INTRASPECIFIC COMPETITION IN SEAWEEDS

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Gathering information about the sea, its chemistry, physics, and biology and their interacting mechanisms, should come right at the top of mankind's list of priorities. The more we know, the better we shall understand how far we can safely go in availing ourselves of the sea's resources, and the consequences of abusing our present powers as a dominant species and recklessly plundering or exploiting its most fruitful regions.

James E. Lovelock

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Summary

The role of intraspecific competition in seaweed populations was reviewed and compared to studies of terrestrial plants.

The natural population dynamics of visible plants of *Fucus vesiculosus* and *Himanthalia elongata* were described by destructive sampling techniques. Also, a non-destructive photographic sampling method was used to assess changes in populations of 'button' stage *H. elongata* populations. Populations were described by density, standing crop, size structure and reproductive potential. While size structures were often positively skewed in *F. vesiculosus*, in *H. elongata* plant size distributions tended to be less variable. Mature stands of *F. vesiculosus* exhibited 'seed' banks. Density manipulations of the two species revealed evidence that intraspecific interactions between plants were taking place. A study of the development of microscopic populations of *Fucus serratus* was carried out using an artificial substratum. While the distribution of sizes of female gametes and recently settled zygotes was normal, a strong positive skew of plant sizes developed. All three species exhibited substantial mortality and traced Deevey Type III survivorship curves. Self-thinning relationships were assessed.

Artificially created variable density populations of *F. serratus* and *Laminaria digitata* were grown in tank culture. Growth rate and survivorship were negatively density dependent. Dominance and suppression was the mechanism which brought about changes in plant size hierarchy, though these changes were sometimes masked by size specific mortality which selectively removed small plants from the populations. Light appeared to be the factor limiting growth. The effect that population structure itself had on constituent plants was assessed by artificially creating populations of *L. digitata* with different population structures. Populations with initially different structures converged through the effects of dominance and suppression, variability in growth rates and size specific mortality.

Intraspecific interactions between propagules of seaweeds was assessed in laboratory cultures. Negative effects of density on the growth and survival of *F. vesiculosus* and *F. serratus* germlings were found. In *F. serratus* germlings nutrient supply rather than light levels seemed to limit growth, though important interactions between density, nutrients and light were found over time.

The spatial pattern of *H. elongata* propagules settled under laboratory conditions was compared to populations of *H. elongata* 'buttons' on the shore. Refined nearest neighbour analysis revealed that while settled propagules exhibited a clumped or random pattern, plants in field populations were highly regular, which indicated that self-thinning resulted in spatial ordering in this species.

General Introduction

Chapman (1986*b*) pointed out that "Nearly all formal demographic studies of seaweed populations (single species) have been reported since 1980", and that "little attention has been given to the ecology of seaweeds at the organismic level". It is pertinent to note that of 150 pages devoted to seaweed ecology in a recent textbook, less than half a page was concerned with population dynamics (Russell and Fielding, 1981), a subject fundamental to our understanding of plant ecology (Silvertown, 1987).

I believe that the historical basis for studies of marine algal population dynamics has largely been dictated by the percolation of ideas from studies of terrestrial plant populations, and the inherent time lag in the take-up of such ideas. This time delay may be partly attributed to the introspective approach taken by many marine ecologists, often out of necessity rather than choice. Marine laboratories are often geographically isolated from their 'mother' institution and library facilities must be concentrated on the marine literature because of financial restrictions. Fortunately, as information technology progresses apace, the dissemination of information across disciplines should improve and with it will come an increased awareness of 'the wider picture'.

While the application of terrestrially derived ideas to marine populations is potentially dangerous if concepts are misapplied, it does allow the comparison of terrestrial and marine plant demography. This may encourage the formulation of generally applicable rules or laws. Furthermore, the different attributes of marine and terrestrial plants (*eg* presence/absence of root and water competition) may allow conclusions to be drawn regarding processes impossible to investigate in either environment alone (Cousens, 1986).

In view of prevailing relationship between terrestrial and marine plant demography I will attempt to synthesize what is known from studies of these two environments.

A few definitions

Population dynamics has been defined as the study of changes in numbers of organisms in populations and the factors influencing them (Russell and Fielding, 1981).

A prerequisite for the study of intraspecific competition is a monoculture (or pure stand) of plants. Naturally occurring algal monocultures are reputedly often found in the marine nearshore environment (Paine, 1984), but frequency of epiphytes, particularly of microalgal species, means that true monocultures are very rare. Paine (1984) pointed out "the spatial and taxonomic vagueness" of the term monoculture, and defined it as at least 80 % space occupation by a single species. It could be argued that a single plant could fill this criterion, and a fundamental definition should consider the scale of study both in terms of target species plant sizes and space.

When plants grow in dense communities, they may undergo competitive interactions for certain resources. For a long time it has been realised that competition has a profound effect on individuals within any monospecific population. Formal definitions of intraspecific competition are as diverse as publications dealing with it, though Clements, a plant ecologist, defined it thus: "when the immediate supply of a single factor necessary (for growth) falls below the combined demands of the individual plants, competition begins" (cited in Donald, 1963). Grime (1973) defined competition as "The tendency of neighbouring plants to utilise the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space".

The 'plastic response' of the competition-density (C-D) effect

The carrying capacity of any habitat is fixed and constant. As a population grows, a point is reached where no more biomass can be accumulated (growth) without loss of plant parts or mortality. When plants are competing for a resource, the form or size of plants in a population may be modified without

mortality taking place. This modification has been termed 'plastic response' (Harper, 1967). Plastic responses occur when plants are growing in a competitive environment and when individuals within the population alter aspects of their growth in relation to the density of the population. The greater the density, the stronger the response to stronger competitive stress within the population. Kira *et al.* (1953) demonstrated that when populations of plants are grown under identical conditions, after an initial period they start to exhibit plastic responses in mean plant weight as a result of intraspecific competition. Such populations can be fitted to a hyperbolic curve that relates mean plant weight to density. When plotted on log-log axes, a number of straight lines are shown. It is important to notice that the densities of the populations do not change with time (*ie* there is no mortality, Figure 1). A generalised equation can be developed which describes how such competing populations change with time (Kira *et al.*, 1953; Harper & White, 1970; Hutchings and Budd, 1981*a*):-

$w = kN^{a}$ Equation 1

where w is mean plant weight, N is plant density, a and k are constants. The linear relationship relating to the log-log plot is :-

$\log_{10}w = \log_{10}k - a\log_{10}N$ Equation 2

At time zero, the value of a is zero, indicating that mean plant weight is independent of density (*ie* the average weight per seed is similar when considering either many or few seeds). As growth occurs, the value of a increases and given sufficiently intense competition may reach 1, which indicates complete compensation for higher densities by lower mean weight. At this point the C-D equation will be:-

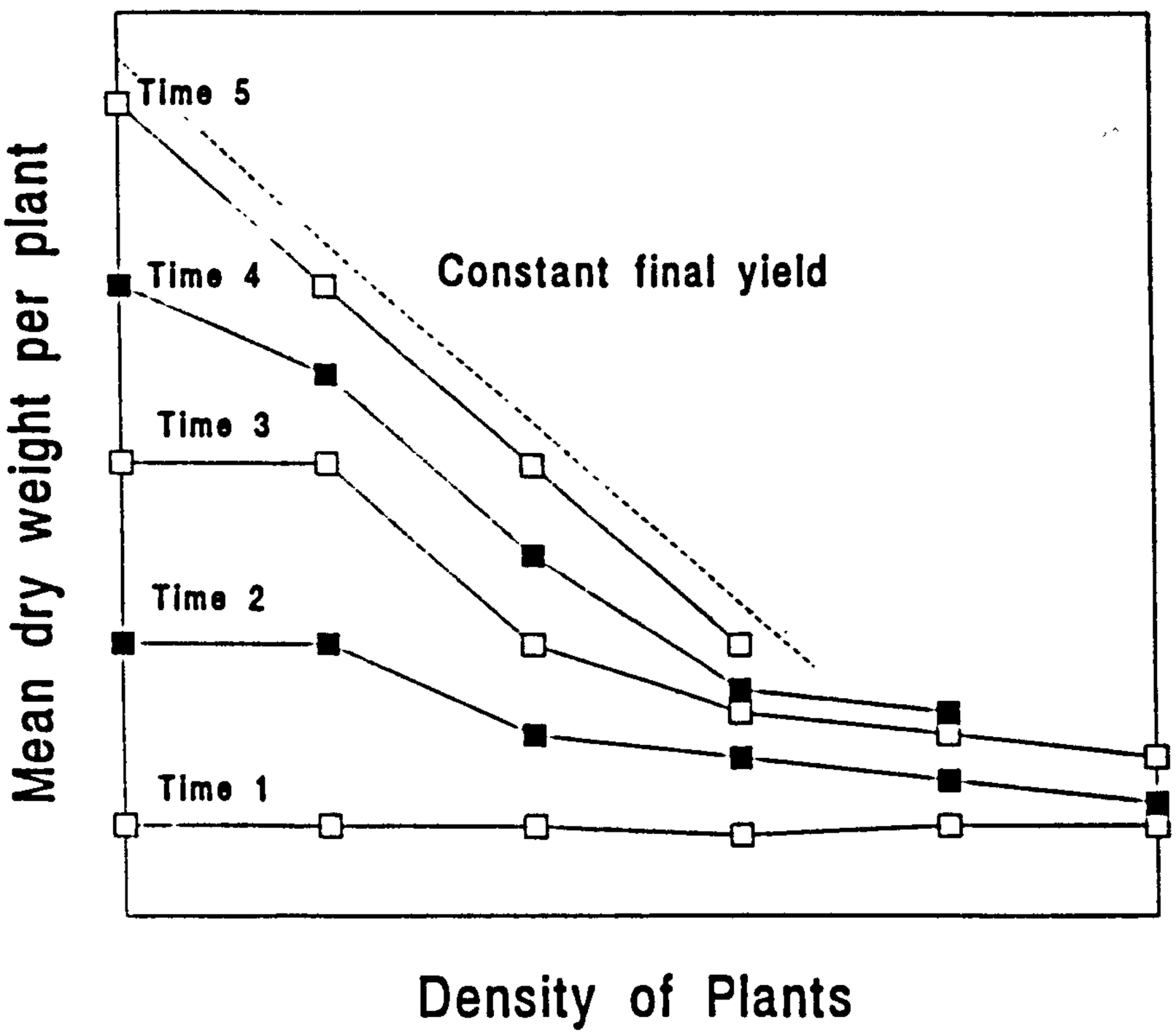
$w = kN^{-1}$ or $\log_{10}w = \log_{10}k - 1\log_{10}N$ Equations 3 & 4

and on the log-log plot will have a gradient of -1 (or 45° slope, see Figure 1). This special line represents the outcome of 'The Law of Constant Final Yield' (Kira *et al.*, 1953).

At very high densities constant final yield may not hold true, as the yield of some plant parts declines (Bleasdale and Nelder, 1960; Bleasdale, 1966; de Wit, 1968; Farazdaghi and Harris, 1968). Some plants do, however, absorb very high degrees of density induced stress by plastic growth responses. Harper and Gajic (1961) found no mortality in *Agrostemma githago* at densities as high as 2300 plants m^{-2}. Also, as Ford (1975) pointed out, plastic responses may reduce the weight of seed produced by each unit of weight of vegetative tissue (and see Donald, 1963; Hiroi and Monsi, 1966)

Certain improvements have been made to Equation 1 in order to provide a more realistic smooth transition from low density, where there is little or no effect from competition, to high density where competition exerts an ever increasing effect (Shinozaki and Kira, 1956; de Wit, 1960; Holliday, 1960 for more detail).

Figure 1 A diagramatic representation of the competition density effect resulting in constant final yield. Note that the density does not change over time.



Seaweeds have been reported as being highly phenotypically plastic by Russell (1986) and Norton *et al*. (1982) who reviewed many laboratory and field based studies. While varied culture conditions such as light intensity, day length, temperature and nutrient status all have effects on individual species, transplant experiments in the field have resulted in altered forms of large brown algae under different wave action or water movement (*eg* Sundene, 1964). Druehl and Kemp (1982) found that blade morphology and growth rate of spatially discrete *Macrocystis integrifolia* populations with differing morphologies converged when transplanted to a common location. Similar results were found by Gerard and Mann (1979) with *Laminaria longicruris*. Norton *et al*. (1982) suggested that *Laminaria* sp. which exhibit longer stipes in forests may be at an advantage where light competition is intense. While plastic responses to density may be theoretically implied from the above studies assuming density limits a suitable resource, few studies demonstrate a link between density and phenotypic plasticity. Black (1974) however, found that plants in sparse stands of the kelp *Egregia laevigata* had more branched rachises (laterals) than more densely packed plants.

Evidence of constant final yield is hard to come by in seaweed populations. Shimo and Nakatani (1969) found that density was not an important determinant of growth rate in the early period of mass cultivation of the red alga *Porphyra tenera*, but Yoshida (1972) concluded that the law of constant final yield was applicable to this species; there was no density dependent mortality, and biomass-density relationships were due to plastic responses in plant growth. Hanisak (1987) reviewed yield studies in *Gracilaria*, and concluded that yield was density dependent.

The lack of substantial evidence of constant final yield in seaweeds may be because most seaweed populations undergo extensive mortality during their growth and development. Whether this mortality is density dependent or not, changes in density exclude the use of such data from interpretation in the context of constant final yield which assumes constant density.

The theoretical basis for self-thinning

As a monospecific plant population grows, often some individuals' ability to absorb competitive stress by plastic responses are exceeded (Harper, 1961; Kays and Harper, 1974). The consequence of this is mortality within the population.

Both mortality and plastic responses may occur simultaneously. Competitively induced mortality is dependent on the density of the population as this is directly related to the competitive stress, and is consequently termed competitively induced or density dependent mortality. During this period of competitively induced mortality (or self-thinning) and continuing growth, the formal equation relating points on a graph has been described as:-

$w = kN^{-3/2}$ or $\log_{10}w = \log_{10}k - 1.5\log_{10}N$ Equations 5 & 6

where w is mean plant mass, N is density of plants and k is a proportionality constant relating to the individual species concerned and compared at the y-intercept (Lonsdale and Watkinson, 1983).

This equation, though suggested by the work of Shinozaki and Kira (1956), was first published by Tadaki and Shidei (1959) and is best known from the work of Yoda *et al.* (1963).

This so called "-3/2 thinning law" (or "self-thinning rule", "power law of self-thinning", "Yoda's Law", "-3/2 power law") was derived by Yoda *et al.* (1963) who also explained it geometrically (elaborated by White and Harper, 1970; Hutchings and Budd, 1983a).

From equation 5 and 6 it is also possible to derive a relationship between stand biomass per unit area (Yield, β) and density (Westoby, 1981; Westoby and Howell, 1981; Zeide, 1987 all cover this). Since $w = \beta/N$ (where β is stand biomass density (yield, gm^{-2}) and from equation 5 $wN = kN^{-1/2}$ then

$\log_{10}\beta = \log_{10}k - 0.5\log_{10}N$ Equation 7

where *k* is "a parameter" (see Westoby, 1984 for elaboration).

Zeide (1987) derived the differential of the law as decrease in plant number (self-thinning, -dd) is caused by increased stand biomass (dB, the differential of the biomass). He defined the relative rate of self-thinning with respect to the relative biomass growth dB/B as -dd/d/(dB/B), and then, according to equation 7 the rate is constant, equal to two, for all species and conditions:-

$$\frac{\left(\frac{-dN}{N}\right)}{\left(\frac{-dW}{W}\right)}=\left(\frac{-dN}{N}\right)\frac{kN^{-1/2}}{\left(-\frac{1}{2}\right)\left(\frac{1}{N}\right)kN^{-1/2}dN}=2 \qquad \text{Equation 8}$$

The rate is thus functionally related to the exponent as the reciprocal of the exponent taken with the opposite sign, and captures in one indicator the outcome of both increase in stand mass and decrease in numbers (Zeide, 1987). The differential form of the law has only one constant and has a clear ecological meaning: as total mass of plants increases by a small fraction *f* (=dd/d), the relative decrease in plant number is *2f* (Zeide, 1987).

Generally, the biomass-density relationship should be used in preference to mean plant weight-density relationship for statistical reasons (Weller, 1987*a*). This is because spurious correlations result from plotting biomass/number (mean plant weight) against number, as number has an influence on both measures.

Exactly how the thinning line should be interpreted has been a cause of substantial controversy in the literature. It describes the way the average volume of surviving plants increases as plant density in a stand decreases due to self-thinning. However, there are three potential interpretations:-

a) The yield-density relationship

This is the time trajectory followed by a single population before and during density dependent mortality (Osawa and Sugita, 1989). This line will have a

changing slope as mortality takes place and it approached the conceptual dynamic thinning line (Figure 2).

