1989 to 1993.

Distributions of Juveniles and Adults at One Site

On 15th November 1993, there was no significant difference in numbers of *Chamaesipho* that settled among places at two Heights (Low, Mid/Upper) on the shore. In April 1994, however, there were significant differences between numbers of juveniles at two places Low on the shore, indicating that differences in post-settlement mortality had occurred between these two places. By July 1994, there were no differences in numbers of older 1993 recruits, nor mixed cohorts of adults, among places at two Heights on the substratum. Patterns of settlement in November 1993 were mirrored both by older 1993 recruits and adult barnacles in July 1994 (Fig. 5.6).

5.4 Post-Settlement Mortality and Distribution of Adults

5.4.1 Juvenile and Adult Mortality

5.4.2 Experimental Method and Design

To standardise data from different sites (see **Chapter 2 : Fig. 2.7**) and heights, percentage mortality was analysed. Annual mortality of adults was estimated in late October or November each year from 1990 to 1992 as the percentage of adults lost from the initial population recorded twelve months previously. Because settlement occurred from August to December, percentage mortality of new settlers was estimated on cumulative settlement for this period, rather than annually, from 1989 to 1993. Mortalities of adults and juveniles were analysed for six sites and three heights of *Chamaesipho's* distribution.

To test the hypothesis that mortality would increase when large densities and percent cover predominated, that is, mortality of *Chamaesipho* was predicted to be density-dependent or cover dependent, correlations were calculated on pooled means ($n = 3$) from six sites (see **Chapter 2 : Fig. 2.7**) and three heights (Low, Mid, Upper) from 1990 to 1992 for adults, and from 1989 to 1993 for total settlers. For adults, relationships of annual percentage mortality between initial density of adults, and between initial percent cover were analysed. For settlers, relationships of percentage

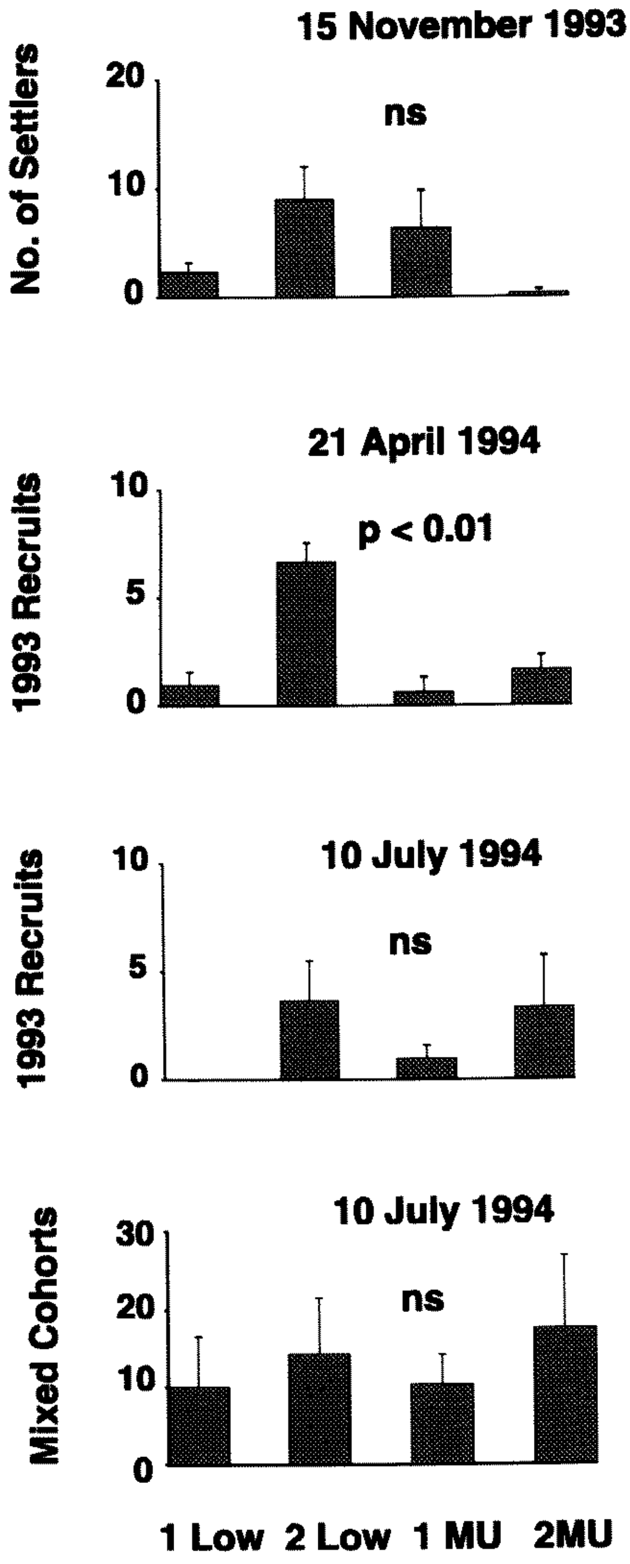

Fig 5.6.

Numbers of *Chamaesipho* counted in random 6 cm quadrats ($n = 3$) at two places nested in each of two heights (Low, Mid/Upper) from settlement in November 1993 through to July 1994. Mixed cohorts of barnacles were also counted in July 1994 in similar sized plots ($n = 3$) so that comparisons could be made between spatial patterns of settlers, older recruits and adults.

mortality between cumulative density of settlers, and between initial percent cover were analysed. Because barnacles inhabit higher levels on exposed shores with more wave-action (Underwood, 1981), greater mortality was expected in these areas. The relationships between percentage mortality of juveniles and adults at different heights were therefore also analysed. Relationships were also calculated between total numbers of barnacles that settled at each site and the final numbers of settlers that remained in December in each site each year from 1989 to 1993.

5.4.3 Results

Percentage mortality of adults did not vary with height from late 1989 to late 1992 (Table 5.4). There were, however, interactions between Site and Time and Site and Height (Table 5.5). That is, some temporal and spatial variation in adult mortality occurred at Cape Banks from 1990 to 1992 and results were not spatially or temporally consistent (Table 5.5). For example, at the exposed Sites 1 and 2, least mortality occurred over three years from late 1989 to late 1992 although, at the end of 1990, Site 2 had most mortality even though there was no significant difference among sites. At the end of 1991 and 1992, there was no significant difference among sites although there were some significant differences between those sites that had the greatest, and those that had the least percentage mortalities. Site 3 had the greatest adult mortality at the end of 1991 and 1992. Over three years from late 1989 to late 1992, percentage mortality progressively decreased from Site 3 to Site 6 to Site 4 to Site 5 to Site 2 and to Site 1 although there were no significant differences among these sites (Table 5.5).

At Low heights, Site 3 had most mortality of adults and there were no significant differences among other sites. At Mid shores, mortality of adults was similar for all sites. At Upper heights, although there were no significant differences among sites, significant differences occurred between sites that had the greatest and least percentage mortalities. That is, most adult mortality occurred on Upper shores at the exposed Site 6 and semi-exposed Site 5. Least adult mortality occurred on these Upper heights at Sites 1 and 2 (Table 5.5).

Table 5.4

Summary of analyses of relationship of annual percentage mortality of adult barnacles between height on the shore, between initial density of adults and between initial percent cover . Annual adult mortality was estimated at the end of each year from 1990 to 1992 as a percentage of adults lost from the initial population recorded twelve months previously. Analyses were calculated on pooled means ($n = 3$) from six sites for three years.

Height			Initial Adult Density			Initial Percent Cover		
df	r	p	df	r	p	df	r	p
52	0.26	ns	52	0.22	ns	52	0.04	ns

Table 5.5

Analysis of annual percentage mortality of mixed cohorts of adult barnacles ($n = 3$) at Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: Annual adult mortality was estimated at the end of each year from 1990 to 1992 as a percentage of adults lost from the initial population recorded twelve months previously. Analyses were performed on annual percentage mortality ($n = 3$) for three years from 1990 to 1992. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data untransformed; Cochran's test, $p > 0.05$.

Source	df	MS	F	p
Time = T	2	79.37	0.15	ns
Site = S	5	596.94	3.60	**
Height = H	2	686.88	0.80	ns
T x S	10	533.64	3.22	**
T x H	4	79.52	0.75	ns
S x H	10	853.99	5.16	***
T x S x H	20	105.68	0.64	ns
Residual	108	165.62		

At Sites 1 and 3, most adult mortality was at Low heights whereas, at Site 6, greatest mortality was recorded at Upper heights. Mortality of adults was similar for all heights at Sites 2, 4 and 5, although marginally more adults died at Low heights at Sites 2 and 4 and at Upper heights at Site 5 (Table 5.5).

Generally, most adults and settlers were recorded Low on the shore and least numbers of adult and juvenile barnacles were recorded at Upper heights at Cape Banks (Figs. 5.1, 5.5; Tables 5.1, 5.3). Although most mortality of adults occurred at Low heights at Sites 1 to 4 (Table 5.5), this was not related to larger numbers of adults inhabiting these sites. There was no relationship between adult percentage mortality and initial density of adults, nor between adult percentage mortality and percent cover of adults for all sites and heights from the end of 1989 to the end of 1992 (Table 5.4). Adult mortality was apparently density-independent.

Similarly, no relationship was found between percentage mortality of juveniles and cumulative density of settlers, nor between percentage mortality of juveniles and percent cover of mixed cohorts for each period of settlement from July to December of 1989 to 1993 for all sites and heights (Table 5.6). Juvenile mortality was also density-independent and spatial patterns of mortality did not reflect spatial patterns of settlement (Total Settlers: Site 3 = 4 > 5 = 2 > 1 > 6; Settler % Mortality : Site 4 > 6 = 3 = 1 > 2 = 5) (Tables 5.3, 5.7).

Table 5.6

Summary of analyses of relationship of percentage mortality of settlers between height on the shore, between cumulative density of settlers and between initial percent cover of surrounding mixed cohorts. Because settlement occurred from August to December each year, percentage mortality of new settlers was estimated on cumulative density for this period each year. Analyses were calculated on pooled means ($n = 3$) from six sites each year for five years from 1989 to 1993.

Height			Cumulative Settler Density			Initial Percent Cover		
df	r	p	df	r	p	df	r	p
88	0.04	ns	88	0.17	ns	88	0.02	ns

Table 5.7

Analysis of percentage mortality of total settlers ($n = 3$) at Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: Juvenile percentage mortality was estimated on cumulative settlement from August to December each year from 1989 to 1993. Arc sine (%) transformation could not stabilise the variances: Cochran's test, $C = 0.13, p < 0.01$. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data untransformed; Cochran's test, $C = 0.10, p < 0.05$.

Source	df	MS	*F*	*p*
Time = T	4	13016.12	7.42	***
Site = S	5	4367.14	15.34	***
Height = H	2	942.78	2.51	ns
T x S	20	1754.76	6.17	***
T x H	8	750.85	1.81	ns
S x H	10	374.99	1.32	ns
T x S x H	40	413.76	1.45	ns
Residual	180	284.62		

Mortality of juveniles was greater than that of adults at Low, Mid and Upper heights of Sites 1 to 6 from 1990 to 1992, except in 1992 at Site 3 (Table 5.8). In 1992, percentage mortality of juveniles and adults was similar at Site 3 and percentage mortality of juveniles was marginally greater than that of adults (Table 5.8). Analysis of variance showed that mortality of juveniles varied both temporally and spatially and that there were interactions between Time and Site (Table 5.7). There was no significant difference in percentage mortality of juveniles among heights (Tables 5.6, 5.7). Generally, the greatest proportion of settlers died at sheltered Site 4 and the least at exposed Sites 2 and 5 (Table 5.7). When settler data for heights (Low, Mid, Upper) were pooled for each site, relationships were evident between total numbers of barnacles that settled at each site from July to December each year and the total numbers of barnacles that remained in December each year from 1989 to 1993 (Fig. 5.7).

Table 5.8

Analysis of annual percentage mortality of mixed cohorts of adult versus percentage mortality of juvenile barnacles ($n = 3$) at Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: Annual adult mortality was estimated at the end of each year as a percentage of adults lost from the initial population recorded twelve months previously. Juvenile percentage mortality was estimated on cumulative settlement from August to December each year Analyses were performed on juvenile versus adult percentage mortality ($n = 3$) for three years from 1990 to 1992. Arc sine (%) transformation could not stabilise the variances: Cochran's test, C = 0.19, $p < 0.01$. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Analysis of Variance, data untransformed; Cochran's test, C = 0.12, $p < 0.01$.