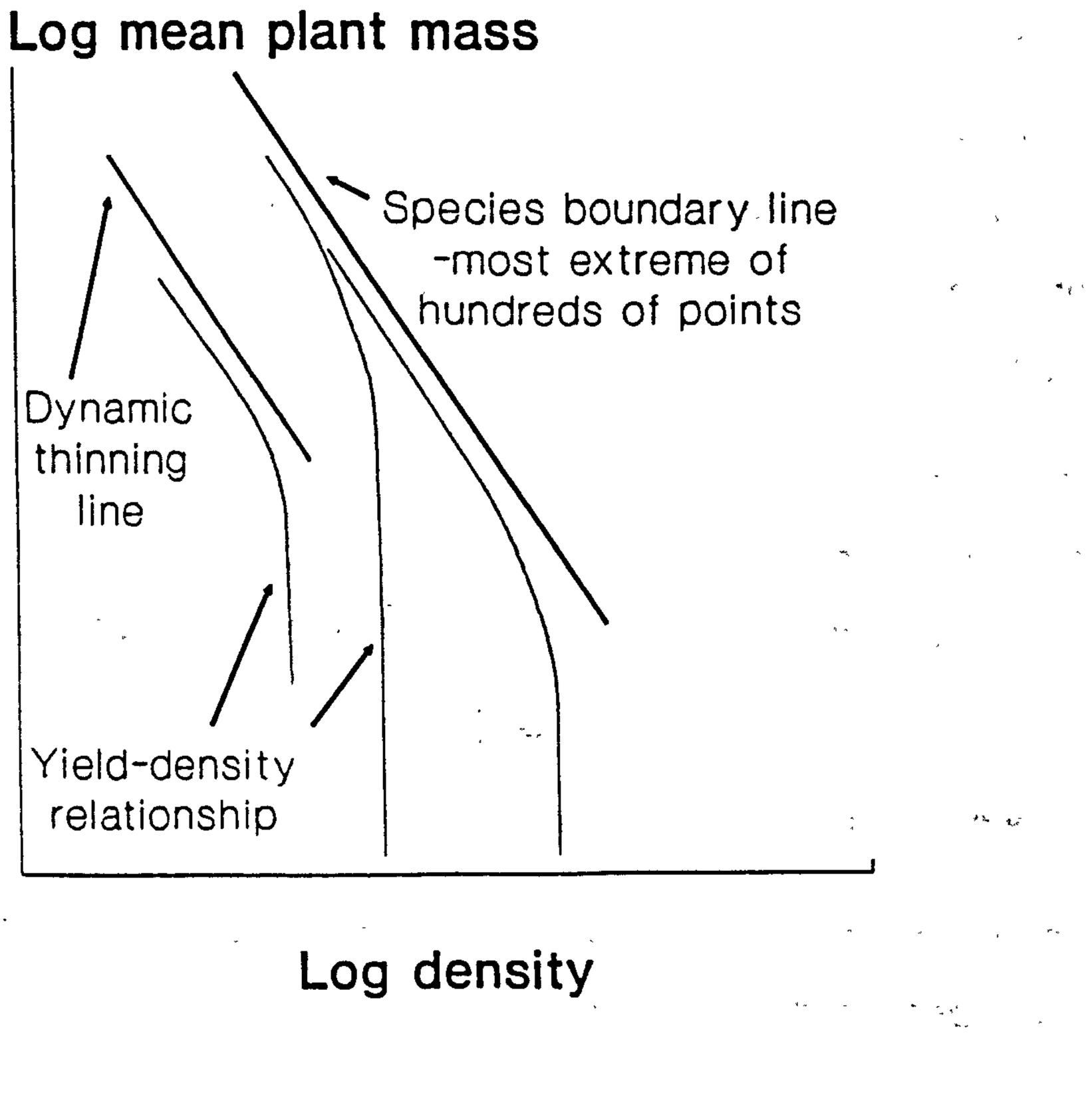
b) The dynamic thinning line

This is "the straight line that is approached, then followed by the time trajectory of an individual crowded stand" (Weller, 1991). Fundamentally, each population of each species may have a different dynamic thinning line dependent on the conditions of growth and the species (Figure 2).

c) The species boundary line

Defined as "The upper boundary of possible yield-density combinations for a species" (Weller, 1991, Figure 2). Data are fitted to the most extreme of hundreds of stands (Osawa and Sugita, 1989; Weller, 1991).

Figure 2 Diagramatic representation of the various types of thinning line



As a population develops, the data points on a log-log plot trace consecutive growth stages of survivors. With the line of constraint, any combination can occur below, but none above (Cousens and Hutchings, 1983). Below the line growth may take place with little or no mortality from competition, thus tracing a steep gradient on a plot of log mean volume and log density. However, as the growing population approaches the line of constraint and competitively induced mortality becomes much stronger, the gradient is deflected and subsequently traces the -3/2 gradient (White and Harper, 1970; Kays and Harper, 1974; Westoby, 1976; White, 1981).

From numerous growth experiments and forestry yield tables many data exist on the process of self-thinning in plant stands which support the -3/2 rule. The rule has been termed one of the most important principles in plant ecology (White, 1980) and considered by J.L. Harper to be "the only generalization worthy of the name law in plant ecology" (cited in Hutchings, 1983).

There are two lines of evidence in support of the 'law'. The first comes from the fact that many reported slopes of self-thinning lines are close to -3/2, with plants ranging in size and form from small herbs to large trees (*eg* Tadaki and Shidei, 1959; Yoda *et al.*, 1963; White and Harper, 1970; Kays and Harper, 1974; White, 1980, 1981; Westoby, 1976, 1984; Harper, 1977). The law also probably applies to some mixed-species stands (White and Harper, 1970) and to some sessile animals (*eg* Hughes and Griffiths, 1988; Frechette and Lafaivre, 1990; Frechette *et al.*, 1992). Depending on the kind of plant, the line's elevation (the *y*-intercept) may vary by a factor of eight (White, 1981).

The second line of supporting evidence comes from across-species regressions of different sized plants (Yoda *et al.*, 1963; Gorham, 1979; White, 1980) which generally form a band of gradient -3/2. This 'interspecific' size-density relationship has also been considered separately (see Weller, 1989 for a review and interpretation).

The 'law', derived empirically, has subsequently been corroborated by much new empirical data (Norberg, 1988) though some deviations exist (White and Harper, 1970; Westoby, 1984; Westoby and Howell, 1986; Weller, 1987*a*; Verwijst, 1989). Recent re-evaluation of the statistical treatment of thinning data should also be noted (Weller, 1987*a*). The law appears to break down only when weights of parts of plants are considered (Mohler *et al*, 1978) and when plants are grown under low light intensities (White and Harper, 1970; Kays and Harper, 1974; Ford, 1975)

Hutchings (1983) has described the -3/2 thinning rule as an ecological law in search of a theory, and the theoretical explanation of the rule is disputed (Westoby, 1977, 1984; White, 1977, 1980, 1981; Miyanishi *et al.*, 1979; Norberg, 1988). The use of modelling may help us to understand the theoretical explanation (Zeide, 1987; McFadden and Oliver, 1988; Valentine, 1988; Voit, 1988; West *et al.*, 1989*b*). For more detailed consideration of self-thinning, the reader is referred to White (1981), Zeide (1987), Norberg (1988), Voit (1988) and Weller (1989).

Intraspecific competition in seaweeds

While many studies of seaweed ecology have been directed towards the spatial distribution of species and communities (*eg* Stephenson and Stephenson, 1949; Lewis, 1964), relatively few workers have considered marine macroalgal organisation at the individual population level (Chapman, 1979). This shortfall in our knowledge is apparently due in part to difficulties in identifying individual genets, especially in the crustose and turf-forming seaweeds (Cousens and Hutchings, 1983; Lobban *et al*, 1985). This has never been cited as a problem in terrestrial studies where studies have long been carried out on grass tillers (ramets) rather than whole plants (genets) which usually behave similarly (Kays and Harper, 1974; Lonsdale and Watkinson, 1982, 1983; Turner and Rabinowitz, 1983). Similarly, sea grasses ramets have been studied(Tomasko and Dawes, 1990). Indeed some authors have successfully used fronds as

functional units in seaweeds equivalent to ramets of higher plants (*eg* Cousens and Hutchings, 1983; Cousens, 1985; Robertson, 1987), and there seems little justification for not doing so. Probably a more fundamental reasons for the lack of plant population studies in seaweeds is that over the life cycle of most species there are enormous variations in plant size and it is over the microscopic and macroscopic ranges (*eg* 'average' gametes 10-20μm, adults 15cm-5m Vadas *et al.*, 1992; sizes span five orders of magnitude, about an order of magnitude greater than trees). It is therefore difficult to study seaweed plants from settlement to death. Also, studies on shores or underwater may be more difficult than on land. On the plus side, seaweed propagules tend to settle on the surface of a substratum rather than in it (as with many seeds) and have no root competition, so they are therefore potentially easier to census.

One often cited effect of intraspecific competition in seaweeds is the effect of an adult canopy on conspecific juvenile recruitment. The evidence has sometimes come to light as a by-product of canopy removals designed to look at synecological aspects of a canopy species (*eg* Burrows and Lodge, 1950; Dayton 1971, 1975; Duggins, 1980; Hawkins, 1983; Santelices and Ojeda, 1984*a*; Benedetti-Cecchi and Cinelli, 1992). Some experiments have used the important manipulative tool of canopy removal to look at adult-juvenile relationships between two species (Hruby, 1976; Ambrose and Nelson, 1982). Many autecological studies have also investigated adult-juvenile relationships (Knight and Parke, 1950; Edelstein and McLachlan, 1975; Kain, 1976; Kirkman, 1981; Keser and Larson, 1984; Santelices and Ojeda, 1984*b*, 1984*c*; Cousens, 1985; Schiel, 1985*a*; Gunnill, 1986; Robertson, 1987). While the majority of authors have reported increased recruitment of juveniles in canopy cleared areas, Chapman (1984), Ang (1985) and Smith (1986) all found no difference in recruitment between canopy cleared and control areas. Harvesting experiments have also yielded the suggestion that intraspecific competition may be important (*eg* Keser *et al.*, 1981). Usually increased light levels have been cited as the reason why large numbers of conspecific recruits have appeared in

cleared areas, or canopy shading as to why they have not (Dayton, 1975; Edelstein and McLachlan, 1975; Kain, 1976; Hay and South, 1979; Kirkman, 1981; Ambrose and Nelson, 1982; Dayton *et al.*, 1984; Keser and Larson, 1984; Santelices and Ojeda, 1984*b*, 1984*c*; Cousens, 1985; Schiel, 1985*a*; Robertson, 1987). Light levels under a canopy are far lower than outside one whether the tide is in or out (Norton *et al.*, 1977; Schonbeck and Norton, 1980*a*; Reed and Foster, 1984; Santelices and Ojeda, 1984*b*, 1984*c*; Cousens, 1985; Kennelly, 1989). The possibility that nutrient levels are reduced directly by adult plants (Dayton *et al.*, 1984; Foster and Schiel, 1985), or indirectly by the effects of adults on water movement (Gerard and Mann, 1979; Norton *et al.*, 1982) has also been suggested. Druehl *et al.* (1988) showed that nutrients in the sea were spatially variable and that there was a correlation between biomass and nutrient status. Nutrient concentrations vary seasonally however, as do many other environmental parameters such as light. Canopy removals nullify whiplash (Dayton, 1971, 1975; Grant, 1977; Gunnill, 1980*a*; Kirkman, 1981; Ang, 1985; Westermeier and Rivera, 1986; Westermeier and Moller, 1990) and sweeping (Kirkman, 1981; Ang, 1985) effects of adults, and these factors cause density independent mortality. Sediment build up (Kennelly, 1989) or scour (Ang, 1985; Kennelly, 1989) and grazer interactions (*eg* Druehl and Breen, 1986; Benedetti-Cecchi and Cinelli, 1992) are also affected by canopy removals. Therefore evidence of intraspecific competition from canopy clearance experiments is only anecdotal, and formal studies of intraspecific competition in seaweeds in which density has been manipulated are rather fewer.

There are four methods which have been used to investigate intraspecific competition in seaweeds by density manipulation. Foster and Schiel (1985) suggested the use of outplanting or artificial thinning of populations to different densities. Outplanting may be particularly suited to early stage population dynamics as propagules may be 'seeded' at different densities before being introduced into the wild. Unfortunately early post-settlement survival may be affected by a host of factors (see review by Vadas *et al.*, 1992) and up to 84 %

(Norton, 1983 in *Sargassum*) or even 99 % (Vadas *et al.*, 1990 in *Ascophyllum nodosum*) of propagules may be quickly lost. Potentially, initially variable densities of propagules may be reduced in a density dependent fashion not because of intraspecific competition *per se*, but for instance because clusters of propagules may be washed off and the size of clusters may be density dependent (*eg* Black, 1974). Artificial thinning of established stands is also potentially useful. It is necessary to ensure that thinning is random with respect to sizes of plants and space, which may be achieved by using minimum nearest neighbour distance and clearing all other plants from within that area (*eg* Reed, 1990*a*) or by thinning proportions of the populations on, for instance, a random point to nearest plant basis. The main criticism of artificial thinning is that density can only be decreased, not increased. The third method involves the creation of populations by attaching plants to artificial substrata (*eg* Chapman, 1990*a*) or moving artificial or natural supports on which plants are growing together effectively to create a range of densities (*eg* Neushul and Harger, 1985). These methods may allow the manipulation of spatial pattern as well as density. Finally, some authors have used natural variations in density and correlated these with growth and survivorship (*eg* Black, 1974). The danger of this method is that variable densities may be the result of variable environmental factors rather than variable recruitment, and consequently the populations could have differing growth and survival rates for reasons independent of density (Schiel, 1985*b*).

a) Outplanting

Schiel and Choat (1980) outplanted artificially settled *Sargassum sinclairii* germlings at different densities but found no effect of density on survivorship. In a most comprehensive study, Reed (1990*b*) outplanted *Macrocystis pyrifera* and *Pterygophora californica* spores at different densities. Both species needed a minimum settlement density of at least 1 spore mm^{-2} for subsequent recruitment, probably to allow fertilisation between male and female gametophytes. Whenever there was recruitment, strong density dependent mortality

occurred. Ang and De Wreede (1992) found a positive relationship between density and mortality, but not growth rate, early on in outplanted *Fucus distichus* germlings.

b) Artificial thinning

The most crude methods involve cutting (the largest) plants to a standard size, and are generally associated with experiments in which commercial harvesting is implicated. This method may not strictly alter density, but does reduce standing crop at least of the larger plants and consequently may reduce competitive stress. Druehl and Breen (1986) concluded that light limitation was important, as partial harvest of *Macrocystis integrifolia* allowed increased growth of *Ulva* sp., but their data did not include a study of intraspecific effects. Reed (1987) found that cutting the top off *Macrocystis pyrifera* plants increased light availability for all plants, but with the trade off that canopy derived photosynthates were lost from translocation. Effects were also site specific. Gomez and Westermeier (1991) investigated various harvesting regimes on *Iridaea laminarioides*, a red alga with a perennial disc and frondose phase. The growth rate of fronds in the untouched control plants was far lower than if pruning to stipe level or to the base had been carried out. Keser *et al.* (1981) experimentally cut *Fucus vesiculosus* and *Ascophyllum nodosum* to different lengths to investigate harvesting effects on biomass. Cleared areas generally yielded higher biomass than cut ones in *Fucus vesiculosus* but not in *Ascophyllum nodosum*. These differences were attributed to large scale repopulation by *Fucus vesiculosus*. Chopin *et al.*, (1992) investigated the effect of dragrake harvesting on the density and biomass of *Chondrus crispus*, and concluded that this method of harvesting selected larger fronds, resulting in lowered biomass and increased density, which may be due to increased light levels after harvesting.

The reduction of density has been carried out in a number of studies. Chapman and Goudey (1983) experimentally thinned a *Leathesia difformis* population so

that plants were 5 cm apart, and found survivorship rates two to eight times higher than in unthinned controls. Density dependent mortality (but not generally growth rate) has been found in older populations of experimentally thinned *Fucus distichus* (Ang and De Wreede, 1992). McCook and Chapman (1991) found lower survival and higher growth in unmanipulated stands of *Fucus vesiculosus* than in those thinned to 1/8th natural density. Percentage cover, which had been reduced to 50 % by the thinning manipulation recovered to a similar level as in the control plots. They suggested that enhanced photosynthesis at low densities allowed better recovery of wave or herbivore damaged fronds. They also found enhanced recruitment at low density. Growth rate, but not survivorship was found to be density dependent in *Pterygophora californica* populations in the most comprehensive experimental thinning experiment carried out so far (Reed, 1990a). He used the minimum nearest neighbour distance method to thin his populations.

c) Creation of populations

Though methods are available for the creation of populations of larger plants in the field (*eg* Sundene, 1964; Luning, 1970) rather few studies have done so in the context of varying density to investigate intraspecific competition. On commercial test farms Kain *et al*. (1990) gave string fragments seeded with *Alaria esculenta* inserted through the twine of rope variable spacings to create a one-dimentional density variation. Plants grew up in groups around the string fragments. They found a significant reduction in biomass per group at small spacings. Hurtado-Ponce (1990) inserted *Gracilaria* sp. fragments directly into the twine of rope at three spacing intervals, and found that while spacing interval did not affect yield, it did affect growth rates, the most dense populations having lower growth rates than higher spaced ones. Using a two dimensional technique Adams and Austin (1979) grew fronds of *Iridaea* at different densities on ropes wrapped round frames, and found that yield and growth rates were density dependent because of intraspecific competition. In probably the grandest experiment in which differing density populations have been created,

Neushul and Harger (1985) constructed three densities of *Macrocystis pyrifera* in a 0.48 hectare test area by differentially spacing anchors with attached plants. Far fewer fronds per plant grew in higher density areas, and biomass per plant was lowest there. Initially differing yields converged. The methods of Chapman (1990a) may be particularly useful for creating intertidal populations. He cut small squares of plant-bearing rock and created mixed and single species stands in a de Wit replacement series experiment with *Fucus spiralis* and *Fucus vesiculosus*, but using monospecific stands of variable density could be most enlightening.

d) Natural density variation

Naturally variable densities have been used to investigate density dependence in macroalgal populations. Ang and De Wreede (1992) arbitrarily divided population squares into high and low density. They found that density did affect mortality at some stages in *Fucus distichus*, though there was no difference in the effect of plant density on plant length over time. Black (1974) found that density was inversely correlated with survivorship in *Egregia laevigata* populations. Schiel and Choat (1980) also used natural variation in density, and correlated increased density with increased yield, dry weight, plant length and reproductive dry weight in *Sargassum sinclairii* and *Ecklonia radiata*. However, they did find positive density dependent survival in juvenile populations followed for a year (Schiel and Choat, 1980). Schiel (1985*b*) also collected data from variable density stands at spatially discrete locations and for *Sargassum sinclairii* he obtained similar results to Schiel and Choat (1980). He also found that *Carpophyllum maschalocarpum* behaved similarly, growing faster in higher density stands. However, Schiel (1985*b*) found that survivorship was negatively density dependent in these species.