Source	df	MS	*F*	*p*
Time = T	2	2343.86	5.55	*
Site = S	5	870.43	4.47	***
Height = H	2	1473.62	1.39	ns
Juvenile/Adult = JA	1	104192.42	107.15	***
T x S	10	422.26	2.17	*
T x H	4	687.35	2.44	ns
T x JA	2	1387.30	2.50	ns
S x H	10	1060.78	5.45	***
S x JA	5	972.41	5.00	***
H x JA	2	224.84	0.79	ns
T x S x H	20	281.21	1.44	ns
T x S x JA	10	554.94	2.85	**
T x H x JA	4	530.86	5.25	**
S x H x JA	10	283.88	1.46	ns
T x S x H x JA	20	101.05	0.52	ns
Residual	216	194.68		

5.4.4 Effect of *Cellana tramoserica*

5.4.5 Experimental Method and Design

Pilot experiments were set up in July 1990 to test for the emigration of *Cellana* out of artificially cleared patches. Three 6 cm patches were cleared within dense populations of *Chamaesipho* at low shore levels of *Chamaesipho's* distribution

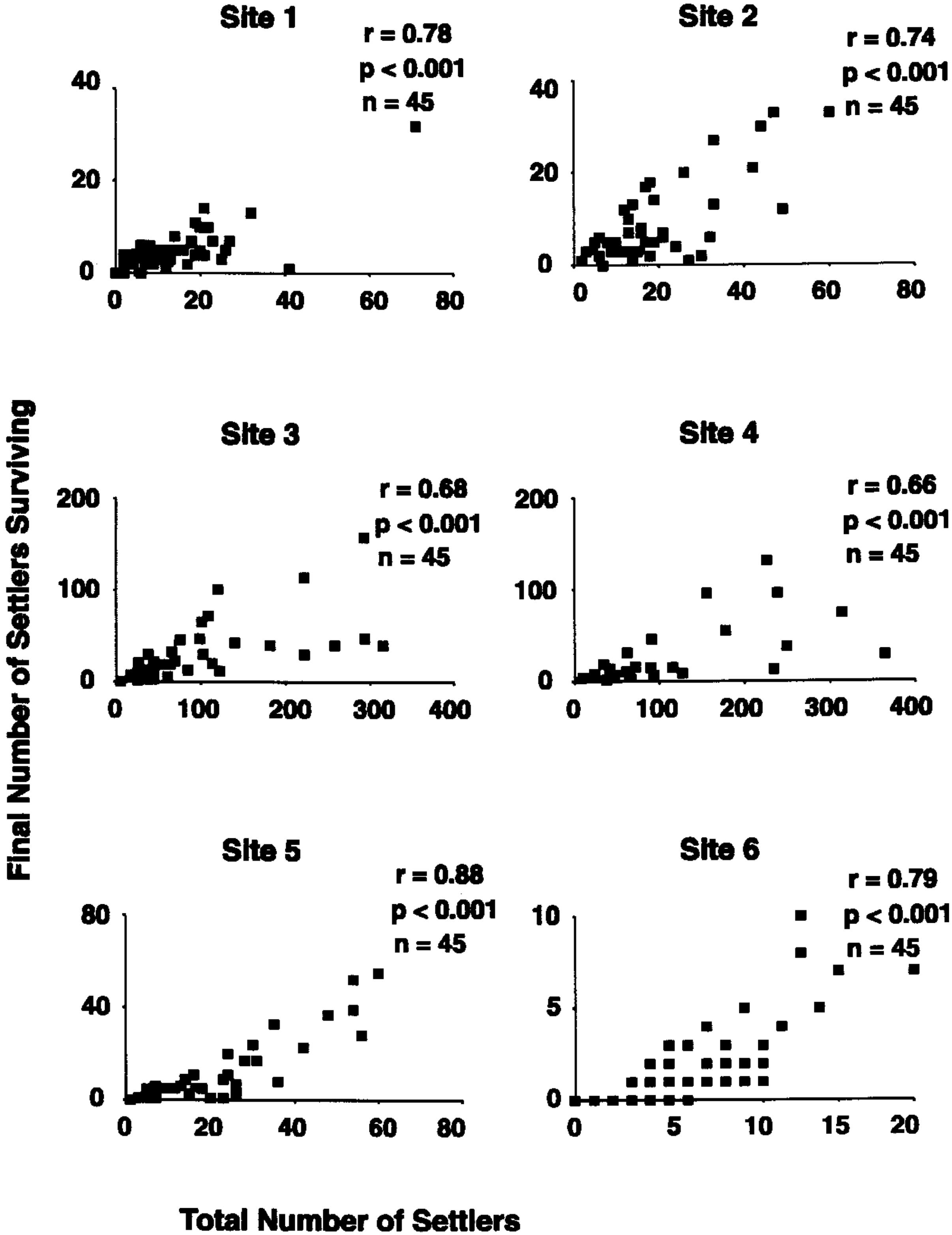

Fig. 5.7

Relationship between final number of settlers surviving and total numbers of barnacles settling each year at Low, Mid and Upper heights of *Chamaesipho's* distribution at six sites from the end of 1989 to the end of 1993. Each point represents total numbers of settlers recorded in each replicate (*n* = 3). There are 45 data points in each correlation.

at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**) using a chisel, mallet and wire brush. Patches were then washed to remove sandstone and shell debris. Each replicate was marked for future identification. Two medium-sized *Cellana* (2.5 cm across shell) were dislodged with a flat blunt knife, moistened and placed in each of the three previously wetted replicates. Each limpet was marked with non-toxic red Humbrol enamel paint.

Over successive days, initial observations emphasised a relatively large degree of emigration and immigration of marked and unmarked limpets. Further investigation of movements of replaced, marked *Cellana* showed a decreased mobility. Homing behaviour in *C. tramoserica* has already been demonstrated (Mackay & Underwood, 1977; Underwood, 1977b, 1988). Thus, it was assumed that limpets that were dislodged and replaced in experimental replicates would eventually remain in those replicates. If variations in numbers of limpets occurred in experimental treatments, these numbers could be corrected daily during sampling.

As an extra precaution, fences were incorporated in the experimental design to exclude any grazers other than *Cellana* such as the snail *Nerita atramentosa* and the limpets *Siphonaria denticulata* and *Patelloida latistrigata*. To account for effects of fences (Underwood & Jernakoff, 1984) and to discount the possibility that ungrazed spores of macroalgae such as *Ulva lactuca* may grow and pre-empt space during settlement (Denley & Underwood, 1979; Underwood & Denley, 1984), some cleared patches on the substratum were left unfenced. Any other species of grazers that ventured in these plots were removed daily because their presence could confound experiments in unfenced areas where grazers were meant to be absent. Of course, because plots were under water during high tides, it was impossible to control for any grazing that may have occurred during submersion.

In July 1990, 1991 and 1992 6 cm patches (*n* = 4) were cleared on the substratum low on the shore of *Chamaesipho's* distribution at Sites 3 and 4 (see **Chapter 2: Fig. 2.7**) for *Chamaesipho* to settle. Settlement was characterised each year by a trickle of few larvae arriving, generally from August to mid November, and a major pulse of one or two events associated with high velocity Southerly winds, 1.2 m to 1.8 m waves and new and full moons (see **Chapter 3**). In some years, virtually no larvae arrived, especially in 1992, 1993 and 1994. In 1992 and 1993, most larvae arrived during peaks on one occasion rather than at other times.

Settlers in cleared patches were counted on 6 to 8 consecutive days, weather, tide and time permitting, during new and full moons from July to December 1990 to 1992. Because fewer other barnacles *T. rosea* and *Tetraclitella purpurascens* were found to settle in areas surrounded by experimental fences (Denley & Underwood, 1979; Underwood & Denley, 1984), fences were only secured to the substratum in November 1990 and 1991 once most settlement had occurred. *Cellana* were also first included at this time. Fences and limpets were not added in 1992 due to insufficient settlement and recruitment of *Chamaesipho* so these 1992 data have not been included.

On 14th November 1990 and 18th November 1991, fences (6 meshes per 2.5 cm: 20 cm x 20 cm x 4 cm) were secured, where appropriate, around 6 cm plots (n = 4) on the sandstone with screws in rawl plugs and lead washers. Some treatments were left unfenced to act as Controls for the effect of fences at two sites. Where necessary, 3 *Cellana,* equivalent to the observed density of *Cellana* in natural patches among *Chamaesipho*, were placed in cleared 6 cm patches (n = 4) containing established juveniles. The substratum was always moistened before adding the limpets and the top of each shell was then splashed with water and tapped gently to ensure attachment. Any variations in numbers of *Cellana* were corrected daily over each 6 to 8 day sampling period by adding or removing limpets. About 6 weeks later, on 27th December 1990 and 6th January 1992, percentage mortality of settlers was estimated from the numbers that had established prior to adding any limpets plus any new barnacles that settled in the interim. From December each year, numbers of remaining barnacles were counted monthly and any new settlers were noted. About 6 months later, in late June 1991 and early July 1992, fences and *Cellana* were removed.

Because densities of settling barnacles vary at very small spatial scales (e.g. within 2 cm) percentage mortality was used. "Natural" mortality of new settlers before *Cellana* was added was disregarded in this experiment and graphs have been included to indicate densities of *Chamaesipho* that recruited before and after limpets and fences were added on 14th November 1990 and 18th November 1991 (see Figs. 5.8, 5.9). Note that from April to July 1992 the whelk *Morula marginalba* invaded all replicates in Site 3 and ate *Chamaesipho* (see Fig. 5.9).

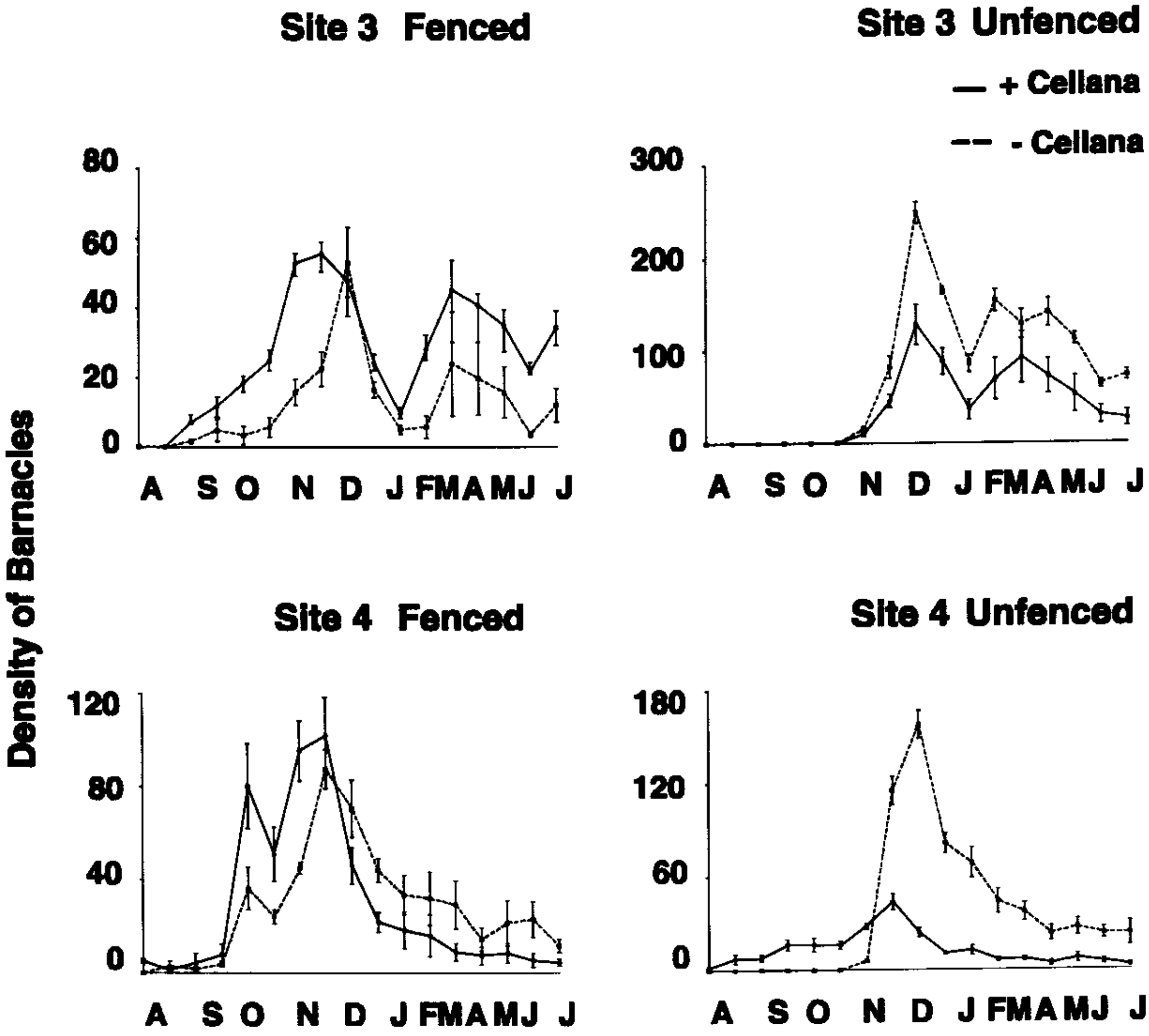

Fig. 5.8

Mean density of barnacles recorded per sampling period from July 1990 to late June 1991 in plots ($n = 4$) where *Cellana* was included or excluded. *Cellana* and fences were added, where appropriate, on 14th November, 1990. Note that some minor settlement occurred January to March 1991. —, + *Cellana*; – –, – *Cellana*.