<u>Negative competition</u>

Begon and Mortimer (1986) termed inverse density-dependence negative competition. It occurs when the benefit of being closer together outweighs any

potential interference competition. Most examples relate to motile animals (*eg* Begon and Mortimer, 1986), though Harper (1977) reviewed a few studies of plants which exhibited this phenomenon. These studies related to seed germination under conditions of stress. For instance while a single seedling may be unable to break through a capped surface a group of seedlings acting together may be able to do so (Harper, 1977). However "such evidence of positive density-dependence in plant populations of a single species is very much the exception" (Harper, 1977).

In seaweeds negative competition has been implicated in quite a number of studies. As on land, most of the studies in which negative competition has been demonstrated occur in propagules. *Enteromorpha linza* and *Blidingia minima* propagules have been demonstrated to survive better at higher densities at the early post-settlement stage as a result of reduced desiccation (Hruby and Norton, 1979). Dense germling stands may be better suited to survive grazing (Lubchenco, 1983). Reed (1990*a*) found that spores of two kelp species needed a minimum density of 1 mm^{-2} in order for fertilisation to take place between gametophytes. Over the generation gap, the higher the density of spores the greater the number of sporophytes (Reed, 1990*a*). Ang and De Wreede (1992) found that *Fucus distichus* germlings under crowded conditions survived better than sparse populations, maybe because of desiccation or grazer effects.

For larger plants Schiel and Choat (1980) and Schiel (1985*b*) found what they assumed to be positive density dependence in stands of *Sargassum sinclairii, Ecklonia radiata*, and *Carpophyllum maschalocarpum* (but see above). Hay (1981) found that rates of water loss and apparent photosynthesis in three species of turf-forming algae was lower when measured on individual plants than plants in turfs when exposed to desiccating conditions, and that there was sometimes an advantage in forming dense turfs. Similar conclusions have been drawn for fucoids (Schonbeck and Norton, 1978; Gunnill, 1980*a*). Some experiments have demonstrated that peripheral thalli of certain red algae grow

less well than central ones (see review by Santelices, 1990*b*). North (1971) found slightly higher growth rates in high density stands which were attributed to localized factors. Finally, higher densities of adult plants may result in release of gametes *en masse* in Fucales (see Foster and Schiel, 1985). Pheromones may be implicated (see review by Brawley and Johnson, 1992).

Self-thinning rule in seaweeds

The applicability of the self-thinning rule to seaweeds has caused some controversy (Chapman, 1986*b*; Santelices, 1990*b*). Unfortunately this is mainly due to the subtle misapplication of the rule. Relatively few data are available on the conformity or non-conformity of monospecific, single-aged stands of marine algae to the -3/2 thinning law and those studies which exist are contradictory (compare Cousens and Hutchings, 1983 and Schiel, 1985b). This is partly due to difficulties in identifying individuals (Cousens and Hutchings, 1983) as discussed above. Kays and Harper (1974) working on self-thinning in *Lolium perenne*, a tillering grass, demonstrated that individual tillers (ramets) as well as plants (genets) were regulated by self-thinning and tended towards the -3/2 gradient. This has been used as justification for studying thinning in seaweeds by using fronds rather than plants as individual units (Cousens and Hutchings, 1983).

Schiel and Choat (1980) examined two species of algae which possess quite different forms and life histories, *Ecklonia radiata* and *Sargassum sinclairii*. They concluded "the 3/2 thinning law is unlikely to apply to these marine algae" (Schiel and Choat, 1980). Their data demonstrated that total yield, plant length, dry weight and reproductive dry weight all increased with increasing density. Brawley and Adey (1981*b*) suggested that Schiel and Choat's (1980) data could be explained by their conclusions studying a coral reef microcosm. Coarse algae were protected from amphipod grazing by their size, but the grazing of epiphytes on the coarse algae did take place, increasing resource availability and thus enhancing the growth potential of the 'host' (*Hypnea*) by as much as

300 % (Brawley and Adey, 1981*a*). Brawley and Adey (1981*b*) hypothesised that in subtidal areas predation of amphipods by fish may be reduced in high density seaweed stands (and consequently amphipod herbivory of epiphytes increased). This contrasts with Schiel and Choat's (1980, 1981) conclusions that at higher densities plants are protected from physical battering and consequently grow faster. Harper and White (1970) also emphasize the possible importance of animal interactions when assessing plant growth. Unfortunately Schiel and Choat's (1980) data did not trace a time series so could only fit the theoretical category of species boundary line for which hundreds of points are needed (see above).

In a different approach Cousens and Hutchings (1983) used data derived from studies by Schiel and Choat (1980), Rice and Chapman (1982), and Fernandez and Niell (1981) as well as their own data. They plotted log mean frond weight and log frond density for a number of natural monospecific stands of a range of species (*Saccorhiza polyschides, Chordaria flagelliformis, Ecklonia radiata, Sargassum sinclairii* and *Ascophyllum nodosum*). To the resultant graph they added the thinning line given by $\log_{10} w = 4.3\text{-}1.5\log_{10} N$ (w = mean frond weight, N = density). They selected $\log_{10} k = 4.3$ because this value was the highest known from previous terrestrial data (White, 1980) and should represent the boundary condition if the law holds true for seaweeds too. Lines were not fitted to the graph by any standard statistical technique, and it is not possible to draw conclusions about the two sets of time course data included on the graph. Most points fell on or below the boundary line (all did so when the *Ascophyllum nodosum* data had been converted to geometric rather than arithmetic means). This they concluded suggests that the law is not violated by these species. Cousens and Hutchings (1983) pointed out that Schiel and Choat's (1980) data did not contravene their 'all species boundary line'.

More recently a few authors have investigated the applicability of the self-thinning rule to single species rather than as a multi species boundary phenomenon, though these authors still compared their data to Cousens and Hutchings'

(1983) study. Robertson (1987) found that some data points relating to a self-thinning *Fucus spiralis* population contravened Cousens and Hutchings' (1983) boundary line, even when geometric means were used to account for skewed population structure. Robertson's (1987) regression fitted line had a slope of -0.93 and intercept of 2.95, and he concluded that "it would seem that responses by terrestrial plants and seaweeds to density are not universally similar and that differences do occur in some instances". Cheshire and Hallam (1988) found similar results in native *Durvillaea potatorum* stands, and that in order for their data to conform with the boundary condition of Cousens and Hutchings (1983), the boundary would have to be moved to $\log_{10}k = 5.0$ (rather than 4.3). This would suggest a carrying capacity of 100 $kg.m^{-2}$ (Cheshire and Hallam, 1988). Russell (1990) found a slope of -0.011 for *Himanthalia elongata*, but did not use pure or even-aged stands. Martinez and Santelices (1992) found that there was no significant correlation between weight and density in *Iridaea laminarioides*, and that points transgressed Cousens and Hutchings' (1983) boundary line.

The influence of intraspecific competition on population structure

One important consequence of competitive-induced mortality is its effect on population structure. It is usually the case that in a population of seeds very few are identical. Seed size, genetic differentiation and slightly different emergence times are some of the factors which shape a population structure and are most important at an early age (Weiner and Thomas, 1986). Ross and Harper (1972) concluded that the growth of an individual seedling is most influenced by the density of previously emerged neighbours, while the spatial pattern of neighbours and effects of seed size were negligible. Furthermore, emergence time influences growth rate divergently, and growth rate was found to be related to the third power of the mean distance from neighbours (Ross and Harper, 1972). This early variability is subsequently enhanced by environmental heterogeneity, differential effects of herbivores, pathogens and parasites as well as intraspecific competition (Weiner and Thomas, 1986)

The consequence of enhanced variability has been described as a 'dominance hierarchy' (Kays and Harper, 1974) or 'size hierarchy' (Harper, 1977) in monospecific communities, plant weight distribution becoming skewed from a normal to 'log-normal' distribution over time (Kays and Harper, 1974). The change in population structure has been reported by a large number of workers studying different species (*eg* Koyama and Kira, 1956; Obeid *et al*, 1967; Ford, 1975; Mohler *et al*, 1978). Harper (1977) suggested that the size hierarchy reflected a 'hierarchy of exploitation'. However, a number of examples show that 'log-normal' distributions are not always forthcoming. Naylor (1976) and Windle and Franz (1979) reported normal distributions in barley shoot weight at successive harvests, while Hedley *et al*. (1983) found the same to be true of 'leafless' pea plants. Andrzejewska and Falinska (1983) suggested that populations were normally distributed in relation to size under favourable conditions. Ford and Newbould (1970) found bimodal distributions of $(\text{diameter})^2$ in sweet chestnut (*Castanea sativa*), and interpreted these as the (usual) positive skew with a second maximum at intermediate sizes. Bimodality has also been reported in high density *Festuca paradoxa* (Rabinowitz, 1979). Several authors have argued that bimodality of population structure can result from asymmetric competition, which produces distinct dominant and suppressed classes (Ford and Newbould, 1970; Ford, 1975; Aikman and Watkinson, 1980; Ford and Diggle, 1981). It should also be noted that bimodality is subjective as no statistical analysis can truely quantify it and the visual appearance of a histogram is dependent on the number of size classes used (Weiner and Thomas, 1986).

Intraspecific competition has important effects on population structure. It is one factor which favours larger plants over small within a population, even when mortality is not taking place, though Ford (1975) pointed out that a 'log-normal' distribution is, in itself, not evidence of competition between individuals in monospecific stands. When self-thinning takes place in a population, the smallest plants are most prone to selective mortality, as they are poor compet-

itors. Numerous data support this observation (Bliss and Reinker, 1964; Hiroi and Monsi, 1966; Ford and Newbould, 1970; White and Harper, 1970; Jack, 1971; Kays and Harper, 1974; Lonsdale and Watkinson, 1982; Watkinson *et al.*, 1983; Gibson and Good, 1986; Weiner and Thomas, 1986; Westoby and Howell, 1986; Weiner and Whigham, 1988).

Predictable changes in population structure may accompany self-thinning (Mohler *et al.*, 1978; Weiner, 1985; Weiner and Thomas, 1986) and these could be useful indicators in the study of self-thinning.

Mohler *et al.* (1978) found that skewness was greatest in populations of trees at the onset of self-thinning and subsequently decreased as mortality proceeded, while Kohyama and Fujita (1981) found that the coefficient of variation decreased as self-thinning occurred in *Abies* stands. Weiner and Thomas (1986) found that size inequality decreased as self-thinning proceeded. They compared these data to two basic models of the interaction between competition and size distribution. They rejected the "resource-depletion" model in which competition acts on all individuals equally or in proportion to their size and concluded that the results supported the "resource pre-emption" model where the effect of small plants on large is less than would be expected from relative sizes while the effect of large on small is greater (see Weiner and Thomas, 1986).

Westoby and Howell (1986) investigated the effect of population structure on self-thinning by a number of experiments which used combinations of different sized seeds, and mixed aged stands. They concluded that population structure was not an important influence on self-thinning paths relative to unexplained variation among stands (Westoby and Howell, 1986). Westoby and Howell (1986) suggested that self-thinning populations develop a relative size distribution which remains constant as mortality and growth rate consistently balance one another. Weiner and Whigham (1988) studied self-thinning in wild rice populations (structurally far removed from trees, above) and found that popu-

lation size variability decreased from high inequality and positive skewness to become more uniform as self-thinning progressed.

In the light of the above studies, two alternative hypotheses have recently been considered as mechanisms which drive the development of plant population structure. Turner and Rabinowitz (1983) demonstrated that a right skewed population structure could develop because (inherent) variance in exponential growth rates of individual plants would result in a positively skewed population structure over time. Schmitt *et al.* (1986, 1987) favoured the dominance and suppression hypothesis where intraspecific competition created dominant and suppressed sizes because of asymmetric competition. Schmitt *et al.* (1987) suggested two tests for these hypotheses; either you can compare size distributions of different density populations at equal mean mass, or compare the slopes of plant size-relative growth rate relationships of different density populations. They also point out the importance of size dependent mortality, which should accompany intraspecific competition (Schmitt *et al.*, 1987). Size variability may be described by a host of statistical methods (reviewed by Weiner and Solbrig, 1984; Weiner and Thomas, 1986; Bonan, 1988; Bendel *et al.*, 1989).

The population structures of numerous seaweed species have been investigated (Table 1). These studies have used measures of age (*eg* De Wreede, 1984), frond length (*eg* Hay and South, 1979), stipe length (*eg* Kain, 1976), stipe diameter (Lawrence, 1986), holdfast height (Santelices and Ojeda, 1984*b*), thallus mass (Russell, 1990), plant volume (Reed, 1990*a*), or combinations of dichotomies and size (Chopin *et al.*, 1992) or age and vitality (Cheshire and Hallam, 1989). Generally population structures are positively skewed, with rather more small plants than large ones (Table 1), though negatively skew populations or normal ones have also been reported. By far the majority of studies have been carried out on large canopy forming brown algae, some on commercially important red algae, and as far as I can gather, none on the greens.

Table 1 Studies of population structure in seaweeds

Species	Skew	Measure	Evidence from	Source
Brown algae				
Ascophyllum nodosum	+	year class	table	Baardseth, 1968
	+	age	table	Keser *et al.*, 1981
	+	length	graph	Aberg, 1990*d*
Carpophyllum maschalocarpum	+	length	histogram	Schiel, 1990
Carpophyllum augustifolium	+	length	histogram	Schiel, 1990
Cystoseira osmundacea	+?	length	histogram	Schiel, 1985a
	=	length	anecdotal	Gunnill, 1986
Desmarestia firma	+	dry weight	histogram	Anderson & Hay, 1986
Durvillaea antarctica	+	length	histogram	Hay & South, 1979
	+	stipe diameter	histogram	Lawrence, 1986
Durvillaea potatorum	+/=	age/vitality	histogram	Cheshire & Hallam, 1989
Ecklonia maxima	+	stipe length	histogram	Velimirov *et al.*, 1977
Ecklonia radiata	+	dry weight	histogram	Kirkman, 1981
	+	length	histogram	Schiel, 1990
Ecklonia stolonifera	+	shoot age	histogram	Notoya & Aruga, 1990
Egregia laevigata	+	size	anecdotal	Black, 1974
Fucus distichus	+	length	histogram	Ang, 1991
	+	coefficient	graph	Ang & DeWreede, 1992
Fucus serratus	+	length	histogram	Knight & Parke, 1950
	+	length	histogram	Burrows & Lodge, 1951
Fucus spiralis	+	length	histogram	Robertson, 1987
Fucus vesiculosus	+	length	histogram	Knight & Parke, 1950
	+	length	histogram	Burrows & Lodge, 1951
Halidrys dioica	=	size	anecodtal	Gunnill, 1986
Himanthalia elongata	+	thallus mass	histogram	Russell, 1988
	+	thallus mass	histogram	Russell, 1990
Laminaria digitata	+	length	histogram	Smith, 1986
Laminaria hyperborea	+/=/-	stipe length	histogram	Kain, 1976
	+	age	table	Norton *et al.*, 1977
Laminaria longicruris	+	length	histogram	Smith, 1986

Table 1 Studies of population structure in seaweeds - continued.

Species	Skew	Measure	Evidence from	Source
Brown algae cont.				
Laminaria ochroleuca	+/=/-	age	histogram	John, 1971
	-	age	histogram	Drew, 1974
Laminaria pallida	+	length	histogram	Velimirov *et al.*, 1977
Laminaria setchellii	+	age	histogram	Dayton et al., 1984
Landsburgia quercifolia	+	length	histogram	Schiel, 1990
Macrocystis pyrifera	+	holdfast height	histogram	Santelices & Ojeda, 1984*b*
Pterygophora californica	=	age	histogram	Dayton *et al.*, 1984
	=/-	age	histogram	De Wreede, 1984
	+/=/-	age	histogram	De Wreede, 1986
	+	volume	histogram	Reed, 1990*a*
Sargassum sinclairii	+	length	histogram	Schiel, 1990
Red algae				
Chondrus crispus	+	length	table	Bhattacharya, 1985
	+	dicots./size	table	Chopin *et al*, 1992
Iridaea cordata	+	stage	graph	Hansen & Doyle, 1986
Iridaea laminarioides	+	length	histogram	Gomez & Westermeier, 1991
Lithophyllum incrustans	+	age	histogram	Ford *et al.*, 1983
Porphyra sp.	+	length	histogram	Yoshihara, 1977

A necessary criterion for self-thinning studies is that populations are even aged (Weller, 1987*a*). The importance of age versus stage has been examined in seaweeds. Chapman (1986*b*) reviewed age in the context of seaweed populations, and concluded the "whilst age class structure is the end product of population dynamics...it is a very poor record of population history". Cheshire and Hallam (1989) reviewed methods of ageing seaweeds, which can generally only be carried out on kelps, though crustose coralline red algae may also be aged (Ford *et al.*, 1983). Many authors have presented population structures based on age (Table 1). Chapman (1986*a*) investigated the effects of age and stage on *Laminaria longicruris*, only occasionally finding size or age as

determinants of mortality, though fecundity was related to size. Notoya and Aruga (1990) found that various linear measurements relating to *Ecklonia stolonifera* plants did not form a linear relationship, but were size dependent. Cheshire and Hallam (1989) used a linear measurement to establish age, and combined age with 'vitality' groups to formulate population structures. Russell (1990) demonstrated the importance of not surmising population age composition from size frequency data. Like many land plants, some seaweeds regularly reproduce vegetatively (*eg Ascophyllum nodosum*) and true age in such species is probably irrelevant.

Another important assumption is that a population of settled propagules is normally distributed. Very few studies have described populations of seaweed propagules either as gamete sizes, or very early post-settlement populations, and most of the studies were not investigating population structure *per se* (Mshigeni, 1976; Ngan and Price, 1979; Fernandez and Menendez, 1991; Destombe *et al.*, 1992). Most seaweed population structures have been reported for plants of a visible size only, which may explain why the possibility of a 'seed bank' in seaweeds has only recently been considered (Hoffmann and Santelices, 1991).

That the majority of seaweed species present age or size distributions that are positively skewed should not be taken as evidence of intraspecific competition (Ford, 1975). Only a few studies have considered size variability of seaweed populations through time in terms of dominance and suppression or exponential growth. Dean *et al.* (1989) considered the role of dominance and suppression in juvenile giant kelp (*Macrocystis pyrifera*), and concluded that intraspecific competition for light acted in this species, though this was the exception for seaweeds generally. However, Reed (1990a) also concluded dominance and suppression by light competition in artificially thinned stands of *Pterygophyra californica*, and employed the formal test of comparing the initial plant size-growth rate relationship between the different densities. Ang and De Wreede (1992) also concluded that dominance and suppression may

operate in *Fucus distichus* and used skewness, Gini and variation coefficients to describe size variability in their populations.

Intraspecific competition and fecundity

The ability to reproduce is fundamental to the survival of any species. The hierarchy of sizes which develops because of intraspecific competition usually results in a large number of small individuals with low or no fecundity, and a small number of large individuals with high fecundity (Obeid *et al.*, 1967; White and Harper, 1970; Weiner, 1985). Also, many plants may not survive at all due to self-thinning. Weiner (1988) produced a model for size dependent reproductive output which has been shown to be successful (Thompson *et al.*, 1991): there is a linear increase in fecundity with plant size. Rice (1990) found that reproductive inequality increased with density and concluded that this could significantly alter the relative importance of genetic drift in the evolution of plant populations. Even gender may be influenced by density (Ackerly and Jasienski, 1990).

In seaweeds, size and biomass have been demonstrated to have a significant effect on fecundity. Many authors have reported a minimum size for reproductive maturity (Knight and Parke, 1950 for *Fucus serratus* and *vesiculosus*; Thom, 1983 for *Fucus distichus*; Ang, 1991 for *Fucus distichus*; Gomez and Westermeier, 1991 and Martinez and Santelices, 1992 for *Iridaea laminarioides*, Kain, 1975 for *Laminaria hyperborea*). Furthermore, as plant size or weight increases, so does reproductive effort or output (Russell, 1979 for *Fucus vesiculosus*; Chapman, 1986a for *Laminaria longicruris*; Robertson, 1987 for *Fucus spiralis*; Aberg, 1990d for *Ascophyllum nodosum*; Ang, 1991 for *Fucus distichus*; Chopin *et al.*, 1992 for *Chondrus crispus*; Mathieson and Guo, 1992 for *Ascophyllum nodosum* and *Fucus spiralis*). Age and reproductive effort have also been linked (Ford *et al.*, 1983 for *Lithophyllum incrustans*; De Wreede, 1986 for *Pterygophora californica*). More specifically Reed (1990a) found an increase in sorus area and sori when densities were reduced by

artificial thinning of *Pterygophora californica* stands, similar to Reed (1987) who found reducing density increased sporophyll production in *Macrocystis pyrifera*. In contrast Schiel and Choat (1980) found an increase in reproductive dry weight with increased density in *Sargassum sinclairii*. Schiel (1985b) found a positive relationship between plant size and reproductive output in *Sargassum sinclairii* and *Carpophyllum maschalocarpum* and a minimum size for reproduction in the latter, though he found reproductive dry weight increased with density in the former species.

Survivorship in seaweeds

Numerous studies have been carried out on survivorship in seaweed populations. Survivorship curves have often been presented, and all types of survivorship have been found in seaweed populations (*eg* compare Chapman and Goudey, 1983 with Santelices and Ojeda, 1984c and Chapman, 1986a). Confusion has surrounded the interpretation of survivorship curves (compare Vadas *et al.*, 1982 with Vadas *et al.*, 1990), because different 'type' curves have been assigned by different authors (*eg* Pearl, 1928; Deevey, 1947; Slobodkin, 1962) and logarithmic or arithmetic plots should be interpreted differently (Begon and Mortimer, 1986; Begon *et al.*, 1986). Most studies have used tagging methods which are not suitable for small plants, and often different survivorship curves are applicable at different stages of the population's development (*eg* Gunnill, 1980a). Some success has been achieved with life table analyses (*eg* Chapman and Goudey, 1983; Dayton *et al.*, 1984), which are also open to many of the same criticisms.

Spatial dynamics and self-thinning

The spatial pattern of individuals within a stand is an important characteristic of a plant population (Clark and Evans, 1954). Greig-Smith (1964) suggested that a regular rather than random or contagious distribution of individuals would be expected as a result of competitive mortality, as resources necessary for plant growth always have a finite concentration at a single point. Antonovics and

Levin (1980) expected a shift to a more regular pattern with time as mortality occurred within a population. A regular pattern offers strong evidence of competition (Pielou, 1962; Greig-Smith, 1964; Antonovics and Levin, 1980) but failure to detect such a pattern does not necessarily mean that competition is not occurring. The effects of environmental heterogeneity (Antonovics and Levin, 1980), uneven age distribution (Phillips and MacMahon, 1981), seed dispersal mechanisms (Fowler, 1986) and other variables must also be considered.

Previous low correlations between plant size and/or reproductive output to location of neighbours in annual plants have been attributed to differences in emergence time and other factors (Firbank and Watkinson, 1987; Fowler, 1984; Mack and Harper, 1977; Matlach and Harper, 1986; Watkinson *et al.*, 1983; Weiner and Thomas, 1986).

Many workers have used nearest neighbour analysis to measure spatial relationships in populations (*eg* Clark and Evans, 1954; Cooper, 1961; Laessle, 1965, see Pielou 1969 for a review), while others used a circle of arbitrary radius centred on an individual plant, with only those plants bounded by the circle actively competing with the target plant (Mack and Harper, 1977; Waller, 1981; Weiner, 1982, 1984; Fowler, 1984; Pacala and Silander, 1985). Other workers used polygons in a similar way (Mead, 1966; Mithen *et al*, 1984; Matlack and Harper, 1986). Fowler (1984) thought of the effects of neighbours as complex cross-interrelationships.

Kent and Dress (1979, 1980) developed models which indicated that random and aggregated patterns were preserved through time, while a regular (lattice) pattern changed to a random one in natural even-aged stands. The influence of neighbours was omitted from their model (Kent and Dress, 1979, 1980). However others have found that in field data from even-aged populations of trees, shrubs and herbs, intensity of aggregation decreased in the course of self-thinning (Kershaw, 1963, 1973; Greig-Smith, 1964, 1979; Williams *et al.*,

1978) or tended to a nearly regular distribution (Cooper, 1961; Laessle, 1965; Tagawa, 1965; Phillips and MacMahon, 1981; Prach, 1981). Ford (1975) found that a regular distribution of first larger and subsequently all plants with self-thinning, and concluded this to be indicative of strong competition. Kenkel (1988) used various spatial statistical methods to investigate the pattern of self-thinning in a 65 year old stand of jack pine. He recorded positions of living and dead trees, and after analysis found that while the initial (live and dead) distribution was totally random, the distribution of live trees was significantly more clumped than random mortality would dictate. Analysis of 'area of influence' for each tree suggested that trees may compete directly only with their immediate neighbours (Kenkel, 1988). A two-phase process has been suggested to explain these results, with an initial two-sided scramble phase of competition for soil resources and a later one sided contest phase for light (Kenkel, 1988)

Leps and Kindlmann (1987) described models of developing spatial pattern over time in even-aged populations, using them to look both at random mortality and individual plant survival dependence on the competitive influence of neighbours. When survival depended on neighbour influence, spatial pattern approached randomness for aggregated or regular initial distribution. This has been used as evidence for the notion that intraspecific competition is the enforcer of regular spatial patterns. It is important to consider possible sampling artefacts when investigating spatial patterns in plant populations (Cox, 1987; Ebert and McMaster, 1981)

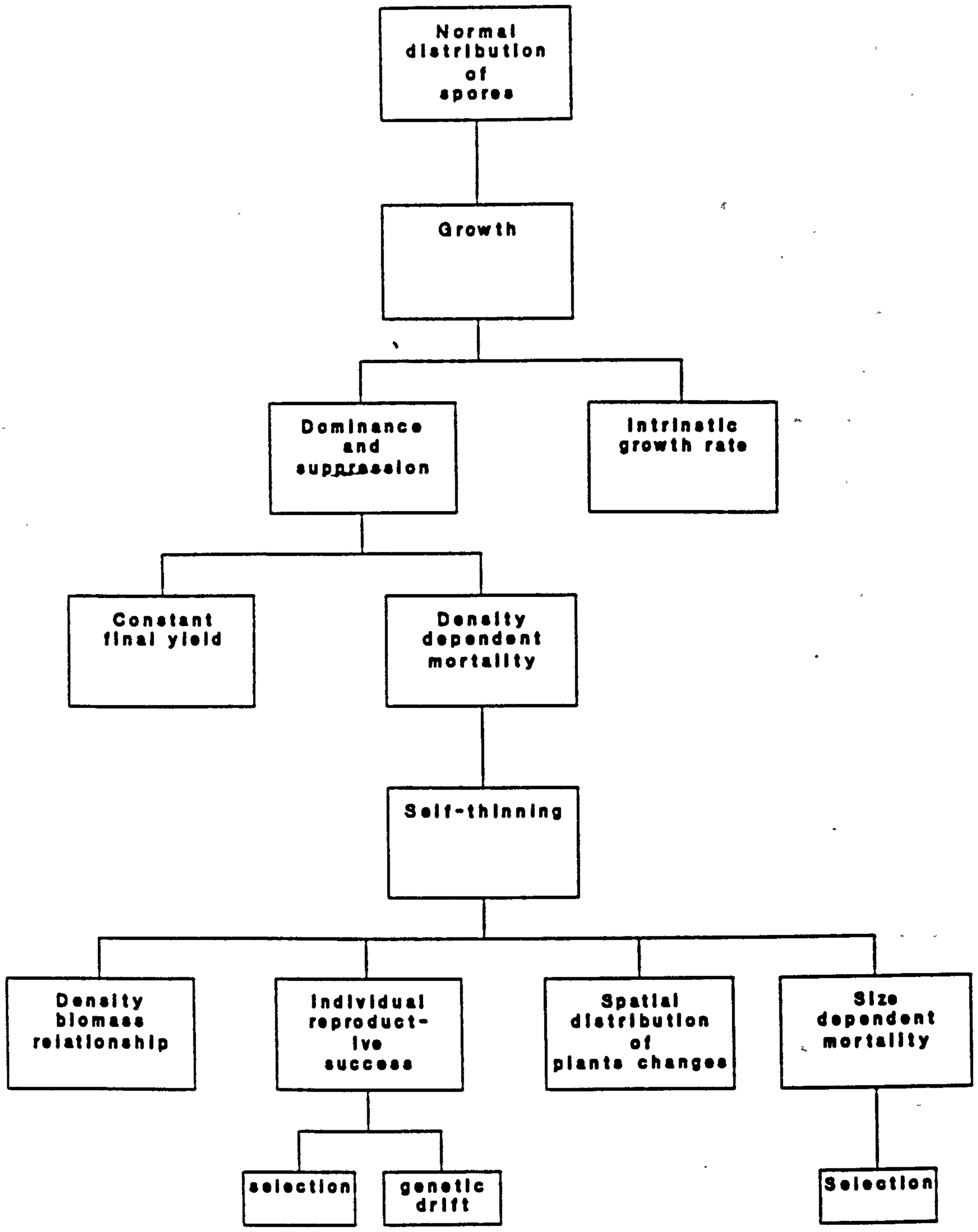
To my knowledge no studies have investigated the spatial dynamics of monospecific populations of marine algae and how they change with time during self-thinning, though one non-temporal spatial study has been carried out (Rice, 1987).

Summary

In the light of the above review, four main areas were identified in which our knowldge on intraspecific competition in seaweed populations is lacking (Figure 3). A knowledge of size distribution of settling propagules is vital if assumptions of the development of size heirarchy are to be made. There is also little information available on the development of size heirarchies in seaweed populations post-settlement, which may be important as seaweed populations in nature are usually found to be positively skewed. Thirdly, there is doubt over the applicability of the self-thinning rule to seaweeds, and little information on the development of self-thinning trajectories over time. The spatial changes which occur in populations undergoing density dependent mortality have also not received attention. When considering intraspecific competition, it is also of great value to identify the factor which is limiting growth. Too often only suggestions have been made.

With these gaps in our knowledge of intraspecific competition in seaweeds in mind, this thesis aims to investigate the natural population dynamics of some intertidal, monospecific, even-aged stands of algae. Futhermore, density will be manipulated in order to investigate the effects of intraspecific competition in these species. Because the sea shore presents many modes of density-independent mortality too, these studies will be supplemented with studies in the laboratory which will aim to minimise confounding factors. Finally, limiting factors will be manipulated in order to try to find what fundamentally drives intraspecific competition in seaweeds.

Figure 3 A diagramatic representation of how intraspecific competition may act on a population of plants



Chapter 1 Statistical Methods

1.1 Description of populations

1.1.1 Histograms

Histograms are indespensible in order to supplement statistical descriptions of a population, and therefore histograms were presented throughout this thesis. It is important that a suitable scale for size classes is selected, which in this case was determined by taking minimum and maximum values and splitting the difference into between 10 and 15 classes depending on a suitable step up value. All the histograms presented here are percentage frequency ones, as often the number of plants between samples varied quite substantially. Percentage histograms break down when *n* is small, and then may present a dubious picture of the population structure.

Three summary statistics have been used in the description of populations in this thesis, each of which quantifies a slightly different aspect of the population structure.

1.1.2 The skewness coefficient or moment skewness

The skewness coefficient (g_1) describes the symmetry of a population. *g1* is invariant to location and scale (Bendel *et al.*, 1989), and has been used as a test for normality. g_1 is derived from the third ($\mu 3$) moment, and is estimated by k_3 and s^3 where

$$k_3 = \frac{n\sum (X_i - \bar{X})^3}{(n-1)(n-2)} \qquad \text{Equation 1.1}$$

and with *s* as the sample standard deviation, then

$$g_1 = \frac{k_3}{s^3} \qquad \text{Equation 1.2}$$

If $g_1 > 0$ the population is positively skewed, most values are small and thus to the left of the mean, and the population is skewed to the right. $g_1 = 0$ signifies

normality, while if $g1 < 0$ the population is negatively skewed, with the majority of values being larger than the mean, and the population is thus skewed to the left.

1.1.3 Coefficient of variation

The coefficient of variation (*CV*) is a simple statistic to use, and describes with relative precision the variability or dispersion of sizes within a population (*eg* Zar, 1984). It is invariant to scale changes (Bendel *et al.*, 1989):

$$CV = \frac{s}{\bar{X}} \qquad \text{Equation 1.3}$$

where s is the sample standard deviation and $\bar{X}$ is the sample mean. Often it is multiplied by 100 to give a percentage for no other reason than the *CV* tends to be a small number (Zar, 1984). *CV* has no units, and *CV*s may be statistically compared for differences (*eg* Sokal and Rohlf, 1981; Zar, 1984).

In this thesis *CV* values were not converted to percentages.

1.1.4 Gini coefficient

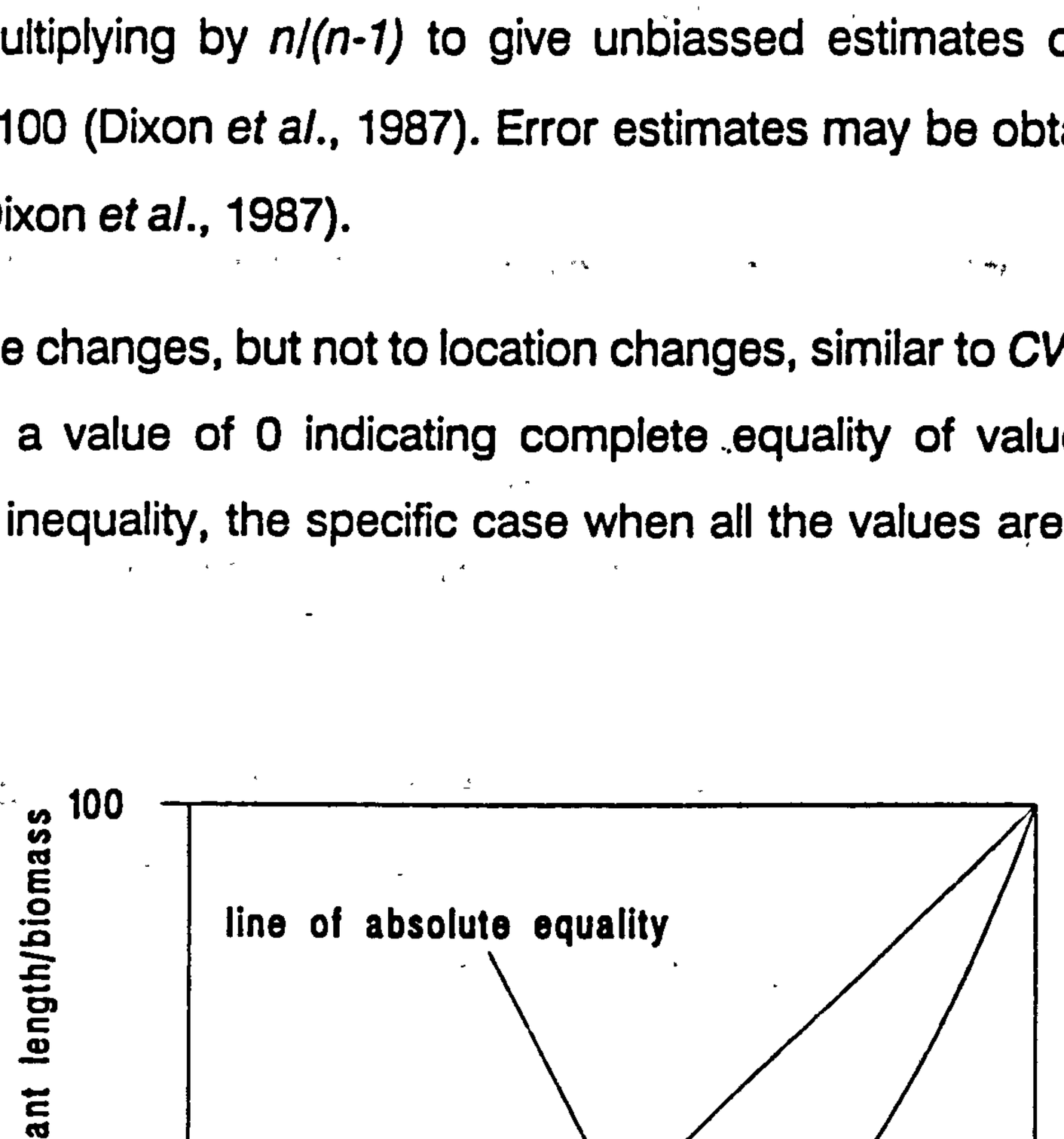
The Gini coefficient (G) is derived from the Lorentz Curve, which describes the cumulative precentage of a variable (*eg* plant size) relative to the cumulative proportion of the population. The Lorentz Curve is compared to the line of absolute equality, a diagonal from (0,0) to (100,100) which indicates that all values of the variable (sizes) are identical. The greater the variation, the greater the deviation of the Lorentz Curve. The ratio of area between the equality line and Lorentz Curve and the (triangular) area below the Lorentz curve describes the Gini Coefficient (Weiner and Solbrig, 1984; Figure 1.1). Statistically, *G* can be calculated by the equation:

$$G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \bar{x}} \qquad \text{Equation 1.4}$$

which is the average of the sum of the sums of all absolute values of each value taken from all other values. As statistical packages rarely include this statistic (originally derived from economics), both Ang and De Wreede (1992), and I used PC based spreadsheet macros to calculate *G*. It should be noted that the time taken to calculate *G* increases substantially with *n*, so random subsampling of values may be preferable for large data sets. However, Weiner and Solbrig (1984) suggest that sample *G*'s can be biased for small samples, and should be corrected by multiplying by *n/(n-1)* to give unbiassed estimates of the population with $n > 100$ (Dixon *et al.*, 1987). Error estimates may be obtained by bootstrapping (Dixon *et al.*, 1987).