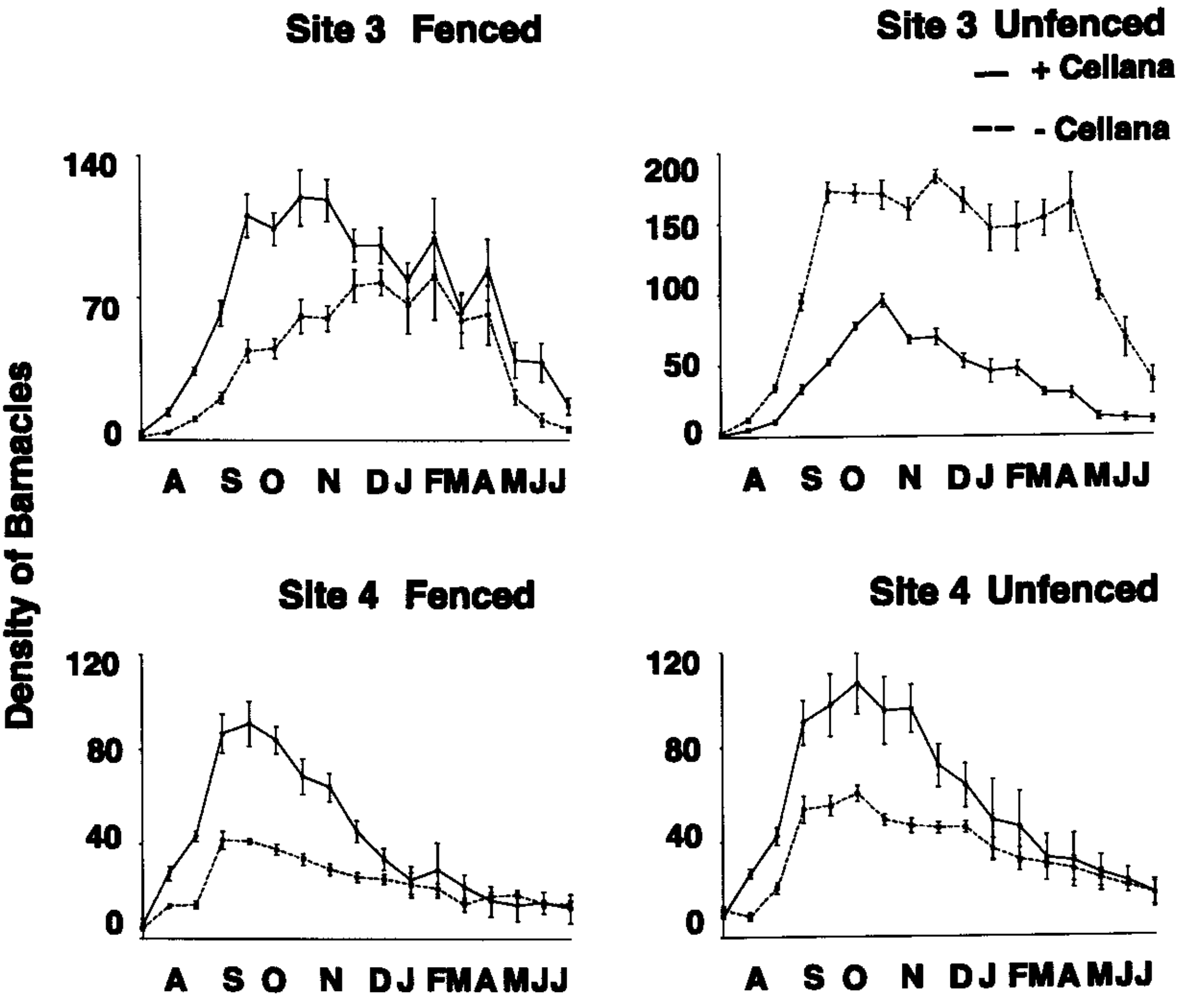

Fig. 5.9

Mean density of barnacles recorded per sampling period from July 1991 to early July 1992 in plots ($n = 4$) where *Cellana* was included or excluded. *Cellana* and fences were added, where appropriate, on 18th November, 1991. Note that some minor settlement occurred January to March 1992. Note also the effect of predation by *Morula marginalba* on all treatments in Site 3 fron April to July 1992. —, + *Cellana*; – –, – *Cellana*.

5.4.6 Results

Temporal and spatial variation in recruitment occurred before and after the limpet *C. tramoserica* was added to or excluded from Fenced and Unfenced plots (Figs. 5.8, 5.9). When data on the effects of *Cellana* on post-settlement mortality of *Chamaesipho* were analysed, SNK tests on means of untransformed data showed that there were interactions among Time x Site x ± *Cellana* (Fig. 5.10; Table 5.9a).

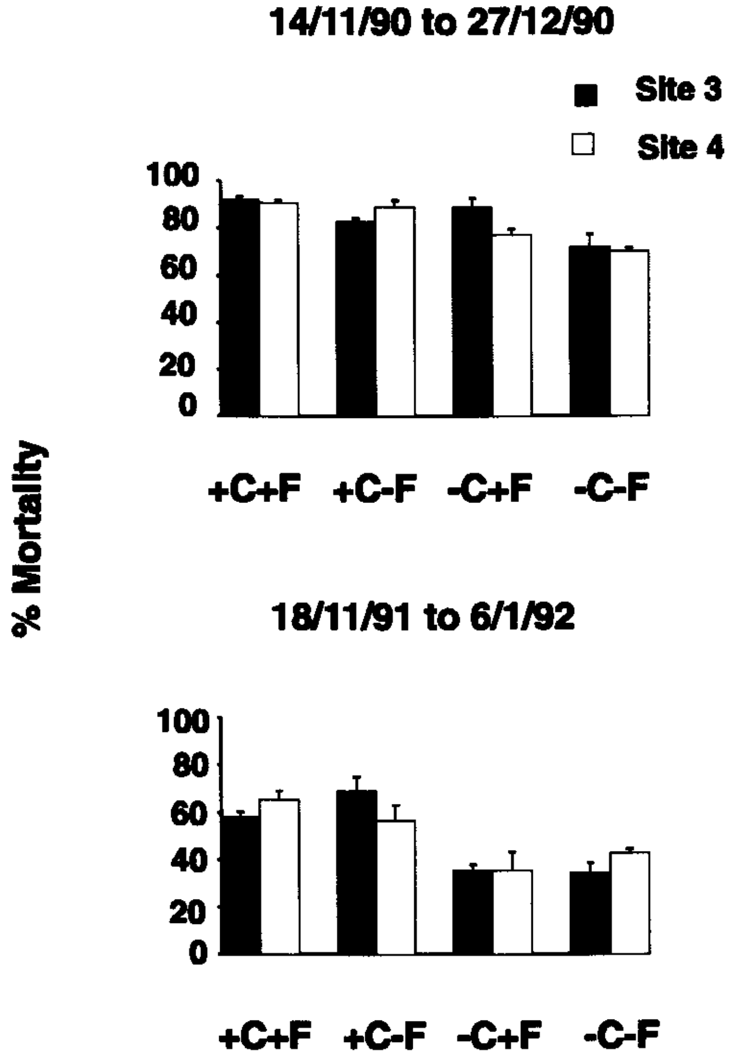

Fig. 5.10

Post-settlement mortality of barnacles for six weeks until 27th December, 1990 and 6th January, 1992. *Cellana* and fences were added to or excluded from plots (*n* = 4) on 14th November, 1990 and 18th November, 1991 respectively when most settlement had occurred. ± C, ± *Cellana*; ± F, ± Fences.

Greater mortality occurred on 27th December 1990 than on 6th January 1992 at both Sites 3 and 4 and in all ± *Cellana* treatments (Fig. 5.10; Table 5.9a). At neither Time was there a difference in post-settlement mortality between Sites. At Site 3, on 27th December 1990 there was no significant difference in mortality between those replicates that had limpets nor those from which limpets were excluded. At Site 4,

Table 5.9

Analysis of post-settlement mortality of juvenile barnacles ($n = 4$) at Low heights of *Chamaesipho's* distribution on the shore at Sites 3 and 4. Post-settlement mortality was estimated over six weeks after major settlement had occurred and after plots were manipulated for ± *Cellana* and ± Fences, that is, from 14th November, 1990 to 27th December, 1990 and from 18th November, 1991 to 6th January, 1992. Post-settlement mortality was estimated as percentage mortality of new settlers and already established juveniles for each six week period. ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

a) Analysis of Variance, data untransformed; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	1	17502.55	508.67	*
Site = S	1	6.91	0.11	ns
± *Cellana* = *C*	1	5469.39	750.84	*
± Fences = F	1	165.51	21.13	ns
T x S	1	34.41	0.56	ns
T x *C*	1	746.30	2.92	ns
T x F	1	469.85	2.31	ns
S x *C*	1	7.28	0.12	ns
S x F	1	7.83	0.13	ns
C x F	1	21.70	0.10	ns
T x S x *C*	1	255.83	4.13	*
T x S x F	1	203.04	3.28	ns
T x *C* x F	1	77.49	0.45	ns
S x *C* x F	1	218.92	3.54	ns
T x S x *C* x F	1	173.12	2.80	ns
Residual	48	61.92		

b) Analysis of Variance, ± Fences pooled, data untransformed; Cochran's test, $p > 0.05$.

Source	df	MS	*F*	*p*
Time = T	1	17502.55	508.67	*
Site = S	1	6.91	0.09	ns
± *Cellana* = *C*	1	5469.39	750.84	*
T x S	1	34.41	0.45	ns
T x *C*	1	746.30	2.92	ns
S x *C*	1	7.28	0.09	ns
T x S x *C*	1	255.83	3.32	ns
Residual	56	76.96		

however, greater mortality occurred where *Cellana* was present. On 6th January 1992, greater mortality was recorded where limpets were present (Table 5.9a).

Because there was no significant difference in mortality between Fenced and Unfenced plots (Fig. 5.10; Table 5.9a), the effect of grazers, other than *Cellana*, on Unfenced *Chamaesipho* can be discounted, as can fence effects, on mortality. When data for ± Fences was pooled, SNK tests on means of untransformed data showed that a greater percentage of barnacles had died by 27th December 1990 than by 6th January 1992. This greater mortality always occurred when limpets were present (Table 5.9b). *Cellana* was therefore responsible for post-settlement mortality of *Chamaesipho* at sheltered Sites 3 and 4 at Cape Banks.

Morula were also responsible for a sudden increase in mortality of *Chamaesipho* in all treatments at Site 3 from April to July 1992 (Fig. 5.9).