G is invariant to scale changes, but not to location changes, similar to *CV*. *G* is bounded from 0-1, a value of 0 indicating complete equality of values, 1 indicating complete inequality, the specific case when all the values are zero except one.

Figure 1.1 The Lorentz curve.



The diagonal represents the case when all plants are the same size. With increasing size inequality the Lorentz curve's deviation from the line of absolute equality increases. The Gini Coefficient is derived from the relationship between the Gini area and the triangular area below it (see text).

1.2 Fitting self-thinning lines

The technique used to fit self-thinning lines is that recommended by Weller (1987a). For the thinning line as a boundary, there are no statistical techniques for fitting such a line. Historically, thinning lines have been fited by using regression techniques through the data (Weller, 1987a reviews these techniques). Only points near the conceptual boundary should be used, and so points below must be rejected before slope fitting can be carried out.

1.2.1 The method of fitting

1. Plots of $\log_{10}$ biomass or $\log_{10}$ mean plant weight against $\log_{10}$ density were prepared.

2. Using both plots, points in common below the potential thinning line were rejected subjectively, with the emphasis placed on rejecting the minimum number of points.

3. The strength of linear association was then investigated by correlation analysis (Pearson's product moment correlation). The null hypothesis was no correlation at $p = 0.05$. Accepting the null hypothesis meant that the data were unsuitable for slope fitting.

4. Slopes were fitted by a principal components analysis (Weller, 1987a) method.

5. The confidence limits of observed slopes were compared to the expected slope of -1.5 for the mean plant weight-density relationship, or -0.5 for the biomass-density relationship. If the expected slope fell within the confidence limits of the observed slope, then the observed slope was considered to conform to expectation.

1.2.2 Fitting slopes by principal components analysis

The methods employed were as follows (Sokal and Rohlf, 1981):-

1. With Y_1 as biomass and Y_2 as density, means, sums of squares and cross products were used to calculate:

$$s_2^1 = \frac{\sum y_1^2}{n-1} \qquad \text{Equation 1.5}$$

$$s_2^2 = \frac{\sum y_2^2}{n-1} \qquad \text{Equation 1.6}$$

$$s_{12} = \frac{\sum y_1 y_2}{n-1} \qquad \text{Equation 1.7}$$

$$\bar{Y}_1 = \frac{\sum Y_1}{n} \qquad \text{Equation 1.8}$$

$$\bar{Y}_2 = \frac{\sum Y_2}{n} \qquad \text{Equation 1.9}$$

2. The eigenvalues (λ_1 and λ_2) were found as follows

$$\text{Let } D = \sqrt{\left(s_1^2+s_2^2\right)^2 - 4\left(s_1^2 s_2^2 - s_{12}^2\right)} \qquad \text{Equation 1.10}$$

$$\lambda_1 = \frac{s_1^2 + s_2^2 + D}{2} \qquad \text{Equation 1.11}$$

$$\lambda_2 = \frac{s_1^2 + s_2^2 - D}{2} \qquad \text{Equation 1.12}$$

3. The slope of the principal axis, b_1 was found by

$$b_1 = \frac{s_{12}}{\lambda_1 - s_1^2} \qquad \text{Equation 1.13}$$

and the equation of this axis was found from Equations 1.8, 1.9 and 1.13

$$Y_1 = \bar{Y}_1 + b_1\left(Y_2 - \bar{Y}_2\right) \qquad \text{Equation 1.14}$$

4. 95% confidence limits (L_1 and L_2) were calculated by

$$\text{Let } H = \frac{F_{0.05[1,n-2]}}{[(\lambda_1/\lambda_2) + (\lambda_1/\lambda_2)-2](n-2)} \qquad \text{Equation 1.15}$$

then from Equations 1.14 and 1.15,

$$L_1 = \tan\left(\arctan b_1 - \tfrac{1}{2} \arcsin 2\sqrt{H}\right) \qquad \text{Equation 1.16}$$

$$L_2 = \tan\left(\arctan b_1 + \tfrac{1}{2} \arcsin 2\sqrt{H}\right) \qquad \text{Equation 1.17}$$

Though this method is an improvement over regression techniques (Weller, 1987*a*), two criticisms may be levelled at it. The points for slope fitting are chosen subjectively, and are therefore open to potential observer bias. Also the greater the number of rejected points, the lower *n* becomes and thus the wider the confidence intervals become. Widening confidence intervals increase the chance of the expected slope being accepted, and Weller (1987*a*) suggests that confidence limits can be imaginary.

1.3 Other methods

ANOVA was used in some chapters, and the methods of Underwood (1981) were used. Some experimental designs incorporated repeated measures, in which case single ANOVAs were calculated for each time. ANOVAs of the population statistics were justified by Rice (1990, *CV*) and Schmitt *et al.* (1986, *G* and g_1).

For other methods commonly used by biologists or specific to certain chapters such as spatial statistical methods of Chapter 9 refer to the relevant chapters.

The significance level used throughout this thesis was $p = 0.05$ (95% confidence level).

Chapter 2 Study sites

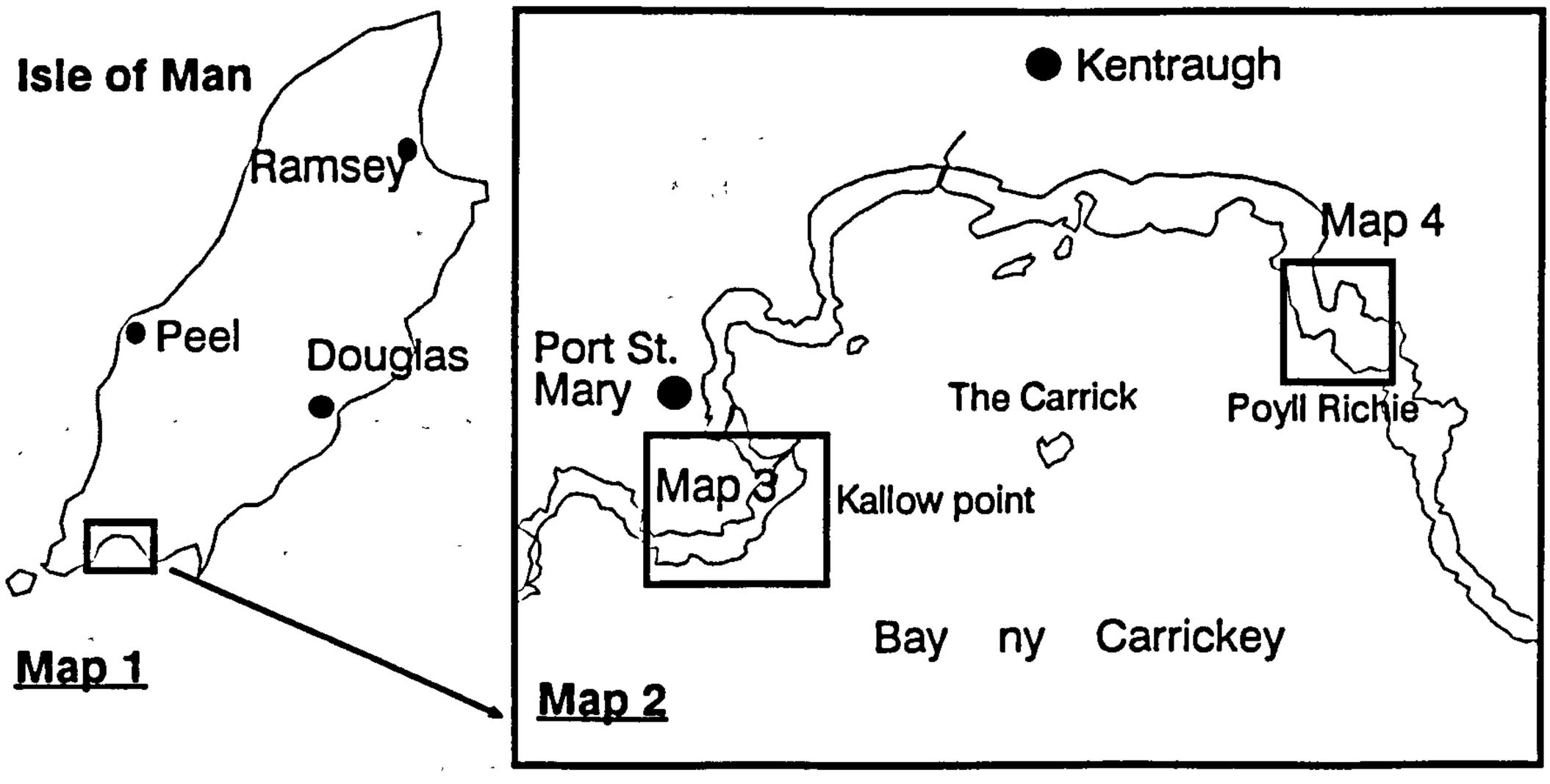
Two main study sites were used in the studies in this thesis, both in the south of the Isle of Man, situated in the Irish Sea (Map 1).

Port St Mary ledges

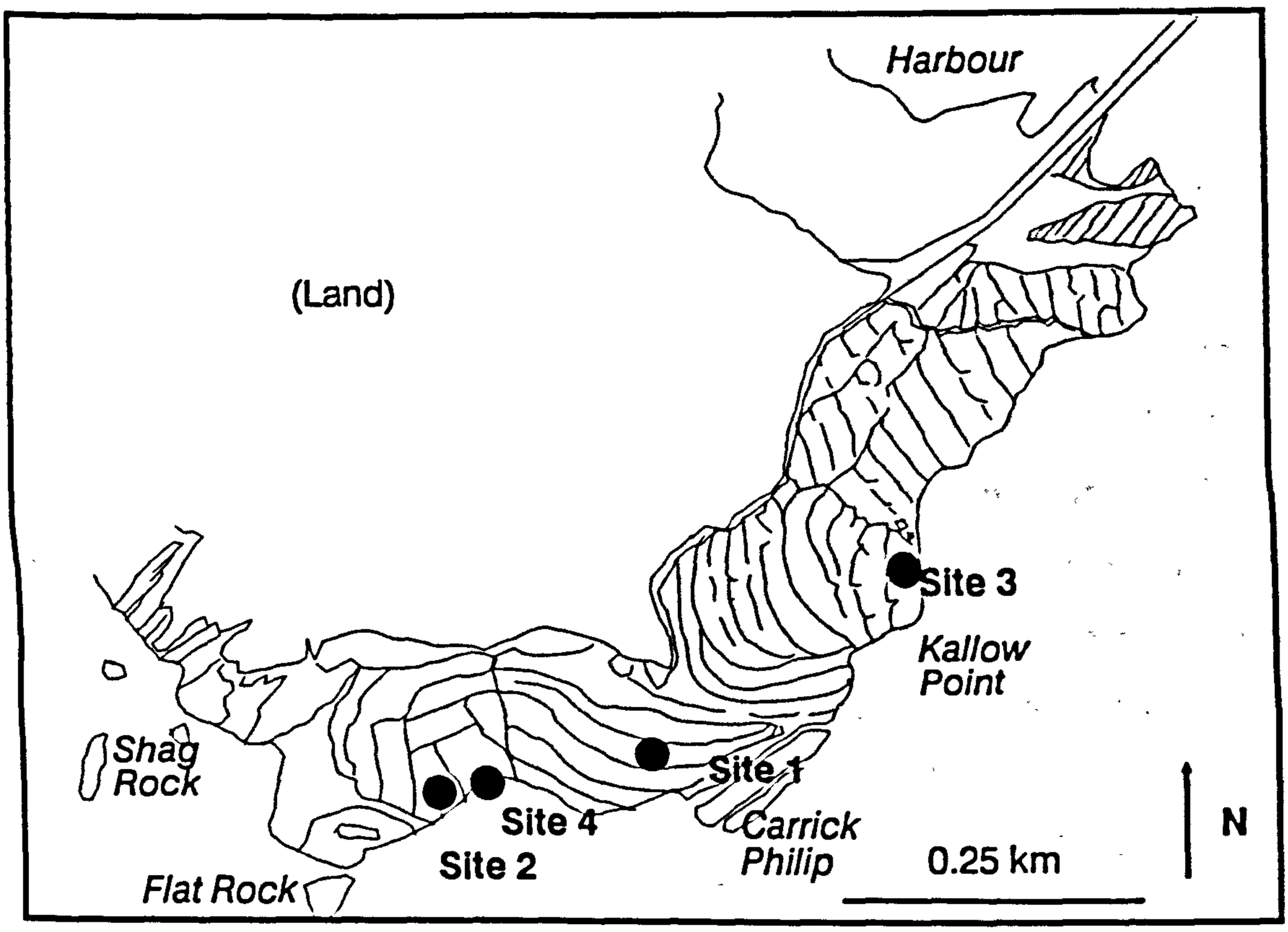
The flora and fauna of Port St. Mary ledges has been extensively studied because of their close proximity to Port Erin Marine Station (see Hawkins and Hartnoll, 1985 for a review). The ledges are situated on the western side of Bay Ny Carrickey (Map 2). The ledges are a series of flat stepped ledges extending from above high water springs to below low water springs (Map 3). Usually the *Pelvetia canaliculata* zone is absent, though distinct areas of *Fucus spiralis, Fucus vesiculosus, Fucus serratus* or *Himanthalia elongata* and *Laminaria digitata* occur intertidally. Some areas of the ledges have boulder fields, though generally they consist of bedrock.