5.5 Discussion

The largest numbers of juvenile and adult barnacles were recorded at sheltered Sites 3 and 4 and at low heights, whereas the smallest numbers occurred at exposed Site 6 and at upper heights. Numbers of already established adults were also found to decrease progressively from late 1989 to late 1993. Because the spatial patterns of settlers were the same as adults and because mortality was similar at all sites and heights, although more pronounced at Site 3 Low and Site 6 Upper, *initial settlement* was found to be more important than *post-settlement mortality* in determining the abundances and distributions of *Chamaesipho.*

In Chapter 3, it was shown that larval supply determines juvenile distributions of *Chamaesipho* at Cape Banks. This corroborates Denley & Underwood's (1979) findings on *T. rosea*. When they studied newly-settled barnacles, they found that mechanisms of settlement, not post-settlement mortality, determined the upper limits of distribution. Results in this chapter emphasise that larval supply and settlement, rather than post-settlement mortality (except in particular circumstances such as when the predatory whelk *Morula* is present), also determine adult spatial patterns of distribution of *Chamaesipho*. Temporal and spatial variations in adult populations were inconsistent with adult or juvenile mortality and the model that differential mortality determines spatial distributions was not supported. In fact, populations of *Chamaesipho* decreased at all sites and heights at Cape Banks from 1989 to 1993 and this was because the numbers that recruited each year were not sufficient to balance the numbers lost. It may be then that in years when settlement and recruitment are negligible, mortality of adults will determine their spatial distribution. Despite this, densities of juveniles and adults varied spatially at Cape Banks, but mortality of adult barnacles was found to be similar among heights and sites on the shore despite differences in height and exposure. This is contrary to the model that fewer adult barnacles exist on exposed and upper shores as a function of greater mortality in these areas. Initial settlement, rather than mortality, is therefore emphasised here as a determinant of distributions of populations of adult barnacles.

Because *Chamaesipho* were found to exhibit density-independent mortality and because many large barnacles were found on upper heights (see **Chapter 6**) mortality of adults may decrease once barnacles are established. This is contrary to Connell's (1961a, 1961b, 1975) findings that extreme physical conditions determined the upper limits of vertical distribution and influenced population densities by increasing mortality on upper exposed shores, and also contrary to the results in this study that greater mortality of adults occurred on upper shores at exposed Site 6. In fact, Fairweather et al. (1984) found that survival of *Chamaesipho* increased with increasing height on the shore regardless of the presence or absence of *Morula*. In this study, however, there were some mixed results which could reflect differences in sites. Most mortality occurred low on the shore at Sites 1 and 3 and on upper heights at Site 6. Mortality elsewhere was similar and may reflect site-specific characteristics. For example, the presence of other barnacles may provide protection from desiccation and so reduce adult mortality when percent cover increases. In fact, Bertness (1989) showed that intense recruitment actually enhanced survival of the barnacle *Semibalanus balanoides* in more exposed areas by providing a buffer from physical stresses. When comparing graphs of percent cover at six sites and analysing SNK tests on means of percentage mortality and percent cover at six sites and three heights this notion is supported. At Sites 1 Low, 3 Low and 6 Upper where percent cover was least, mortality was greatest. When data for six sites were pooled, mortality and percent cover, and mortality and density of barnacles were not, however, negatively correlated and no relationship was found between percentage mortality and initial adult density, nor between percentage mortality and percent cover of adult barnacles. Despite this, survival of *Chamaesipho* was detrimentally affected in some areas of least cover at 1 Low, 3 Low and 6 Upper. It seems that site-specific characteristics may be implicated in determining these differences in mortality in these areas.

Juvenile mortality at six sites was also density-independent. Spatial patterns of settlers and adults were similar and did not reflect juvenile nor adult mortality patterns. Although adult mortality was similar among sites, most juveniles died at sheltered Site 4 and least at exposed Sites 2 and 5, and no differences in juvenile mortality occurred among heights. This does not fit the proposed model that fewer barnacles are found on exposed and upper shores as a function of differential mortality in these areas. Post-settlement mortality did not therefore determine adult populations of *Chamaesipho.* Also, because both juvenile and adult mortality of *Chamaesipho* were found to be density-independent at Cape Banks, this study supports Connell's (1985) statement that initial settlement determines adult densities when juvenile or adult mortality of barnacles is density-independent.

Even though percentage mortality of juveniles was estimated only for the period of settlement from July to December of each year whereas adult percentage mortality was an annual estimation, juvenile mortality was still found to be much greater than adult mortality. This difference in juvenile and adult mortality at six sites suggests that different mechanisms are operating to influence mortality at different stages of the life cycle of *Chamaesipho* and that juveniles are more "fragile" than established adults.

In fact, juvenile populations of *Chamaesipho* at Sites 3 and 4 were modified by the presence of the limpet *Cellana* but results do not suggest that this effect was sufficient to carry through to adult populations. *Cellana* occurs in patches of free space among *Chamaesipho* and was found to affect numbers of juveniles that occupied these spaces. *Cellana* possesses a radula with a few large teeth in each row which enables the limpet to forage for diatoms and algal spores among cracks in the substratum (Underwood, 1975, 1978). This could explain its influence on survival of young barnacles. Analysis of pooled fenced and unfenced data emphasised that the presence of *Cellana* had a deleterious effect on survival of young *Chamaesipho.*

Although juvenile mortality was much greater than adult mortality at six sites, it is interesting that in this study from late 1989 to late 1993, the spatial paterns of settlement of juveniles (Site 3 = 4 > 5 = 2 > 1 > 6) reflected adult patterns (Site 3 = 4 > 5 = 2 = 1 > 6). That is, despite great post-settlement mortality of settlers, juvenile patterns were retained in the adult stage and post-settlement mortality merely acted to reduce juvenile populations evenly across sites and heights. Also, at Site 4 when settlers from November 1993 were monitored on the substratum, in July 1994 patterns of older 1993 recruits corresponded to patterns of randomly selected adults, and to the earlier patterns of settlement. At six sites, relationships were also found between total numbers of barnacles that settled each year and the numbers of these settlers that remained at the end of each year from 1989 to 1993. In Chapter 4 it was also shown that, when data was pooled for six sites and three heights from 1989 to 1993, there was a strong relationship between total annual density of settlers and total annual density of adults. This again indicates that *initial settlement,* rather than *post-settlement mortality,* is an important determinant mechanism for distributions of populations of *Chamaesipho.*

Earlier in this thesis (see **Chapters 3 and 4**) it was shown that larval supply determines juvenile distributions of *Chamaesipho* and behavioural responses of cyprids will influence numbers that settle. Results in this chapter on juvenile and adult mortality, and spatial patterns of settlers and adults, also suggest that larval supply and settlement, *not* post-settlement mortality, are crucial to the formation of adult distributions of *Chamaesipho.* Even though post-settlement mortality of juveniles was high, especially when *Cellana* was present, and juvenile densities were modified, its effect was not sufficient to change the original juvenile patterns of distribution. That is, patterns of differential numbers of cyprids that arrived and settled at Cape Banks were maintained in adult distributions despite juvenile and adult mortality.

CHAPTER SIX

SIZE AND GROWTH

6.1 Introduction

Other studies have shown that environmental cues will influence growth of barnacles (Bertness, 1989; Bertness et al., 1991). Rates of growth in barnacles will vary under differing conditions of wave-exposure (Bertness, 1989; Bertness et al., 1991) and in species of barnacles where adjoining walls fuse (Connell, 1961a; Luckens, 1975; Hui & Moyse, 1987). Bertness et al. (1991) recorded greater growth in *Semibalanus balanoides* in low tidal areas where barnacles were dense and where water velocity and wave-exposure were large, rather than in upper habitats or those with smaller wave-exposure or velocities. Crisp (1955, 1960) also found an association between increased current flow and growth of barnacles. Increased growth of *Semibalanus* in exposed habitats (Hatton & Fischer-Piette, 1932; Moore, 1934, 1935; Crisp, 1955) can also be linked to reduced algal cover in these areas (Barnes, 1955). Similarly, Luckens (1970) found that the barnacle *Chamaesipho brunnea* in New Zealand grew faster when submerged for longer periods but rates of growth were density-independent. That is, the more dense populations in the upper range of distribution of this species had slower rates of growth than sparse populations lower on the shore.

Apart from faster growth, adults may be of different sizes because they grow for longer periods or because they survive longer in some areas. Three models were therefore proposed to explain the differences in size of adult *Chamaesipho tasmanica* in different sites at Cape Banks. The first model is that barnacles may grow faster at some sites - they therefore finish up larger in these areas. It was predicted that, if the same cohort of barnacles was measured from juvenile (< 1 mm) to adult sizes, rate of growth of these juveniles in different areas should be correlated with the sizes of adults in these areas. The second model proposed that barnacles grow at the same rate, but have longer periods of growth in some areas - they therefore finish up larger in these areas. It was predicted that, if juveniles from the same cohort were measured from settlement, the periods during which barnacles in different areas grew should be correlated with sizes of adults in these areas. The third model is that barnacles keep growing but live longer at some sites - they therefore finish up larger in these areas. Therefore, if juveniles from the same cohort were measured there should be a correlation between longevity of these juveniles and size of adults. Greater longevity will be recorded in areas where barnacles are relatively large.

6.2 Size

Earlier studies used basal-length of barnacles as a measure of size and growth (Barnes & Powell, 1950; Crisp, 1960). In dense populations of *Chamaesipho*, shells of adults fuse. Aperture-length along the rostro-carinal axis, as used in studies on other local barnacles (Denley & Underwood, 1979; Otway & Anderson, 1985; Otway & Underwood, 1987), is also a good estimator of size and growth in this species because aperture-length was positively correlated with shell-length (Fig. 6.1).

6.2.1 Sampling Design and Methods

Measurements were taken from processed black and white negatives of barnacles photographed in the field at Sites 1 to 6 (see **Chapter 2: Fig. 2.7**) using an Image Analyser with binocular microscope and camera attachments (for method see **5.2.1**). To determine the sizes of *Chamaesipho* in different places at Cape Banks, five barnacles were randomly selected and measured from black and white negatives of each replicate from 1989 and 1992 .

Size-frequency distributions of *Chamaesipho* at Sites 3, 6 and 2 (see **Chapter 2: Fig. 2.7**) at Low, Mid and Upper heights, respectively, within the barnacles' range, were also measured from black and white negatives of each replicate (n = 3) in October 1989 and October 1992. Again, aperture-lengths were measured with an Image Analyser (for method see **5.2.1**).

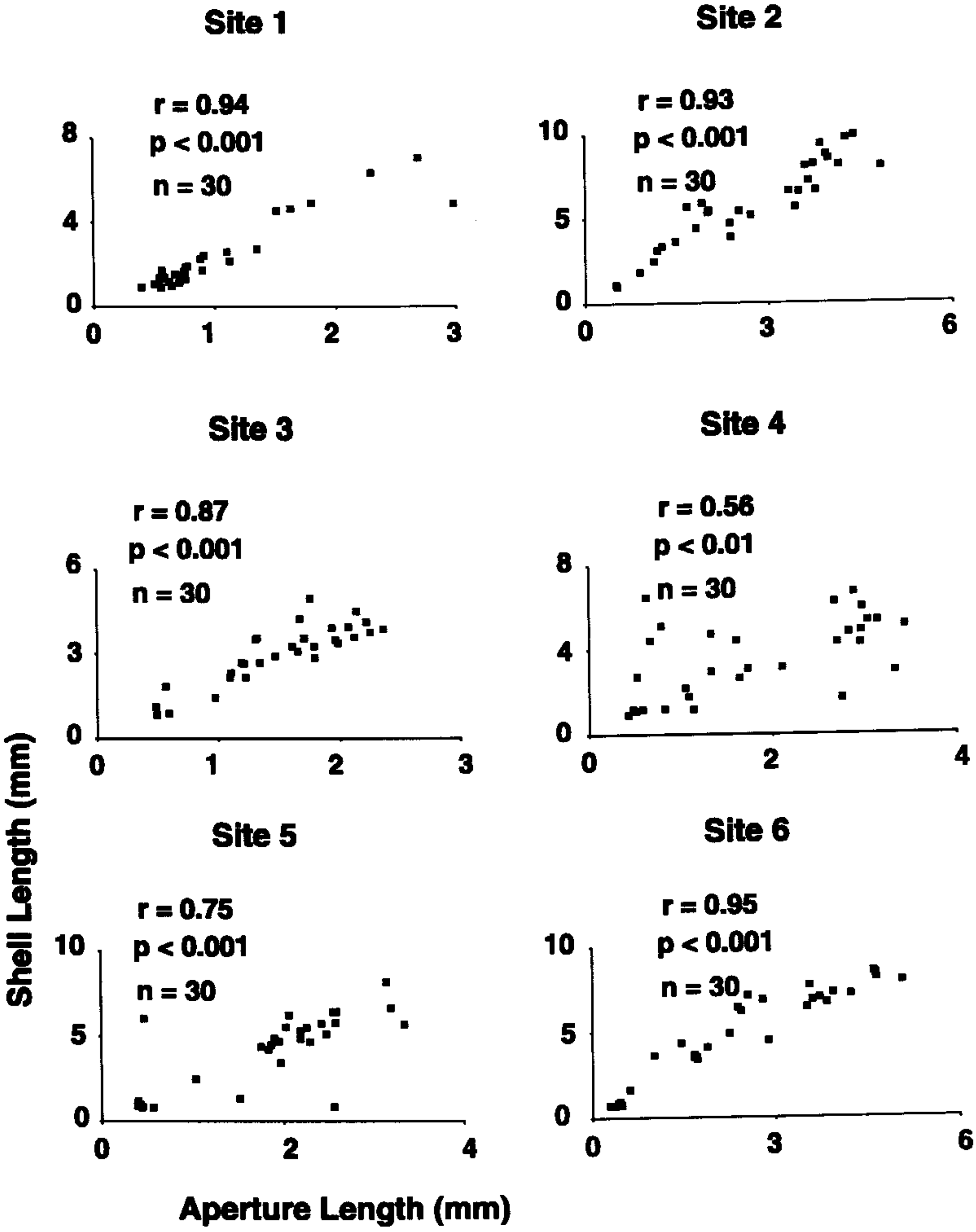

Fig. 6.1

Relationship of shell-length (mm) and aperture-length (mm) of *Chamaesipho* at six sites. Correlations were calculated separately for each site on pooled raw data from 10 barnacles randomly sampled from black and white negatives photographed in October 1989 on Low, Mid and Upper heights at each site.

6.2.2 Results

The largest barnacles were found at exposed Site 6 and the smallest at sheltered Site 3. Barnacles were generally larger on Mid and Upper heights at Cape Banks (Fig. 6.2; Table 6.1). Size differences were recorded among sets of replicates on semi-exposed Site 5 and exposed Sites 1, 2 and 6, and all of these sites are higher than the sheltered Sites 3 and 4 (see **Chapter 2: Table 2.1**).

Table 6.1

Mean size (mm) of mixed cohorts of barnacles ($n = 5$) in each of three replicates nested in Low, Mid and Upper heights of *Chamaesipho's* distribution on the shore at six sites: data are from the end of each year in 1989 and 1992.

	1989		**1992**	
Place	Mean	SE	Mean	SE
Site 1 Low	1.14	0.23	1.83	0.20
Site 1 Mid	1.28	0.2	2.18	0.18
Site 1 Upper	1.37	0.2	1.83	0.18
Site 2 Low	1.53	0.24	1.27	0.12
Site 2 Mid	2.23	0.32	1.87	0.24
Site 2 Upper	2.2	0.31	1.9	0.19
Site 3 Low	1.04	0.06	1.22	0.04
Site 3 Mid	1.74	0.15	1.8	0.13
Site 3 Upper	1.48	0.13	1.62	0.08
Site 4 Low	1.42	0.18	1.73	0.17
Site 4 Mid	1.84	0.18	1.79	0.14
Site 4 Upper	2.38	0.28	2.39	0.17
Site 5 Low	1.95	0.17	1.72	0.16
Site 5 Mid	2.1	0.31	1.87	0.15
Site 5 Upper	1.67	0.22	1.98	0.11
Site 6Low	2.45	0.22	2.32	0.18
Site 6 Mid	3	0.41	2.56	0.26
Site 6 Upper	1.73	0.23	2.06	0.14

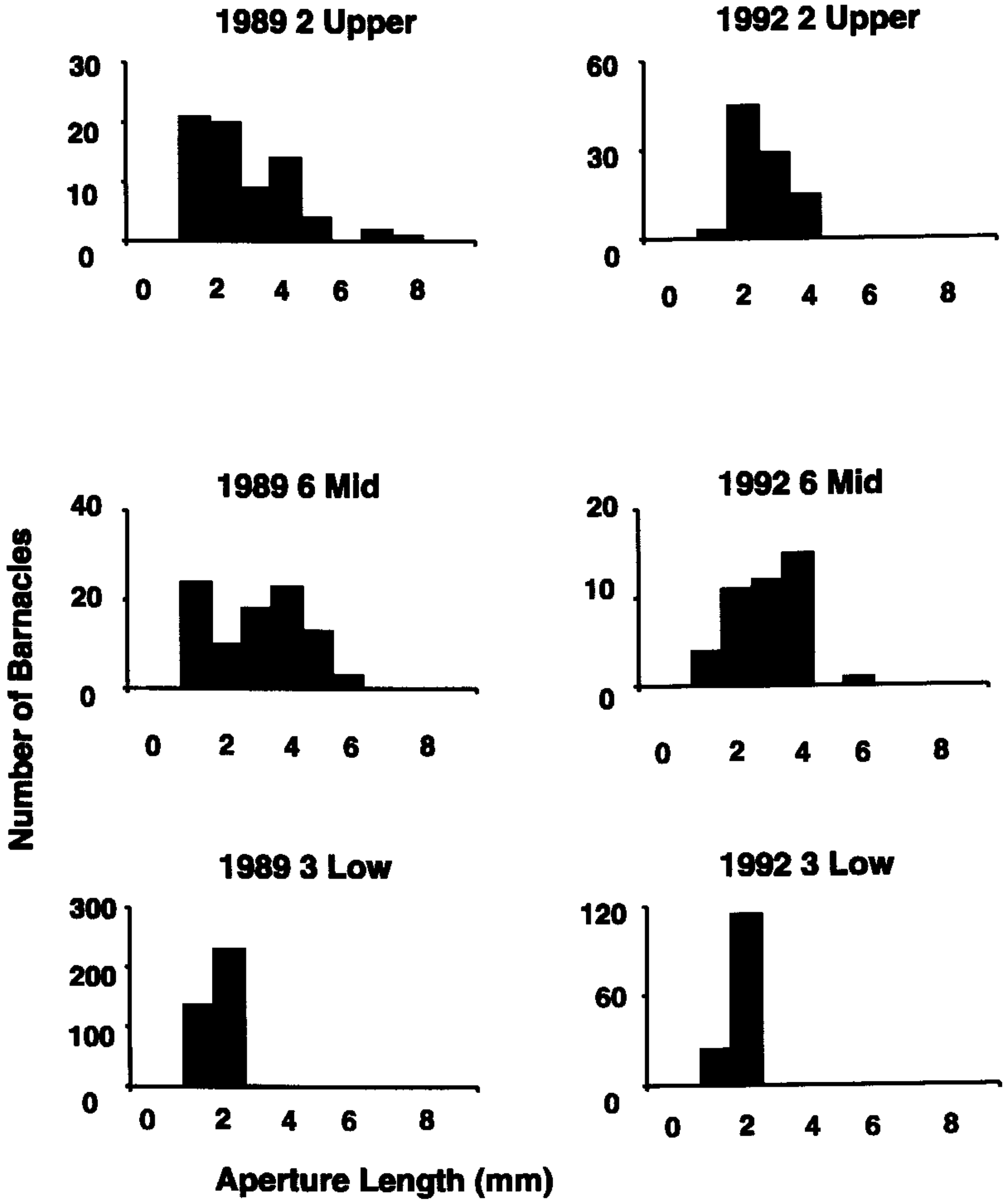

Fig. 6.2

Size-frequency distributions of *Chamaesipho* measured in three replicates on Low, Mid and Upper heights at Sites 3, 6 and 2, respectively, in late 1989 and again in late 1992.

6.3 Growth

6.3.1 Sampling Design and Methods

Using an Image Analyser and black and white negatives of each replicate at Low, Mid and Upper heights at six sites (for method see **5.2.1**), barnacles were sampled independently at the end of each year from 1989 to 1992. Barnacles were also mapped so that they could be aged at the end of 1992, so that longevity (the numbers of years that individual barnacles survived from when first measured in 1989) could be recorded. Growth was therefore calculated over three years from first settlement in 1989.

To test hypotheses derived from *Model 1*, correlations were first calculated between annual rates of growth and aperture-lengths for data at separate sites for juveniles (< 1 mm) first measured in 1989 and the same cohort measured again in 1992. (Because in most places very few barnacles settled in 1989 and survived to the end of 1992, only two juveniles in each replicate (n = 3) could be followed through adulthood over three years. Data are incomplete for Sites 4, 5 and 6 because juveniles that settled in some replicates in 1989 failed to survive to the end of 1992 (see **Fig. 6.3**)). The slope of regression b for growth-rate of these juveniles (< 1 mm) was used as the measure of growth-rate. So, correlations were calculated on b (see **Fig. 6.3**) at each of six sites from 1989 to 1992 and mean size of thirty adults (> 1 mm) randomly chosen from Low, Mid and Upper heights within *Chamaesipho's* distribution at each site. Correlations were also calculated between mean annual growth-rates of seven juveniles (because only seven juveniles survived at Site 6 in 1992) and mean size of thirty adults (> 1 mm) at each of six sites.

To test hypotheses derived from *Model 2*, aperture-lengths of two juveniles (< 1 mm) from each replicate (n = 3) at Low, Mid and Upper heights of *Chamaesipho's* distribution were measured at the end of 1989. Individuals from this cohort were subsequently measured at the end of each year to the end of 1992 and the data plotted. Graphs were examined and periods of growth (years) were estimated for each of six

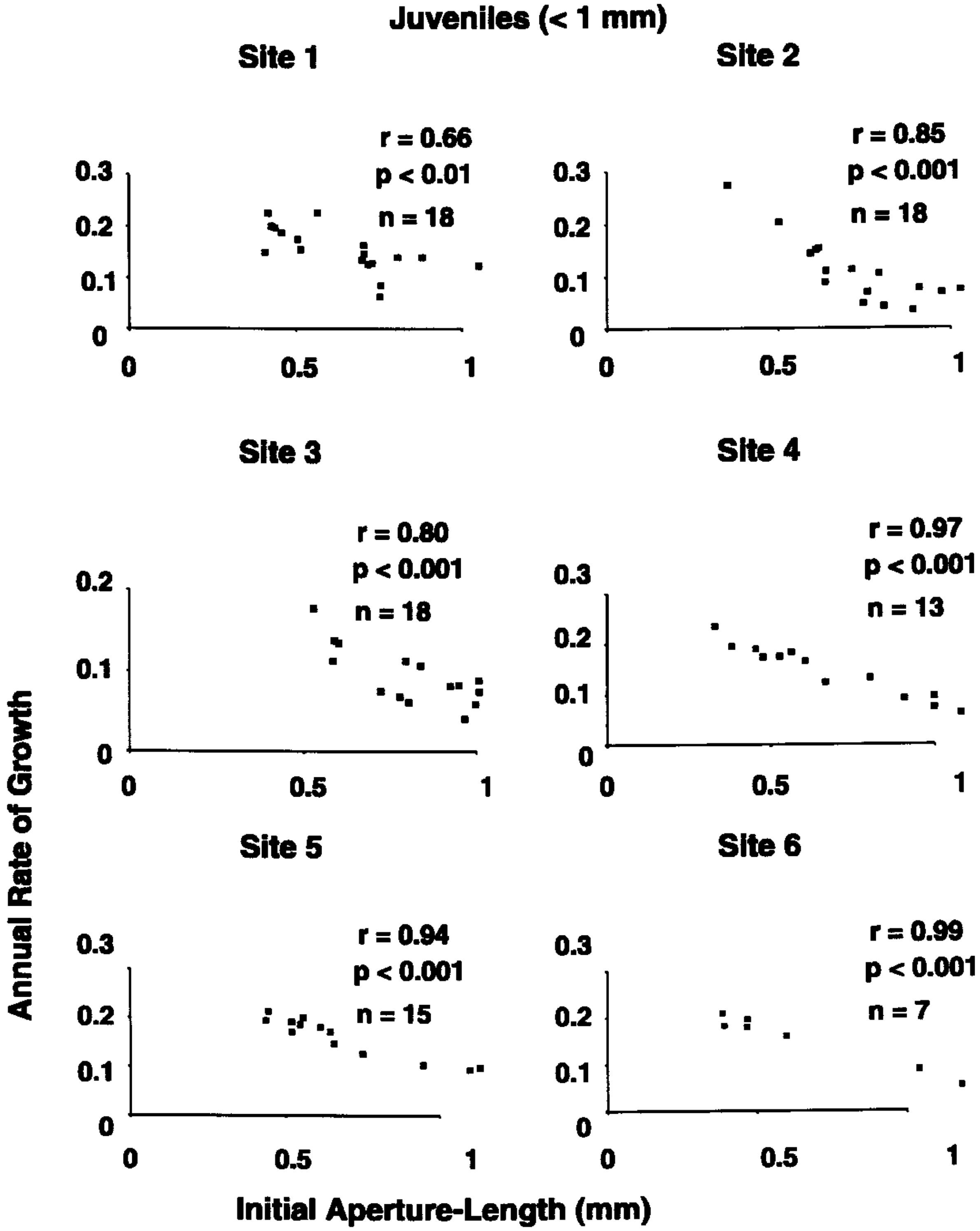

Fig. 6.3

Relationships between annual growth-rate and initial size of barnacles at each of six sites when two juveniles (< 1 mm) were measured from each of three replicates on Low, Mid and Upper heights at the end of 1989 and individuals in the same cohort were measured at the end of 1992. Numbers of cases varied because, in some replicates at Sites 4, 5 and 6, juveniles that settled in 1989 did not survive to the end of 1992.

sites by extrapolating down to the X axis from where each graph line first decreased in slope (see **Fig. 6.6**). A correlation between periods of growth and size of adults at each site was then calculated.