Poyll Richie

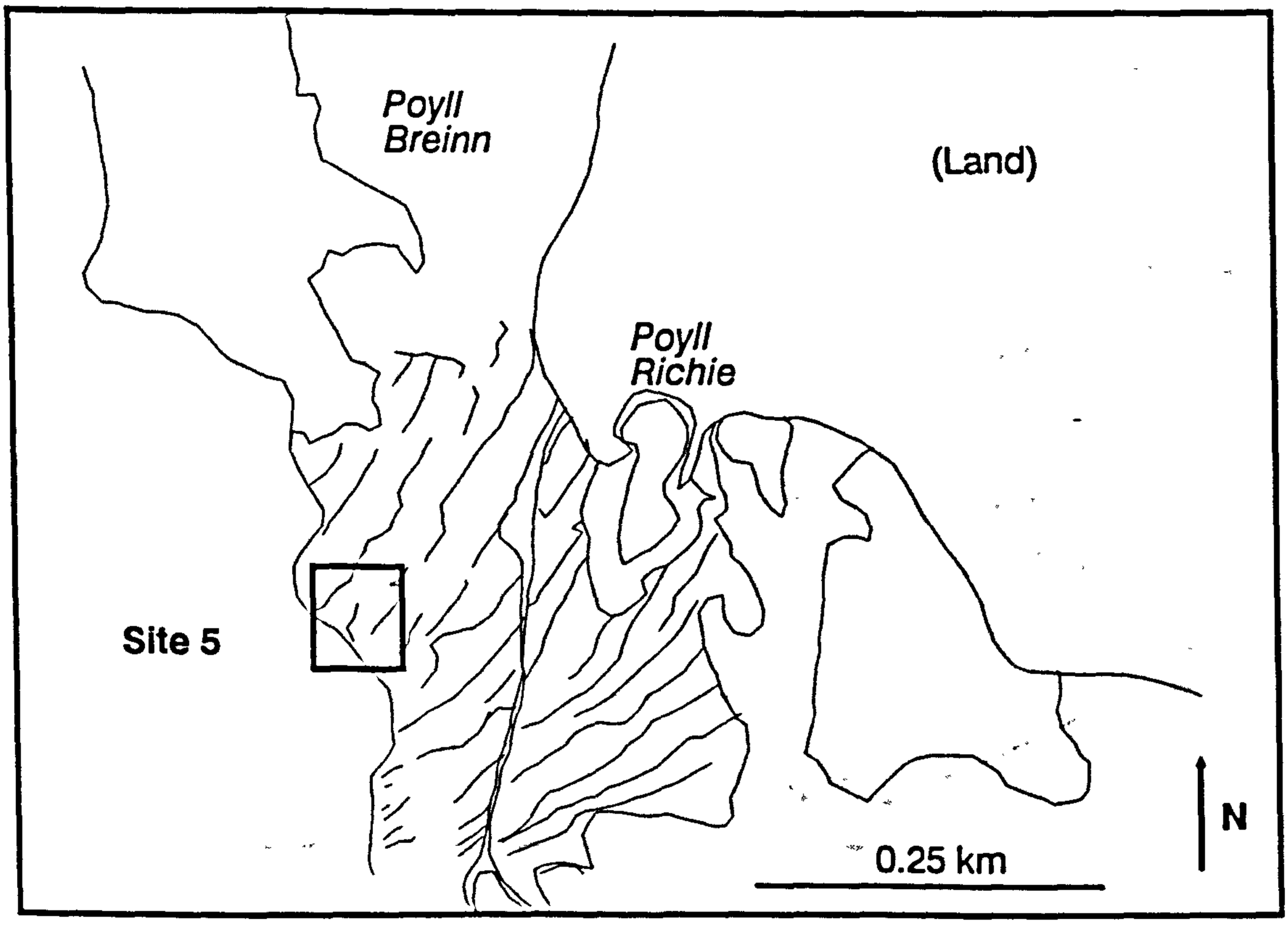
The Poyll Richie site is relatively untouched by scientists. It is on the eastern side of Bay ny Carrickey (Map 2). In many ways it is rather similar to the Ledges



Map 3 Port St. Mary Ledges, showing study and sample sites



Map 4 Poyll Richie, showing sample and study sites



at Port St. Mary as it has flat rock strata at least at the northern end (Map 4). The *Pelvetia canaliculata* zone is fully evident on the upper shore, though other zones are similar to the Ledges, except that *Himanthalia elongata* is not present. There is probably a greater abundance of littorinids at this site than the Ledges, particularly on the upper shore.

Meteorological data

Ronaldsway meteorological center is about five miles away from the study sites, and is therefore an accurate source of meteorological data appertaining to the two study sites. Temperature, rainfall, sunshine and windspeed and seawater surface temperature data are presented in Figure 1.1a-e. Seawater measures were made at Port Erin Marine Laboratory.

The location of individual study areas

Chapter 3

Fucus vesiculosus - Site 1

Fucus serratus - Site 5

Himanthalia elongata (Non-destructive) - Site 2

Himanthalia elongata (Destructive) - Site 3

Chapter 4

Fucus vesiculosus - Site 1

Himanthalia elongata - Site 3

Chapter 5

Fucus serratus - Site 5

Laminaria digitata - Site 4

Chapter 6

Fucus vesiculosus - Site 1

Chapter 7

Fucus serratus - Site 5

Chapter 8

Laminaria digitata - Site 4

Chapter 9

Himanthalia elongata photographs - Site 2

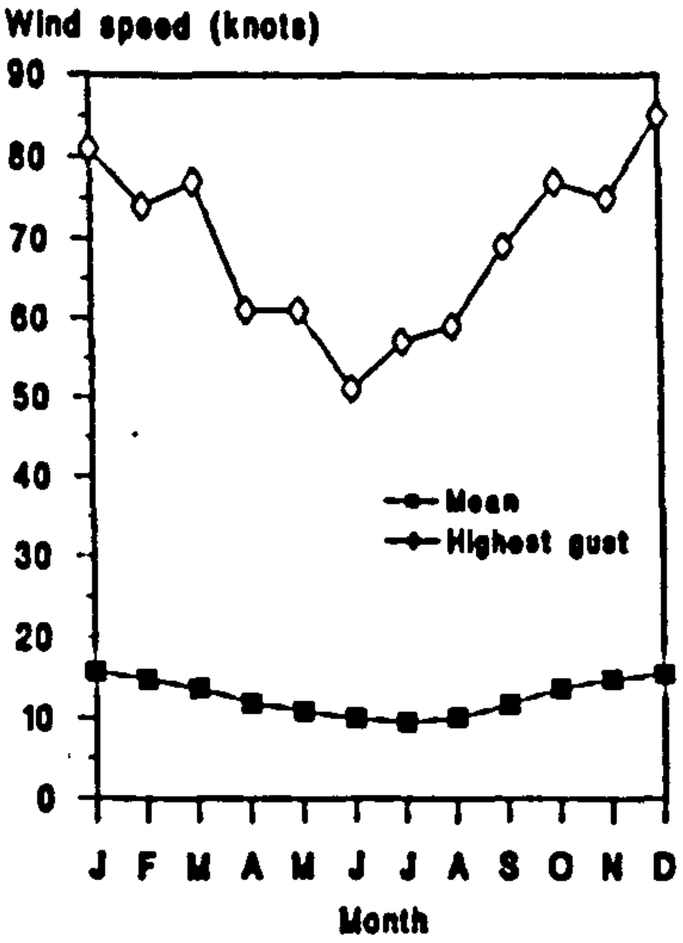
Himanthalia elongata settlement - Site 3

Rationale for choosing sites

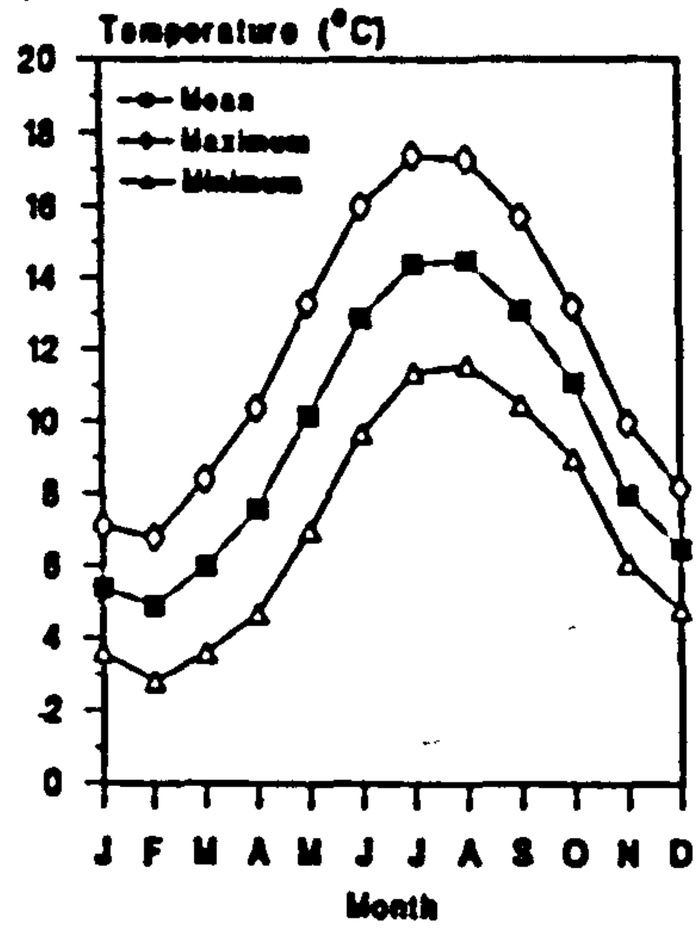
For field experiments, the major reason for the choice of site was the presence of even-aged, predominantly monospecific stands of the study species. Furthermore they were all close to the laboratory to minimise travelling time as a large number of visits had to be made.

Figure 2.1 Various meteorological observations for the Isle of Man, 1947-1986, except e).

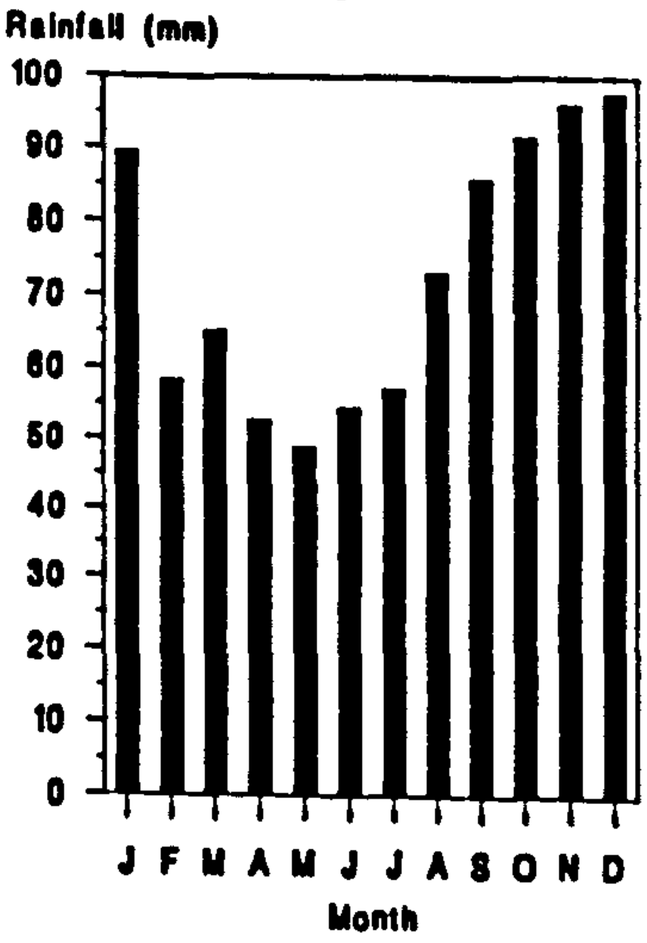
a) Mean monthly wind speed



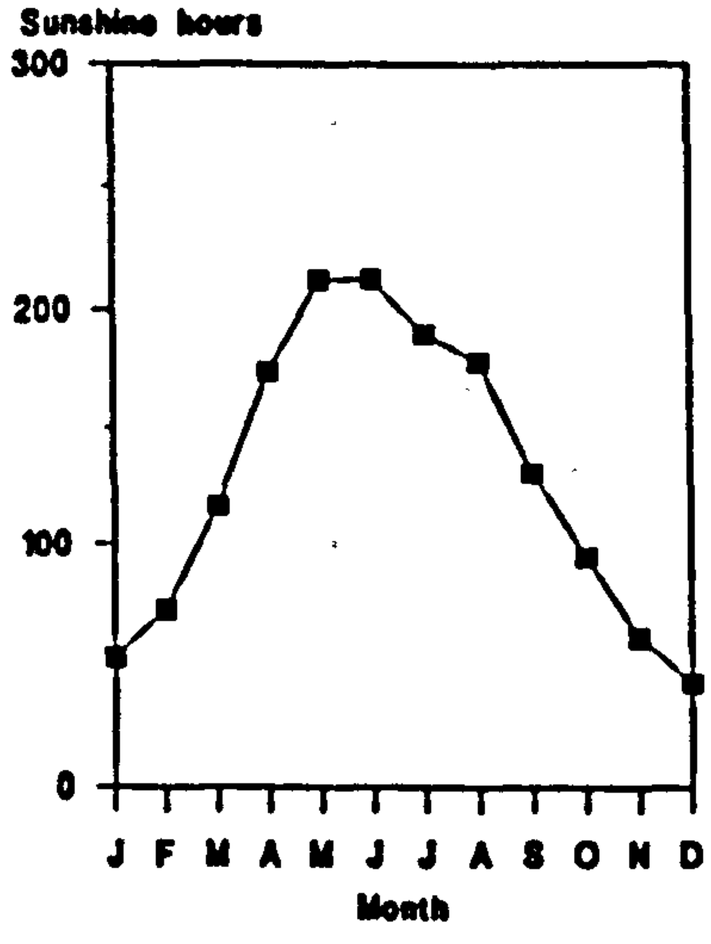
b) Mean monthly air temperatures



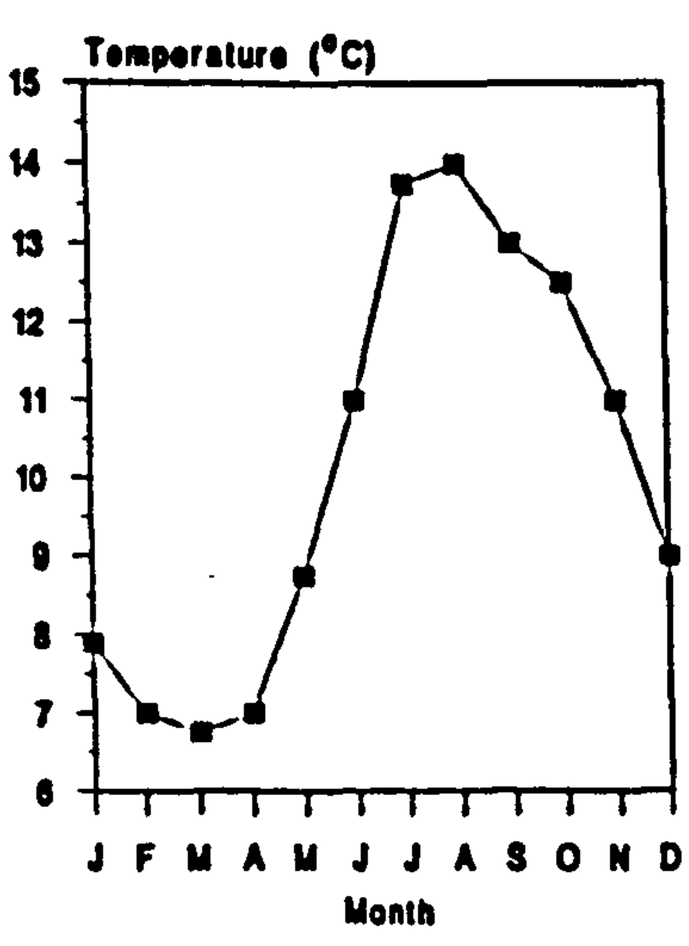
c) Mean monthly rainfall



d) Mean monthly sunshine



e) Mean monthly sea surface temperature, Port Erin Bay, 1976-1979.



Site 1 (*Fucus vesiculosus*) was chosen because it was a wide ledge with an even barnacle cover onto which *F. vesiculosus* propagules had recruited particularly heavily despite only a small number of adult plants being present. This made the site suitable for destructive monitoring and manipulations, for which quite a large area was required.

Site 2 and 3 consisted of particularly dense aggregations of *Himanthalia elongata* buttons, which usually have a patchy distribution on the Ledges. The study areas probably arose after winter storms had cleared away areas of reproductively mature adult plants, opening up space for new plants.

Site 5 (F*ucus serratus*) was at Poyll Richie, and had a dense canopy of large reproductively mature adult plants with almost no understorey species other than the crustose coralline alga *Phymatolithon purpureum*. It was easy to clear areas for experimentation as there were fewer, larger plants, though the plants around cleared areas ensured a large supply of propagules.

Apart from field-experiments, material had to be collected for laboratory based work. Site 4 (*Laminaria digitata*) was one such site which was particularly suitable as it had been used in a previous manipulation experiment by a postgraduate student and had a large number of suitably sized plants.

Chapter 3 The population dynamics of three Fucoid algae

3.1 Introduction

Fucus vesiculosus is an important component of the contingent of marine macroalgae to be found intertidally on British and other northern temperate shores (Knight and Parke, 1950; Keser *et al.*, 1981; Chapman, 1990*a*). It is often found in predominantly monospecific stands. Furthermore, frequently it occurs in even aged patches. It therefore makes an ideal study organism for the elucidation of intraspecific competition.

Various aspects of the population dynamics of *F. vesiculosus* have previously been studied. These studies include observations on the dynamics of *F. vesiculosus* itself (Knight and Parke, 1950), studies of effects on other plant species (Chapman, 1990*a*) and studies of population interactions in multispecies communities (McCook and Chapman, 1991; 1992). The genus *Fucus* is a complex of species, subspecies, hybrids and ecads, and *F. vesiculosus* is no exception (*eg* Burrows and Lodge, 1951).

It was therefore considered necessary to study a natural monospecific even-aged cohort of *F. vesiculosus* as an entity, incorporating the most recent methods in data collection and analysis in order to relate natural dynamics on the shore to experimental manipulations on the shore and under the more controlled conditions of the laboratory.

Himanthalia elongata also commonly occurs on British rocky shores (Gibb, 1937). It may compete directly with *Fucus serratus* (Norton, 1986) as it is usually found at a similar height on the shore. Silt inhibits the survival of *H. elongata*, and this may be responsible in part for its preference for wave exposed sites. Though often a minor consituent of the flora of certain locations, *H. elongata* becomes the dominant species forming dense monocultures in semi-exposed areas (Russell, 1988). As a deciduiphyke (Chapman and Chapman, 1976) *H.*

elongata has a macroscopic attached thallus which remains for part of the year while the basal portion is perennial. This life form strategy has brought about some confusion regarding *H. elongata*'s longevity until recently (*eg* Russell, 1990). However, this same attribute also makes *H. elongata* a potentially useful subject in the study of density biomass relationships because it essentially changes form during its life. Furthermore, because this species is found in dense populations, it may be a useful ally in the study of intraspecific competition.

F. serratus is a very common component of rocky shores. It has been extensively studied before (*eg* Knight and Parke, 1950). However, no published studies have investigated the development of population structure early in its life. This species was chosen to test the assumption that the size structure of seaweed propagules is initially distributed normally as is usually the case in seeds of land plants (Harper, 1977). *F. serratus* makes a useful subject as dense aggregations of propagules may settle in a short time. A knowledge of early population structure is fundamental to our understanding of plant population dynamics, though there seems to have been no work directly examining population structure in seaweeds at a microscopic stage. This may partly explain why the possibility that algal equivalents to a 'seed bank' have only recently being recognised (Hoffman and Santelices, 1991).