To test hypotheses derived from *Model 3,* fifteen small (1 – 2 mm) barnacles were randomly selected at each site and were traced from maps of replicates from 1989 to 1992. The number of years that each of these barnacles survived (longevity) was recorded. Correlations were then calculated between mean number of years that these barnacles survived and mean size of thirty adults (> 1 mm) randomly selected from six sites. Also, the percentage of older barnacles (> 3 years of age) in ten places in areas where barnacles were relatively large was compared with ten places in those areas where barnacles were relatively small.

Annual rates of growth were calculated as: $R = \log (L_t/L_0)/t$ where R = rate of growth; L_t = Aperture-Length at Time t; L_0 = Aperture-Length at Time zero; and t = Time in years (see Denley & Underwood, 1979; Underwood, 1984).

6.3.2 Results

When correlations were calculated on *b* the slope of regression from Fig. 6.3 and between mean size of adults (> 1 mm) at each site, no significant relationship was found (Fig. 6.4). Nor was there a significant correlation between annual growth-rates of juveniles first measured in 1989 and later in 1992 and mean size of adults at each site (Fig. 6.5).

When juveniles (< 1 mm) were first measured at the end of 1989 and individuals of the same cohort were measured at the end of each year up to the end of 1992 so that periods of growth (years) at each site could be estimated (see **Fig. 6.6**), periods of growth were found not to vary among sites (Fig. 6.7).

While no significance was recorded, there was a relationship between years surviving (longevity) of small (1 – 2 mm) barnacles and mean size of adults at each

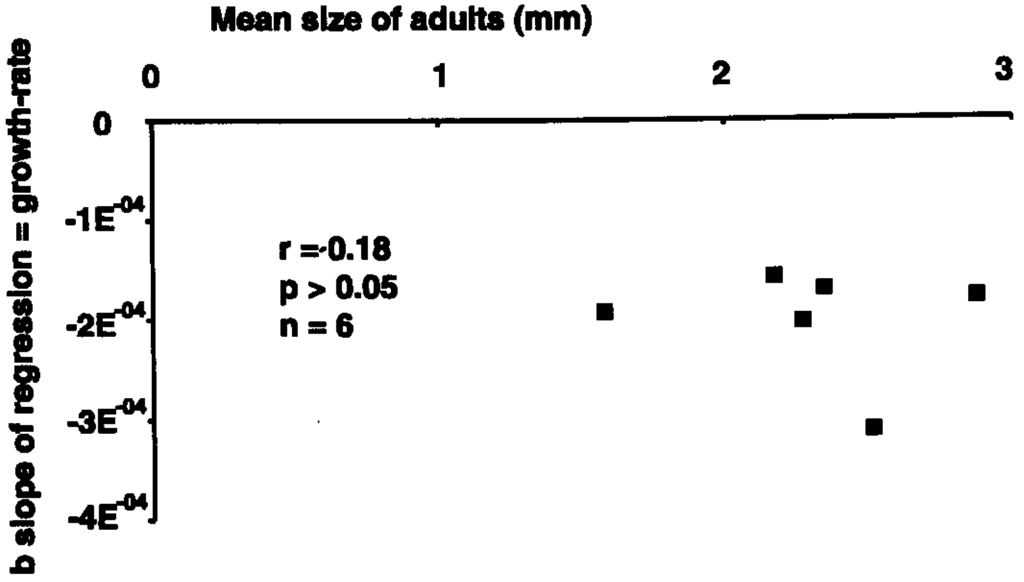

Fig. 6.4

Relationship between *b*, the slope of regression (see **Fig. 6.3**) for rate of growth of juveniles (< 1 mm) first measured in 1989 at each of six sites and mean size of 30 adults (>1 mm) on Low, Mid and Upper heights of *Chamaesipho's* distribution in six sites.

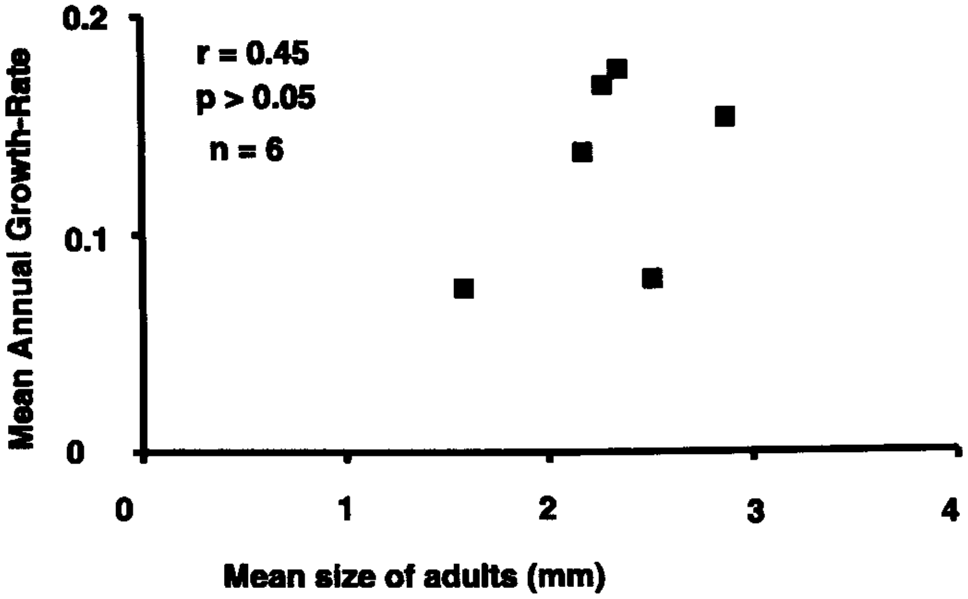

Fig. 6.5

Relationship between mean annual rates of growth ($n = 7$) of juveniles (< 1 mm) first measured in 1989 (see **Fig. 6.3**) and mean size of 30 adults (>1 mm) on Low, Mid and Upper heights of *Chamaesipho's* distribution in six sites.

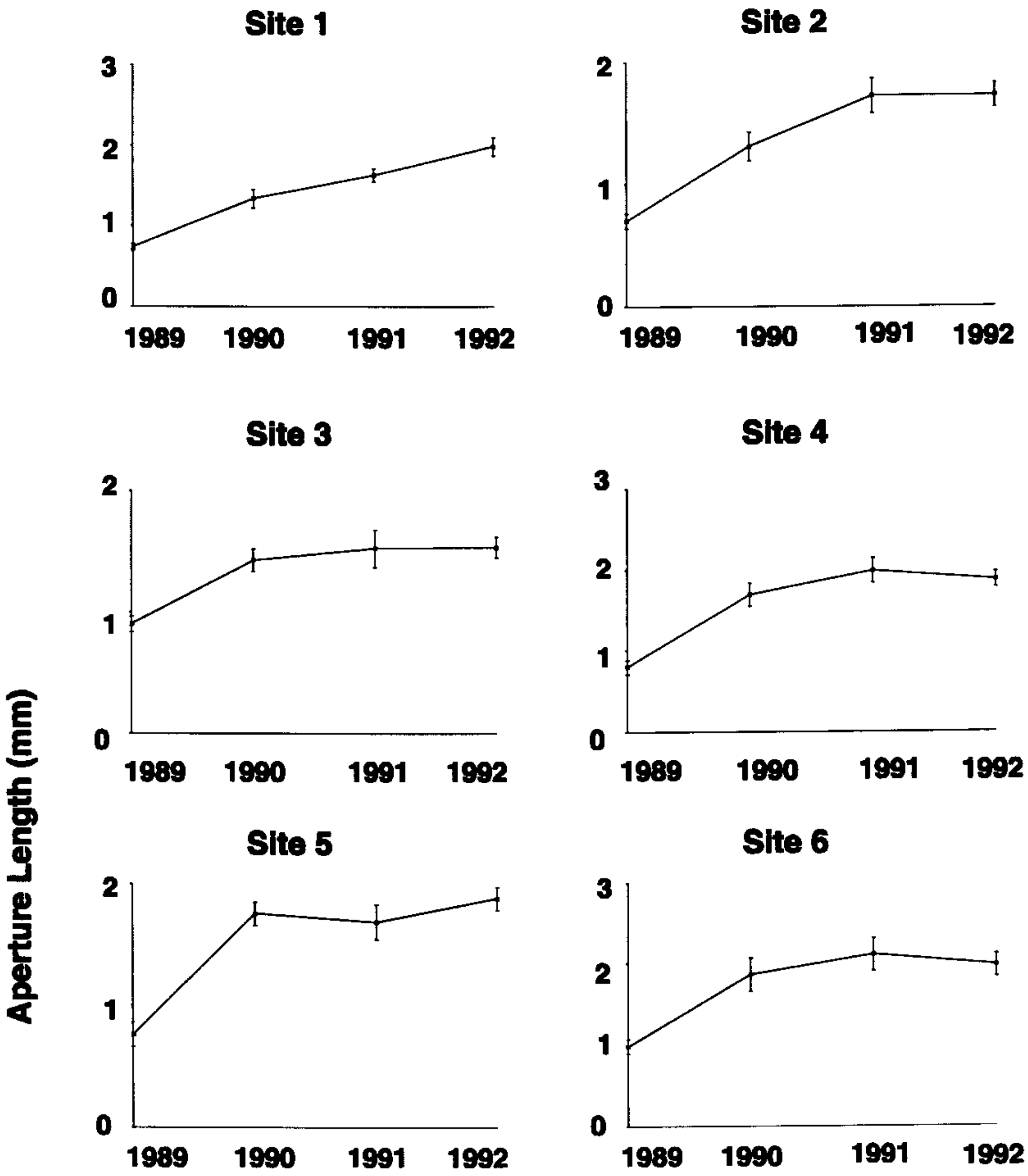

Fig. 6.6

Mean size of juvenile (< 1 mm) barnacles (n = 18) measured at the end of each year from 1989 to1992 in each of six sites at Low, Mid and Upper heights of *Chamaesipho's* distribution.

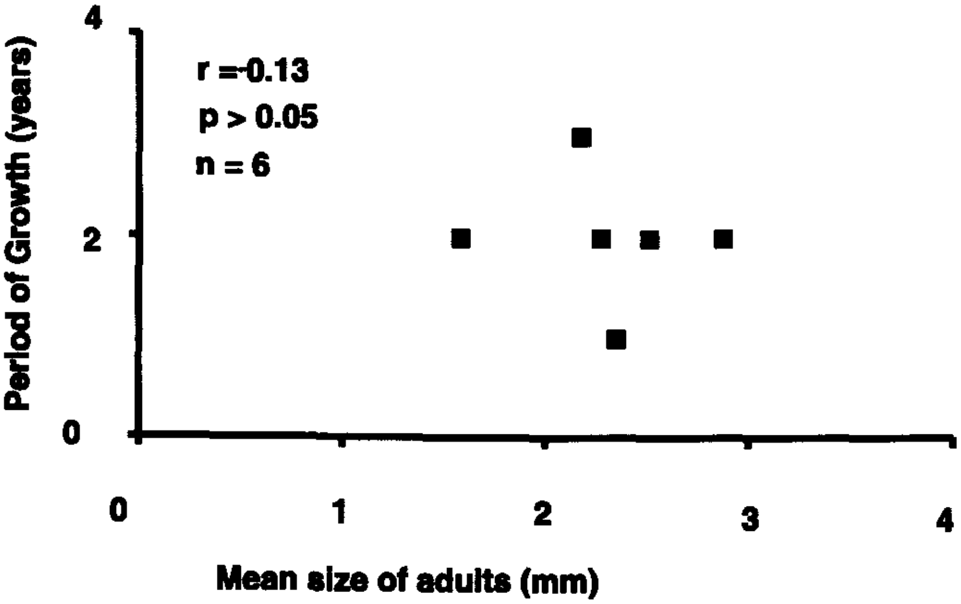

Fig. 6.7

Relationship between periods (years) of growth of juvenile (< 1 mm) barnacles (*n* = 18) measured at the end of each year from 1989 to 1992 and the mean size of 30 adults (> 1 mm) at each of six sites at Low, Mid and Upper heights of *Chamaesipho's* distribution.

site (Fig. 6.8). That is, where barnacles were larger, longevity was also greater. When percentages of old barnacles (> 3 years of age) recorded at the end of 1992 were compared in areas predominated by large and small barnacles, respectively, a greater mean percentage of older barnacles (> 3 years of age) was found in areas predominated by large barnacles (60.36%; SE = 4.04) than in areas with mainly small barnacles (19.27%; SE = 3.45). These results indicate that longevity varies among areas at Cape Banks and that increased longevity of juveniles through adulthood in some areas will determine that larger barnacles will predominate in these areas.

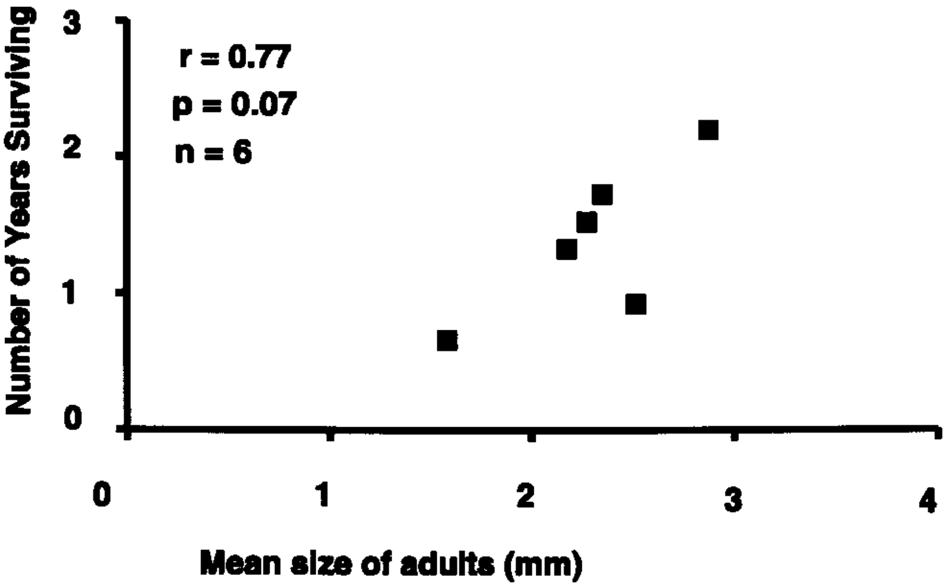

Fig. 6.8

Relationship between mean survival years (n = 15) of barnacles and mean size of 30 adults (> 1 mm) in each of six sites at Low, Mid and Upper heights of *Chamaesipho's* distribution.

6.4 Discussion

Hypotheses pertaining to the proposed three growth models were tested to determine the influence of rates of growth, different periods of growth and longevity on size of barnacles. There was no relationship between the growth of juveniles from the end of 1989 to the end of 1992 at each site and the mean size of adults at each site. That is, faster rates of growth were not found to influence the presence of large barnacles. Similarly, periods of growth did not differ when juveniles were measured from 1989 to 1992.

While variation in rates of growth and in periods of growth did not determine that larger barnacles occupied some areas at Cape Banks, longevity was found to influence the size differential of *Chamaesipho*. For example, longevity of small barnacles was correlated with mean size of adults at each site. Also, a greater percentage of older barnacles (> 3 years of age) occupied areas predominated by large barnacles, especially on upper and exposed shores. That is, in areas with predominantly large barnacles, survival is greater and barnacles live longer. These results emphasise that differential longevity functions to determine size distributions of *Chamaesipho*.

Although factors determining differences in longevity are unknown, because a size differential was recorded at Cape Banks, site-specific characteristics are implicated. Earlier (see **Chapter 5**) it was shown that the whelk *Morula marginalba* influenced distributions of *Chamaesipho* at sheltered Site 3 Low so that only small barnacles of one or two cohorts inhabited these low areas. In very exposed areas *Morula* are swept away by waves (Moran, 1985a). Perhaps barnacles are larger on exposed and upper shores such as Site 6 because there are fewer *Morula* to prey on barnacles. Larger barnacles may also be better equipped to withstand the greater physical extremes of temperature and desiccation in these exposed areas. It could also be that, because other studies have found that differential availability of food may influence growth in barnacles (Bourget & Crisp, 1975; Otway & Anderson, 1985; Bertness et al., 1991), availability of food may also influence longevity of *Chamaesipho*, and therefore the size differential, so that larger barnacles were recorded on exposed shores at Cape Banks. Site-specific influences are therefore emphasised in processes determining the size distribution of *Chamaesipho* at Cape Banks and more research is necessary.

CHAPTER SEVEN

GENERAL DISCUSSION

7.1 Local Consequences of Studying *Chamaesipho*

Unlike some previously described species, the rocky shore honeycomb barnacle *Chamaesipho tasmanica* in New South Wales has abundant free space for settlement in areas where barnacles do not coalesce, but relatively few cyprid larvae arrive. These larvae are gregarious when settling. This behaviour is similar to that of some other Chthamaloid barnacles *Chamaesipho brunnea* and *Chamaesipho columna* in New Zealand (Luckens, 1970, 1975) and *Chthamalus anisopoma* in California (Raimondi 1988a, 1988b, 1990, 1991). Raimondi (1991) contrasted the models of *larval delivery* (larval supply) and *larval behaviour* (larval choice) and found that larval behaviour at settlement determined the distribution of adult barnacles.

There have been very few examples in the literature where most stages of the life-cycle of barnacles have been studied to explain the observed patterns of abundance (but see Yoshioka, 1982; Roughgarden et al., 1988; Hurlbut, 1992; Ross, 1992; Carlon & Olson, 1993; Meekan et al., 1993). Yet any stage may influence patterns of distributions of adults. In this thesis, the life-history of *Chamaesipho* after arrival from the plankton was studied to elucidate the relative importance of each stage in determining the spatial and temporal distributions of adults at Cape Banks. Underwood and Denley (1984) emphasised the importance of recruitment as a process for determining the abundance and distribution of populations. By its very nature, however, an intensive sampling programme precluded many previous workers from quantifying larval supply and settlement in the field. This study concentrated on larval supply and settlement and compared the effects of these processes with the influences of mortality on abundance of *Chamaesipho*.

Otaiza (1989) suggested that spatial abundance and distribution of *Chamaesipho* at Cape Banks in 1986 and 1987 were determined by differences in total recruitment, survival or both. The present study found that *initial settlement* (larval supply and larval choice) determined the demography of *Chamaesipho* at Cape

Banks. The alternative model that *post-settlement mortality* determined the distributions and abundance of juveniles and adults was not supported by experiments. Otaiza (1989) also suggested that recruitment of *Chamaesipho* was episodic, rather than continuous. Here, larval arrival and settlement were typified by trickles of larvae from late July to December. Major pulses of arriving cyprids were also recorded once or twice each year from 1989 to 1993.

A consistent spatial pattern of greater larval arrival at one site indicated that site-specific characteristics have much more influence on the demography of populations of this species than was previously thought. Cyprids of another species, *Tetraclitella purpurascens*, were also, at times, caught in traps with *Chamaesipho*. Cyprids of the two species are similar in size, but had consistently different patterns of larval arrival when submersion times and water-flow were similar. Thus, passive movement of cyprids must be discounted. Other studies have shown that larval dispersal is generated by meteorological conditions and the associated hydrodynamics (Farrell et al., 1991; Roughgarden et al., 1991, 1994; Milicich, 1994; Pineda, 1994b) although currently very little is known about dispersal patterns of broadcast nauplii and cyprid larvae. *Chamaesipho* larvae arrived at Cape Banks from late July to early December, with main peaks once or twice each year, generally in September, October and November, 1989 to 1993. Intense storms with high speed Southerly winds and huge waves were also recorded from July to October each year although no cyprids arrived and settled when very strong winds and seas predominated. Wave height and direction are implicated in mechanisms determining larval supply of *Chamaesipho*, and major peaks of larval arrival were always close to, or on, new and full moons in association with high velocity Southerly winds.

Larval supply, enhanced by the gregarious response of larvae to adult conspecifics, determined distributions of juvenile *Chamaesipho*. Cyprids settled gregariously in response to the presence of adults and (sometimes) to the presence of barnacle extract. They settled in decreasing numbers with increasing distance from adults. Settlement was not induced by the presence of other, already established new settlers, but older recruits did induce settlement. Otaiza (1989) transplanted cores of rock from inside to below the normal distribution of adults. Larvae only settled on cores with adults. Here, above the distribution of adults, there was a positive response to barnacle extract. Within the distribution of adults, extracts of crushed shells and tissues of barnacles did not always elicit a response by settlers. The causes of mixed results in response to the presence or absence of barnacle extract are, as yet, unknown.

Previous studies on settlement in different-sized patches have standardised data by dividing by surface areas (Sousa, 1984; Le Tourneux & Bourget, 1988; Raimondi, 1990). In gregarious species, because of the influence of resident adults at perimeters of patches, (Raimondi, 1990; Minchinton, 1997 in press) there is a need to measure perimeter, especially when data from different sizes of patch are to be compared. When numbers of total settlers of *Chamaesipho* in different-sized patches (6 cm, 3 cm, 1.5 cm) were multiplied by Perimeter/Surface Area ratios, barnacle extract was detected to induce settlement. Thus, most larvae may have settled in smallest patches because these patches have the greatest exposure to adults along their perimeters. This means that larvae arriving to settle in small patches would be more susceptible to chemical cues produced by adults along the edge of these patches than would be larvae arriving to settle in larger patches, regardless of the presence of extract. Similarly, in densely populated areas, when new settlers were removed (Removals) or not removed (Controls) daily from different-sized patches painted with extract, settlement was greatest in smallest (1.5 cm) patches. In sparsely populated areas there was no difference in settlement with size of patch. Therefore, cues from barnacles on the fringe of patches effectively overrode any cues from extracts of barnacles. Where there was no extract, most colonisation occurred in the smallest patches examined. These results have important ecological implications for the survival of this gregarious barnacle because fewer cyprids would settle in large areas of bare space typical of disturbed areas.

Jernakoff (1985c) found that the barnacle *Tesseropora rosea*, which occurs in association with *Chamaesipho* in some places at Cape Banks, also settled more densely in smaller (25 cm^2) than in larger (200 cm^2) patches. In contrast, Denley (1981) found that there was no difference in densities at settlement of *T. rosea* in large (400 cm^2 and 100 cm^2) and small (25 cm^2) patches. In even smaller (4 cm^2) patches, however, her results were very variable and often no barnacles were recorded in these patches, even in similar sized subquadrats within larger quadrats. This is consistent with findings that *Tesseropora* settle on bare spaces (Denley & Underwood, 1979).

In this study, where small patches were 1.77 cm^2 in area and large patches were 28.28 cm^2, generally more *Chamaesipho* were recorded in small patches. This corroborates Otaiza's (1989) findings and other results from this study which have shown that *Chamaesipho* is gregarious. Although gregarious versus non-gregarious behaviour when settling may be causing different patterns of settlement between *Chamaesipho* and *Tesseropora*, respectively, the actual mechanisms which contribute to inconsistent results within each species, with respect to numbers settling in different patch sizes, are as yet unknown. I suspect, however, that spatial variation in larval supply may be a major causative factor and larval choice when settling may also be implicated.

Overall, when the effects of initial settlement on populations of *Chamaesipho* were investigated at Cape Banks, many more larvae arrived within the area of *Chamaesipho's* distribution than at upper heights outside the limits of distribution. Numbers of settlers recorded on the substratum varied at a spatial scale of a few centimetres. Despite this, manipulated settlement cues, such as the presence of barnacle extract, older recruits and small patch size, induced settlement. In some areas there was no significant difference between treatments. This may be because fewer larvae arrived, or fewer larvae settled due to unknown interactions. The importance of site-specific characteristics in determining differences in larval supply and larval choice cannot be overemphasised.