3.2 Materials and Methods

3.2.1 Fucus vesiculosus

An area of shore at The Ledges, Port St. Mary, Isle of Man was selected in August 1990. The area was a ledge of rock approximately 10 x 5 m and roughly rectangular. The fall in height from the top of the study site to the bottom was 20 cm, which equated to a delay of 30 minutes between cover of bottom and top of the study site with a rising or falling tide. The area consisted of a barnacle-limpet-*Fucus* matrix. The area was initially delineated by marking four corners with ring bolts to which were attached 30 cm long pieces of fluorescent plastic tape in order to make site relocation easy. To achieve this, holes were drilled into the rock using a compressed air drill and compressed air cylinders, while rawplugs were used to hold the ringbolts in place.

Having delineated the area, thin rope was used to divide the area and facilitate its subsequent treatment. Initially any *Fucus* plants over 1 cm tall, and therefore not recent recruits, were removed. Any other plant species present were also removed (if large enough). The limpet *Patella vulgata*, the predominant herbivore at this site, was also removed along with other visible gastropods so as to reduce herbivory and barnacle predation.

Eleven 25 x 25 cm quadrats were permanently marked in this area approximately 2 weeks later, by subjectively locating quadrats within the areas with 100% barnacle cover. This precluded areas which limpets had previously occupied, which were covered by a layer of green algae by this stage. Also the areas were selected on the basis of evenness of *Fucus vesiculosus* population cover, and care was taken to avoid the edges of patches.

Quadrats were marked permanently on the shore by drilling holes with a 2-stroke Riobi drill using lead-free petrol. The holes were marked with screws screwed through a 1 cm^2 piece of fluorescent plastic tape into Plasplug rawplugs. Preliminary experiments revealed that drilling holes and marking in

this way did not damage the barnacle matrix or make it susceptible to destruction by waves. A map was drawn of the quadrat layout and quadrats on it numbered for the purpose of relocation.

Quadrats were selected at random for destructive sampling. Preliminary work revealed that 5 x 5 cm quadrats were initially required to estimate with accuracy the population density (Figure 3.1). The position of each sample in each quadrat selected was also randomly placed within a grid of 25 squares. Later in the study larger sample areas were required, of 10 x 10 or 15 x 15 cm areas in order to estimate population dynamics with accuracy. The decision as to when to step up the sample size was based on reviewing the smoothness of size class transition of population structure for the previous sampling period.

Sampling was initially fortnightly. Later, samples were taken at monthly or two monthly intervals (Table 3.1). Three sample areas were generally taken at each time. Samples of barnacles and attached *Fucus* were carefully scraped from the rock using an ordinary cutlery knife and placed in marked plastic bags for subsequent analysis in the laboratory.

Samples were processed by removing any visible *F. vesiculosus* plants from the barnacles. This was done as quickly as possible to remove the risk of herbivory by the few amphipods invariably also collected in the sample. The length of each individual plant was then measured to an accuracy of 1mm with a ruler. Biomass was measured as a collective dry weight of all plants in each sample (giving three replicate samples for each time). Samples were oven dried at 60 °C in aluminium pie dishes until two consecutive dry weight measurements agreed to within 0.001 g. Dry weight was measured using a Sartorius balance accurate to 0.0001 g.

When plants became reproductive three additional parameters were measured: the number of receptacles on each reproductive plant, the number of reproductive plants in the population and the total dry weight of excised receptacles of the population, this being an estimate of reproductive potential.

Figure 3.1 Estimating the minimum sample area by density at the start of an experiment assessing the population dynamics of *Fucus vesiculosus*

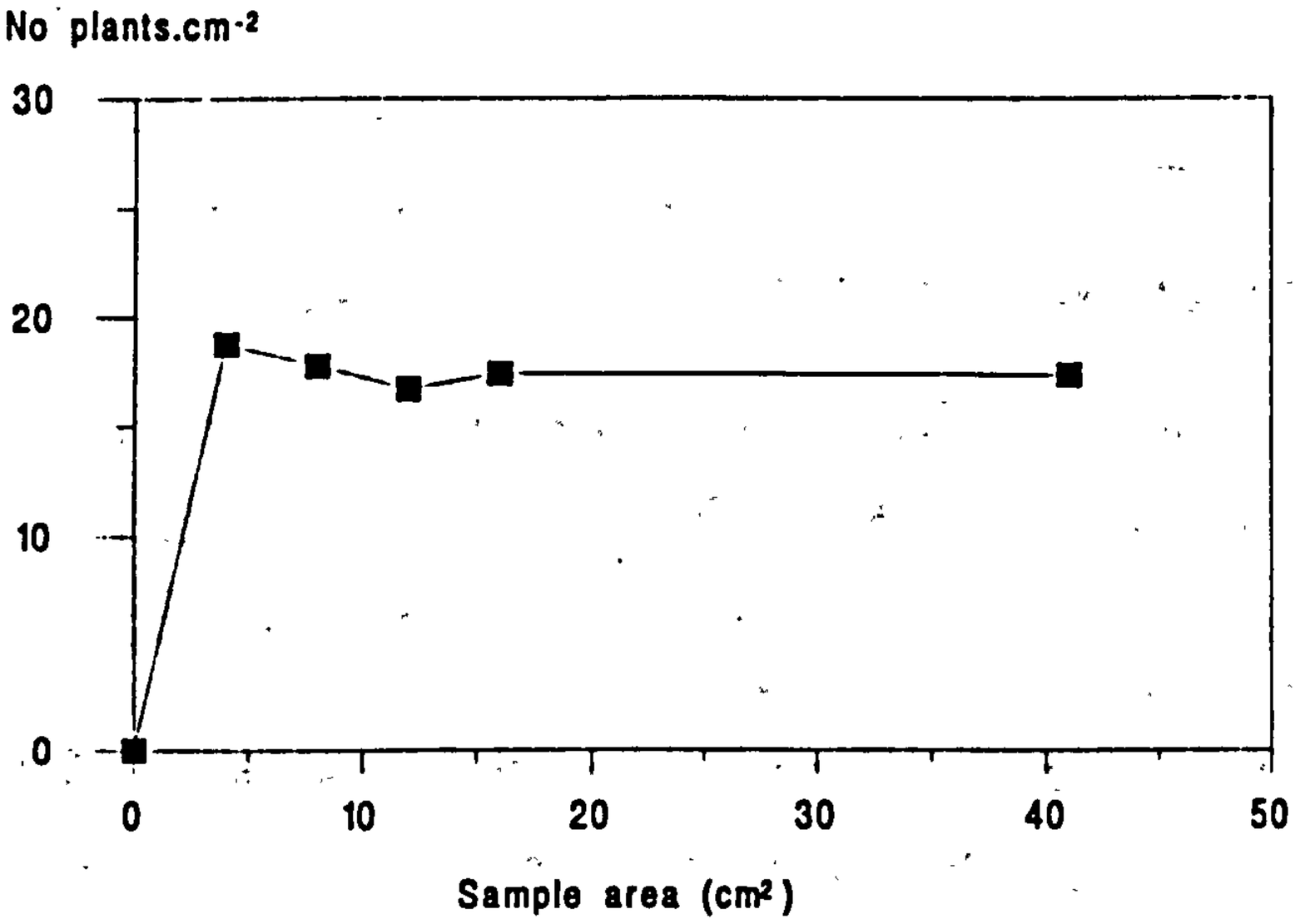


Table 3.1 Sample details for *Fucus vesiculosus* experiment

Sample	Date	Sample size	Day	n
1	09/09/1990	25	0	3
2	23/09/1990	25	14	3
3	07/10/1990	25	28	3
4	21/10/1990	25	42	3
5	05/11/1990	100	58	3
6	21/11/1990	100	73	3
7	05/12/1990	100	87	3
8	03/01/1991	100	116	3
9	05/02/1991	225	147	3
10	05/03/1991	225	175	3
11	03/04/1991	225	204	3
12	21/05/1991	225	252	3
13	30/7/1991	225	322	3
14	06/10/1991	225	380	3
15	06/03/1992	750	531	2

The statistical analyses performed are those in Chapter 1 unless otherwise stated.

3.2.2 Himanthalia elongata

3.2.2.1 Non-destructive monitoring

Eight young populations of *Himanthalia elongata* at the early 'button' stage were selected on the Ledges, Port St. Mary, Isle of Man in March 1990 (see Chapter 2 for site details). They were permanently marked as above.

A non-destructive photographic sampling technique was used. A Canon A1 SLR camera with a 70-210 Macro zoom lens was suspended 1m directly above a population on a standard photographic tripod. Ilford HP5 or HP5Plus 400ASA black and white print film was used. Fast film was used because the subject matter was dark and the populations were only accessible on low spring tides, which occur in early morning and early evening around Manx shores, when light availability was often poor. Where necessary natural light levels were supplemented with flash.

Preliminary monitoring was conducted to verify the technique. Photographs were taken with a scale in the picture to check that peripheral aberration of picture quality was minimal. It was. The five of the eight populations originally marked that were most advanced were photographed and immediately destructively harvested. All plants were measured for maximum button width using callipers accurate to 0.1mm, and then oven dried at 60 °C as above. Button diameters measured from the photographs tallied closely with direct 'ground truth' measures, as did the number of plants. This confirmed that in such populations, which were closely packed, there was no understorey of small plants missed by the photographic technique. Other investigations of mine revealed that overgrown plants died quickly.

Separately, over the proceeding four months, buttons had been collected from a number of sites on the Ledges on a number of occasions in order to

investigate whether any linear measure of the buttons was a good descriptor of plant dry weight. Maximum button width, button width perpendicular to this measure, above holdfast diameter, half-height diameter, button heights and button type were measured for all plants (see Figure 3.2). For later stage plants (4-6) button top thickness (as a mean of three measures) was taken and where plants had thongs (developing receptacles), maximum thong length was recorded. Blotted wet weight and oven dried dry weight were also measured. Ninety four plants were measured in this way, and maximum button width was found to be the most accurate predictor of dry weight (Table 3.2). Other measures were therefore dropped, and effort was concentrated on supplementing data on dry weight-maximum button width measures until a large number of measures had been taken. A robust linear relationship was found which could be used as a predictive tool in conjunction with the photographs to estimate population standing crop from the sum of the weights of individual plants (Figure 3.3). Actual measures of standing crop agreed very well with predictions.

Photographs of the three remaining populations were taken at fortnightly intervals unless the weather was bad (Table 3.3). Photographs were always taken with 0.5 mm black square scales so that variation in magnification could be corrected. Photographs were developed and printed on 20 x 25 cm paper on return to the laboratory so that a revisit could be made if problems occurred. Monitoring stopped when buttons began to produce thongs. Seperately, seven plants growing individually, close to the photographed populations, were measured at regular intervals in order to see whether there was any difference in growth rates of plants in populations to those growing individually.

Photographs had acetate sheets overlaid, and each plant was given a unique identifying number. Photographs were then digitized using a sonic Graf/Bar MARK II (Science Accessories Corporation) digitizer and pen cursor operating with DesignCAD 2-D v4.2, an off-the-shelf computer aided design program running on an IBM compatible personal computer with a '286 processor.

Figure 3.2 The stages of *Himanthalia elongata* buttons and the various measures taken in order to find a predictor for dry weight

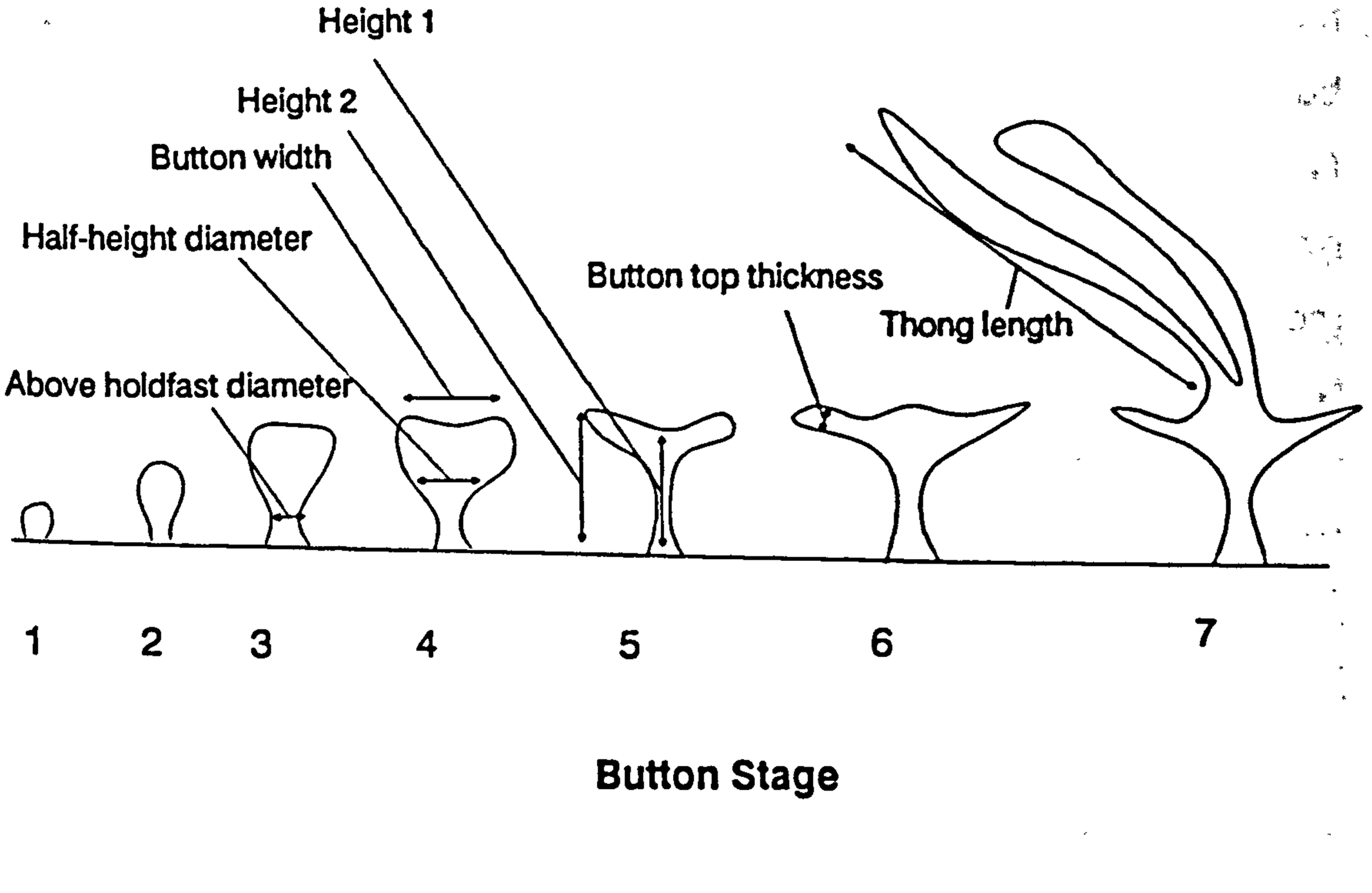
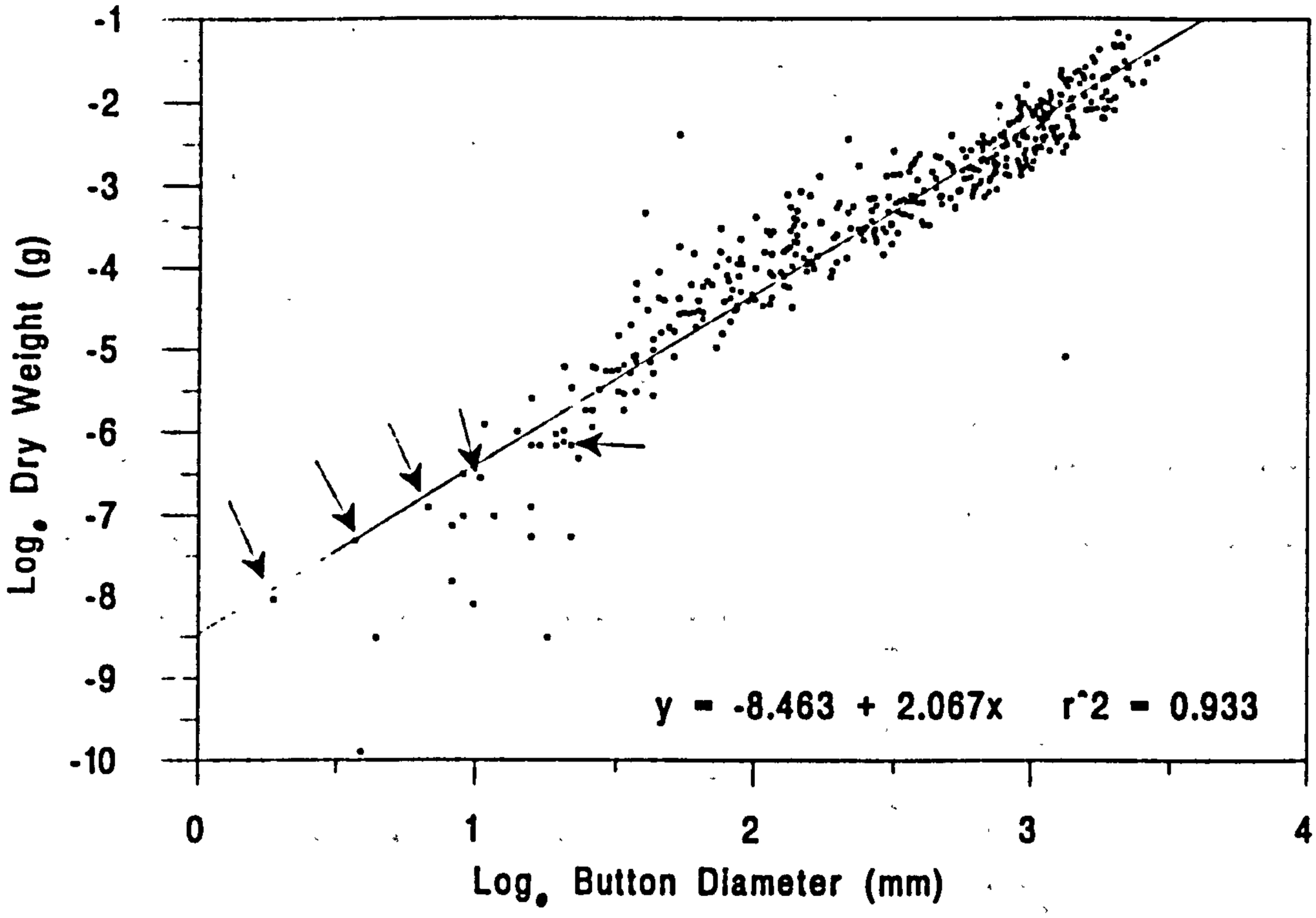


Table 3.2 Correlations of various *Himanthalia elongata* button measures with dry weight in order to find a suitable estimator measure

Measure	Correlation Coefficient	n	Significance @p=0.005
Button diameter	0.952	94	S
Button type	0.764	94	S
Above holdfast diameter	0.705	89	S
Half diameter	0.248	89	NS
Top thickness	-0.480	40	S
Wet weight	0.904	94	S
Height central	0.148	89	NS
Height inclined	0.400	40	S

Figure 3.3 The relationship between button diameter and dry weight in *Himanthalia elongata*



Arrowed points represent means of ten plants

Digitizing was simplified by assuming that plants could be described by a central point and radius point defining a circle. Each plant also had its identifier input into the drawing, and drawings were saved as ASCII text files. These files were imported into a Lotus 123 v2.2 spreadsheet and a bespoke macro was developed which sorted the data, calculated plant diameters based on *xy* coordinates, calculated the population Gini, skewness and variation coefficients, generated size- and weight-frequency tables, as well as calculating plant density and estimating standing crop.