Historically, post-settlement mortality was thought to be implicated for other species of barnacles (Connell, 1985). In this study, analyses of data showed that, despite great post-settlement mortality of juveniles, spatial patterns of settlers and adults were similar and were not altered by juvenile nor adult mortality. That is, juvenile spatial patterns were retained by adults. Post-settlement mortality merely acted on settlers evenly across the six sites studied. Differential mortality was therefore rejected as a model for causing the sparse populations of barnacles on exposed and upper shores.

There were, however, some differences among heights among sites, particularly at Site 3 Low and Site 6 Upper. Variation in spatial abundance and distribution of populations of *Chamaesipho* was therefore not considered to be due to differences in adult mortality except in unusual circumstances such as in years when settlement and recruitment were negligible, or at Site 3 Low where predation by the whelk *Morula marginalba* occurred, or on very high exposed shores, or when sheets of older larger barnacles were detached (pers. obs.). These isolated incidences of intense adult mortality are, however, relatively uncommon and, overall, have only localised influences on patterns of distribution.

For example, Site 3 Low was characterised by very small barnacles only one to two years old with aperture-lengths less than 1 mm. Large densities of small (10 mm) *Morula* were recorded preying on *Chamaesipho* at Site 3 Low from April to July 1992 when many replicates contained 50% empty shells. Predation may therefore maintain the uniform small size of *Chamaesipho* characteristic of Site 3 Low and determine adult patterns even though large numbers of larvae initially settled and recruited. Where the habitat is suitable for predators, post-settlement mortality may be more important than initial settlement for the demography of *Chamaesipho*. Similarly, Connell (1970) found that on low shore areas at San Juan Island where predation was great, populations of the barnacle *B. glandula* were diminished.

Although there has been excellent work by Fairweather et al. (1984) on predation by *Morula* on *Chamaesipho*, they obtained conflicting results at different locations. Further research is required to elucidate the effects of *Morula* on populations of *Chamaesipho* at different sites, because it seems that site-specific characteristics have much more influence on barnacle populations than was originally thought. Here, predation was sporadic and only isolated areas (particularly Site 3 Low) were heavily preyed on by *Morula*. Similar to Moran et al.'s (1984) observations, very small whelks preyed on tiny barnacles although *Chamaesipho* is not a preferred prey species (Fairweather et al., 1984). Only at Site 3 Low were there plenty of crevices and this is consistent with the relationship between availability of crevices and predation (Fairweather et al., 1984; Moran, 1985b; Fairweather, 1988c, 1988d). It may therefore be that not only do properties of a site determine the numbers of larvae that arrive and then settle, but properties such as microtopography, food and shelter, will determine whether a habitat is also favourable for predators. Mortality of *Chamaesipho* is normally density-independent, but, when conditions favour the presence of *Morula*, mortality may become density-dependent so that initial settlement no longer has a primary role in determining population densities (Connell, 1985).

Site 6 had the most wave-action and was the highest site sampled in this study. There was virtually no difference in height above MLWS between low (2.95 m) and upper (2.96 m) heights at Site 6 even though the upper height was more than 1 m further up the shore. Despite this, barnacle numbers progressively decreased from low to mid to upper heights within *Chamaesipho's* distribution as distance up the shore increased at Site 6. It may be that differential larval supply and recruitment determine these differences in demography in this area. Early studies on barnacles, however, showed that physical factors such as temperature and desiccation determined the upper limits of vertical distribution and influenced population densities (Connell, 1961a, 1961b, 1975). In this study, there was greater mortality of adult *Chamaesipho* only on the upper shore at Site 6. Here, mortality may override the process of larval supply to influence numbers of barnacles. An investigation into larval supply on exposed shores is therefore warranted.

Experiments using the limpet *Cellana tramoserica* showed that more mortality of new settlers of *Chamaesipho* occurred when *Cellana* was present, and that there was no significant difference in mortality when fences were present or absent. This indicates that other grazers either had no effect on young *Chamaesipho*, or that *Cellana* densities in experimental plots were high enough to swamp the effect of natural grazers on juvenile populations of barnacles.

Because *Cellana* does not affect adult populations of *T. rosea* (Denley & Underwood, 1979; Denley, 1981; Underwood et al., 1983) and because, in this study, mortality of adult barnacles was similar among sites and heights whether the limpet and other grazers such as *Patelloida latistrigata* and *Nerita atramentosa* were naturally present or absent, *Cellana* was not thought to cause mortality in adult populations of *Chamaesipho*. Because this study has also shown that spatial patterns of adults were the same as those of settlers, it is assumed that *Cellana* can only affect distributions of early juveniles and, once new barnacles establish, the influence of *Cellana* is reduced.

Different processes operate after settlement to determine the variation in sizes of *Chamaesipho* recorded at Cape Banks. Hypotheses from three growth models were tested for their influence on differential size of barnacles. When juveniles were measured from the end of 1989 to the end of 1992, it was found that differential longevity, rather than variations in rates of growth or in periods of growth, drove the size distributions of *Chamaesipho* at Cape Banks, with larger barnacles inhabiting exposed shores. Also, a greater proportion of older barnacles (> 3 years of age) occupied areas dominated by large barnacles, especially on exposed shores. That is, increased longevity influenced the presence of large barnacles on exposed shores at Cape Banks and determined that larger barnacles continued to predominate in these areas.

In summary, *initial settlement*, **not** *post-settlement mortality*, is paramount in determining spatial abundance and distributions of *C. tasmanica*. While differential longevity will influence sizes of adults in some areas, this study has shown that both larval supply and larval choice are important processes that determine the initial patterns of distribution and abundance of juveniles as well as the ultimate distributions of adults. Mechanisms determining larval availability and settlement are very complex: dispersed, metamorphosed larvae must return (or arrive from another source) and then select substrata on which to settle. Factors influencing larval supply include currents, wind direction, wind speed, wave direction, wave height, lunar cycles, small-scale hydrodynamics, topography of the substratum and position in the water column, whereas those found to enhance larval choice at settlement include the presence and proximity of adult conspecifics and older recruits, and small patch size.

At Cape Banks, in areas which favour the arrival and settlement of large numbers of cyprid larvae, if it were not for predation by the whelk *Morula*, bulldozing and pre-emption of space by the limpet *Cellana* (Underwood et al., 1983), smothering and pre-emption of space by algae (Denley & Underwood, 1979; Underwood & Denley, 1984), artificial and natural disturbances, *Chamaesipho* could probably eventually occupy all available space. This assumes that the larval supply was sufficient. In this study, however, very few larvae arrived and settled relative to the free space available.

7.2 General Issues from a Study of *Chamaesipho*

Many previous studies in the northern hemisphere have emphasised adult interactions as determinants of demography (Connell, 1961a, 1961b; Dayton, 1971; Paine, 1974) whereas, now, the importance of variable settlement and recruitment of juveniles has been recognised in processes determining populations of adults (Underwood et al., 1983; Underwood & Denley, 1984; Caffey, 1985; Minchinton & Scheibling, 1991; Pineda, 1994a). In fact, mechanisms which determine the abundance and distribution of adults may not be similar worldwide (Underwood, 1994). Currently, there is dissension in the literature about the relative importance of influences of juveniles and adults. Some authors have stressed the importance of *post-settlement mortality* (Connell, 1985) whereas others have emphasised *initial settlement* and the associated processes (Underwood & Denley, 1984).

In this study, *initial settlement* was found to determine the spatial patterns and abundance of juvenile and adult *Chamaesipho* despite relatively few cyprid larvae arriving to settle. Results of this study therefore fit the more recently proposed model that sparse recruitment will determine that patterns of adult numbers will match patterns of numbers of recruits (Connell, 1985; Carroll, 1996). The earlier models on settlement and survivorship pertained to those species which had unlimited numbers of larvae arriving, but limited space for these larvae to settle. Gaines and Roughgarden (1985), however, extended these ideas to include models which incorporated variable (small to large) settlement with space-limited recruitment. They postulated that populations with steady-state abundance were derived from small rates of settlement, whereas temporally oscillating populations were derived from large rates of settlement.

While the earlier studies emphasised that competition, predation and disturbance influence populations of sessile marine invertebrates (Connell, 1961a, 1961b; Dayton, 1971; Paine, 1974), more recently, *supply-side ecology* (Underwood & Denley, 1984; Underwood & Fairweather, 1989) and the influence of recruitment (Underwood et al., 1983; Underwood & Denley, 1984) as a driving force in determining demography of populations has gained momentum. It is interesting that, in the 70's and 80's it was also recognised that, if larval settlement was sparse, competition, predation and disturbance had relatively no influence on population abundance and distribution (Paine, 1974; Underwood & Denley, 1984; Sutherland & Ortega, 1986). Currently, *variation* in larval supply, and therefore, recruitment (Underwood et al., 1983; Caffey, 1985; Minchinton & Scheibling, 1991; Pineda, 1994a), and the *consequences* of variable settlement (Caffey, 1985; Fairweather, 1988a) have also gained attention, especially as an influence on interactions which maintain intertidal assemblages (Fairweather, 1988a; Underwood & Fairweather, 1989). The earlier ecological theory was based on northern hemisphere species with abundant larval supply and space-limitation when settling (Connell, 1961a, 1961b, 1985; Gaines & Roughgarden, 1985; Roughgarden et al., 1985, 1988), whereas now it is recognised that other processes operate when numbers of larvae arriving are relatively few (Roughgarden et al., 1985, 1987, 1988; Menge & Sutherland, 1987). That is, while species with these characteristics are still extant, maintenance of their status quo depends on a concordance of factors, as highlighted by this study on *C. tasmanica.* While the demography of *Chamaesipho* follows contemporary trends, its position in the realm of barnacles is compromised by the tenuous link between the adult and juvenile stages and its dependence on a combination of physical and biological factors acting in tandem to ensure adequate larval supply and maintenance of population abundance. In fact, during this study, numbers of *Chamaesipho* at Cape Banks decreased and, prior to Otaiza's (1989) study in 1986 and 1987, larval supply was scant or non-existent (Underwood, pers. comm).

Adult *Chamaesipho* occupy large tracts of substrata on sheltered mid-littoral estuarine shores in south-eastern Australia. Because numbers of barnacles at Cape Banks have noticeably decreased over the five years of this study and because larval supply is dependent on a concordance of numerous processes, long-term ecological studies are needed. Because this study demonstrated a consistent pattern of larval supply in one area at Cape Banks, larval supply of *Chamaesipho* also needs to be studied at various places.

Like *Chamaesipho*, the intertidal barnacle *Chthamalus fissus* on tropical rocky shores in Costa Rica is characterised by poor larval supply and abundant space for settling cyprids (Sutherland, 1990) but predation by fish and gastropods maintains space (Sutherland & Ortega, 1986). In the northern hemisphere, patterns of assemblages are influenced by predation by the seastar *Pisaster ochraceus* (Paine, 1974, 1984) but there is no similar major predator in Australia. Whelks are also important predators in the United States (Dayton, 1971; Menge, 1976; Lubchenco & Menge, 1978) and very much so in New South Wales (Underwood, 1994). In fact, predation in Australia is complex with different patterns exhibited in different areas with similar species (Underwood & Fairweather, 1986; Underwood, 1994). Australian research, however, implies that predation may be minor compared with the effects of recruitment on diversity of populations (Underwood et al., 1983). This study has also emphasised the importance of larval processes in determining numbers of *Chamaesipho* at Cape Banks, and has indicated that mortality, especially predation by whelks, plays a secondary role.

This study on barnacles has reinforced theory that encapsulates many other marine intertidal species. While it is recognised that arrival of larvae and their successful settlement and recruitment maintains assemblages on rocky shores (Underwood et al., 1983; Underwood & Denley, 1984; Underwood & Fairweather, 1989), terrestrial ecologists also accept that transport of propagules is inherent in processes governing population dynamics and maintaining assemblages of organisms (Roughgarden, 1989; Underwood & Fairweather, 1989). While *initial settlement* (including larval supply and larval choice) is integral to the spatial patterns of juvenile and adult *Chamaesipho* at Cape Banks, long-term ecological studies of larval supply, settlement and recruitment of *Chamaesipho* at various sites and shores on the eastern Australian coast are necessary to determine processes governing patterns of variation of this barnacle at larger spatial scales. Effects of *site-specific characteristics* on larval supply *and* on settlement *and* on longevity after settlement will then become even more apparent as major causative mechanisms for the demography of *Chamaesipho*. Ecological theory would therefore be enhanced by these proposed studies and could be extrapolated to concurrent studies on multiple marine and terrestrial species in Australia, and worldwide.

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