3.2.2.2 Destructive sampling

During the winter storms of 1990-1991 an area of the Ledges, Port St. Mary was naturally cleared of most mature, receptacle bearing *H. elongata* plants by wave action, exposing a large area of small dense *H. elongata* buttons (see Chapter 2 for study site details).

Table 3.3 Sample details of the two *Himanthalia elongata* experiments

Sample	Photographic monitoring		Destructive sampling	
	Date	n	Date	n
1	27/04/1990	3	05/02/1991	3
2	11/05/1990	3	05/03/1991	3
3	14/06/1990	3	03/04/1991	3
4	24/06/1990	3	21/05/1991	3
5	13/07/1990	2	30/07/1991	3
6	23/07/1990	2	06/10/1991	2
7	10/08/1990	2	06/03/1992	2
8	21/08/1990	3		
9	06/09/1990	2		
10	23/09/1990	2		
11	20/10/1990	2		
12	01/11/1990	3		

A rectangular area of 3 x 6 m was marked within this patch by attaching ringbolts to the rock at 1 m intervals around the study area. The ringbolts were then used as anchors for string which divided the area into eighteen 1 m^2 areas. Any older *H. elongata* plants and all other macroalgal species (predominantly *Fucus serratus* and *Laminaria digitata*) were removed from the area. A 'roundrat' (circular sampling frame) 10cm diameter was constructed from a plastic bucket (see Chapter 4, Figure 4.3). Areas with 100 % *H. elongata* cover were selected and the roundrat pushed into the plant patch. A knife was used to remove any plants from round the outside of the roundrat and the roundrat taken away to reveal a round population of plants. A circular shape was selected over a square or rectangular one for two reasons. Such a shape minimises the perimeter to area ratio, and thus minimises edge effects. Also plants at the edge of a circular population will all experience the same intensity of potential edge effects, while

in a quadrat, plants in corners will experience a greater influence of edge effects than those half way along a side.

Populations were marked with brass screws and fluorescent plastic tape. Populations were numbered and random numbers generated to select populations for sampling at different times. Whole populations were sampled at each time, usually three each time (Table 3.3). Maximum button width, and where appropriate, maximum thong length were measured to 0.1 mm using callipers and 1mm using a ruler respectively. Whole populations were then oven dried (as above) and population dry weight measured.

3.2.3 Fucus serratus

3.2.3.1 Preparation of the study area

The study was carried out on an area of rocky shore near Poyll Richie on the eastern side of Bay ny Carrickey, Isle of Man (see Chapter 2). Five discrete (20m apart) 4 x 4 m areas were permanently marked as above. The areas, consisting of dense *F. serratus* canopy were cleared of visible macroalgae (excluding the crustose coralline species). Holes were drilled within each area and clean discs (see below) were screwed into the rock. Allowing a 1 m boundary band around the area 33 discs were randomly sited in each area. The experiment was set up from 25th-28th October 1991.

Monitoring was conducted to investigate the early development of a population of *F. serratus*. Artificial surfaces were used in preference to the natural substratum for three reasons. The discs used were distinct standard units which satisfied the criteria of statistical independence and could be easily handled. The discs could be brought to the laboratory for analysis without disturbance of the populations on them. Finally, the substratum in the study area was the red coralline crustose alga *Phymatolithon purpureum*. *Phymatolithon* spp have been shown to slough the epithallus (Johnson and Mann, 1986), and this was an unwanted effect in my study.

3.2.3.2 The manufacture of settlement discs

In order to make a mould, a positive was created out of acrylic sheet on which settlement discs were represented by acrylic discs with sandpaper glued to the upper surface to provide a rough textured surface. The mould was made from silicone rubber (Sylastic) made up to manufacturers instructions, which was poured onto the positive and allowed to set. The mould could make ten discs each time. Discs were made from an epoxy adhesive (Sikadur 31 Rapid, Sika Ltd, Welwyn Garden City, UK). The mould was dampened with washing up liquid before being filled with epoxy, application being made with a round-ended cutlery knife. The epoxy had a thixotropic quality, and once the mould was filled gentle tapping of the mould settled the epoxy and excluded air bubbles. The mouldings were set in an oven at 80 °C which substantially reduced the setting time and allowed a quicker turn around time in the manufacture of the discs. After manufacture the discs were soaked in running fresh water for two days before use. 180 discs were made in this way.

3.2.3.3 Settlement of propagules

In order to estimate the settlement rate of zygotes of *F. serratus* the 'same' three discs were regularly collected and replaced with fresh ones in each of the five areas. Thus settlement (actually settlement and short term survival) could be regularly monitored. The sample details are presented in Table 3.4. Counts were made of the numbers of propagules on each disc using a stereomicroscope and fibre optic incident light source. If the numbers of propagules were large four random stratified fields of view (one from each quarter of the disc) were sampled, and the number per disc was estimated by multiplying up.

3.2.3.4 Population dynamics

Destructive samples of the 30 remaining discs were carried out at intervals, with three discs collected from each area at each time. Sampling details are presented in Table 3.4.

As well as young *F. serratus* germlings, a layer of diatoms and detritus soon built up on the discs and a method was developed to remove this so that buried spores could be seen. Seven sacrificial discs were collected. Ten ml of water in a syringe was squirted onto each disc through a fine hypodermic needle at a fairly constant pressure. This removed most of the diatoms and detritus. The dregs from each disc were collected and examined under a microscope to see what proportion of spores had been blasted off the disc, and whether any particular size of spore was preferentially removed. No particular size of sporeling was selected, and only between 0.5 and 2.7 % of germlings were removed with the diatoms, a negligible amount (Figure 3.4).

Once the discs had been cleaned they were censused. For each disc the outlines of all the propagules in four seperate fields of view were drawn with the aid of a *camera lucida*. As some plants in the population got larger, and the population density got smaller, so the fields of view were increased to take account of this change. For discs from the last two sample times, all the largest plants were removed with forceps and drawn seperately, and then the smaller plants were subsampled by fields of view. This was done because the large plants were much more sparse than the smaller ones and they often hid smaller plants beneath them. The images were digitised and processed (Figure 3.5) as for *H. elongata* photographs (above), except drawings were of length rather than circles (diameter).

3.2.3.5 Oospores

To supplement data from the wild, the sizes of artificially released oospores were also measured. All the receptacles from a mature female plant were excised and shocked to encourage the release of oospores (for method see Chapter 6 for *F. vesiculosus*). The suspension of oospores were analysed for size with a Coulter Multisizer.

Table 3.4 Sample details for the monitoring of settlement (discs replaced) and growth (destructive disc sampling) in a population of *Fucus serratus* germlings

Sample	Date	Settlement	Settlement and Growth
1	10/11/1991	√	√
2	26/11/1991	√	√
3	10/12/1991	√	√
4	12/01/1992	√	√
5	23/01/1992	√	x
6	08/02/1992	√	√
7	20/02/1992	√	x
8	22/03/1992	√	√
9	22/04/1992	√	x
10	09/05/1992	√	√
11	16/07/1992	√	√

Figure 3.4 The loss of spores of *Fucus serratus* from discs when washed to remove diatoms

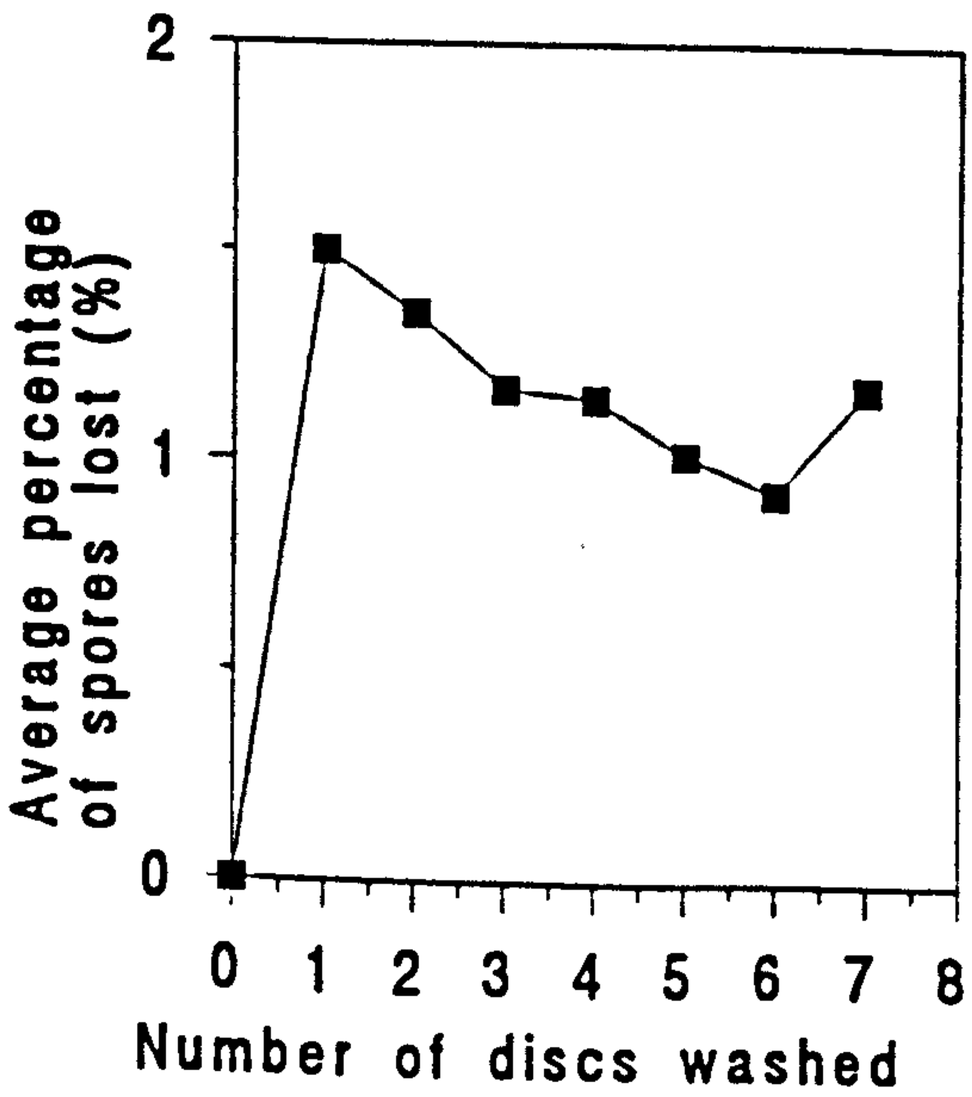
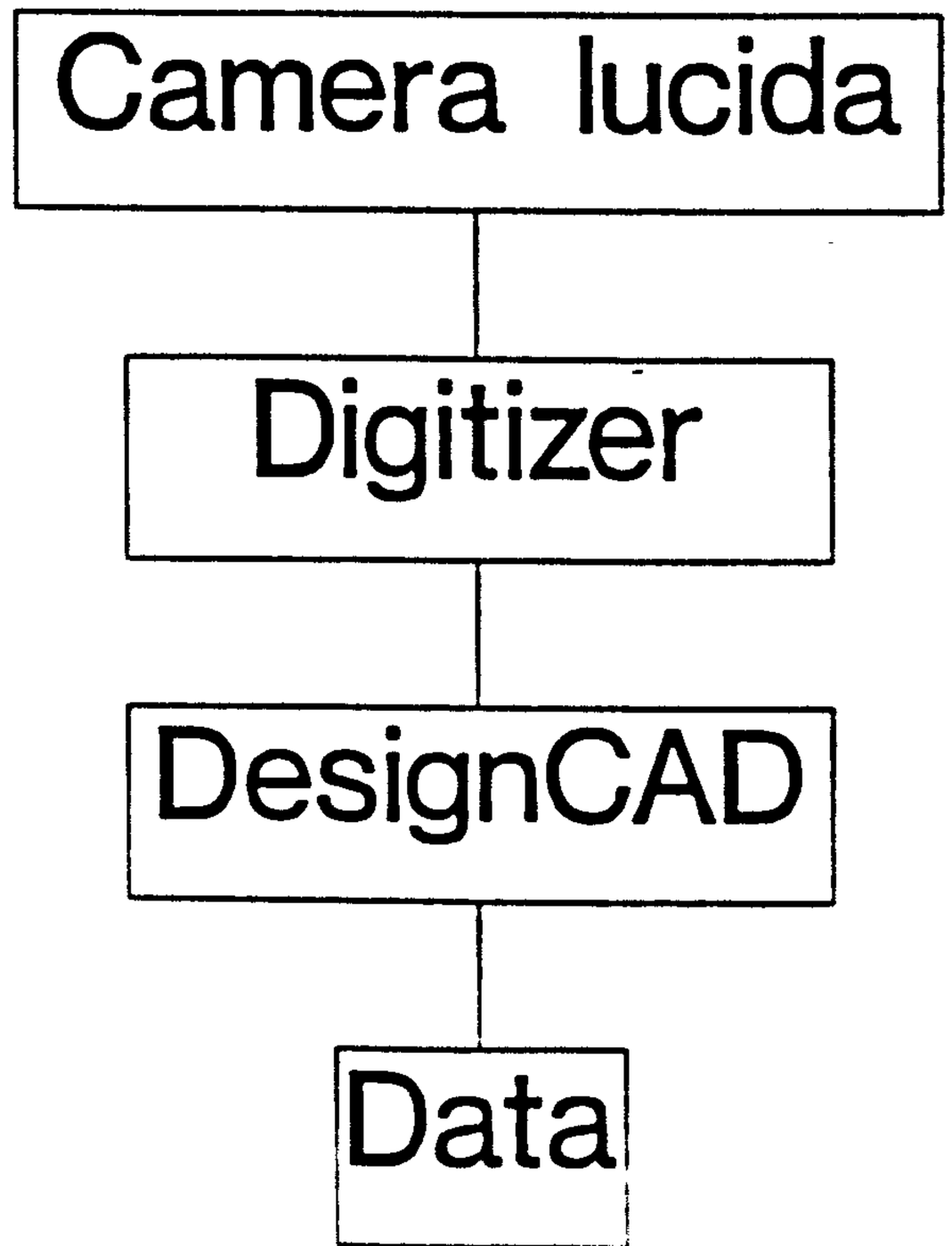


Figure 3.5 The analysis of populations



3.3 Results

3.3.1 Fucus vesiculosus

3.3.1.1 Population structure

Initially, the population structure of plant sizes was positively skewed (Figure 3.6). By October, population structure had started to differentiate into two separate features, a large initial size class (more than 80 % of plants were less than 20 mm in length), and a secondary peak in the third size class (40 - 60 mm, Figure 3.6). The population structure then developed in a similar fashion until May 1991. This consisted of a large first size class and a second peak of larger plants. While the first peak remained stationary over time, the plant sizes of the second mode became more variable. Statistical analyses of these data quantified aspects of the population structure and its development.

Variability (as coefficient of variation) was quite high during early winter (Figure 3.7). This variability decreased throughout late winter and over the spring, summer and autumn was fairly stable, though increasingly variable from sample to sample. In terms of the Gini coefficient (Figure 3.8), the population behaved similarly to the coefficient of variation. Initially the distribution of plant sizes was half way between complete equality and inequality, with a coefficient of 0.5 (Figure 3.8). In the following early winter the value of the coefficient varied between higher inequality and higher equality. Between December and May 1991 Gini coefficients were characteristically low, though still variable. Through-out the summer, autumn and winter of 1991 the Gini coefficient gradually increased indicating an increase in population inequality.

The statistical skewness of the population changed through the study period (Figure 3.9). Initially the population was highly positively skewed (*ie* consisted of many small plants and few big ones). Within the next month the population became more positively skewed, though by the third week of October the skewness coefficient had fallen considerably. By December, and throughout

Figure 3.6 Length frequency histograms for a population of *Fucus vesiculosus*. All scales are identical.

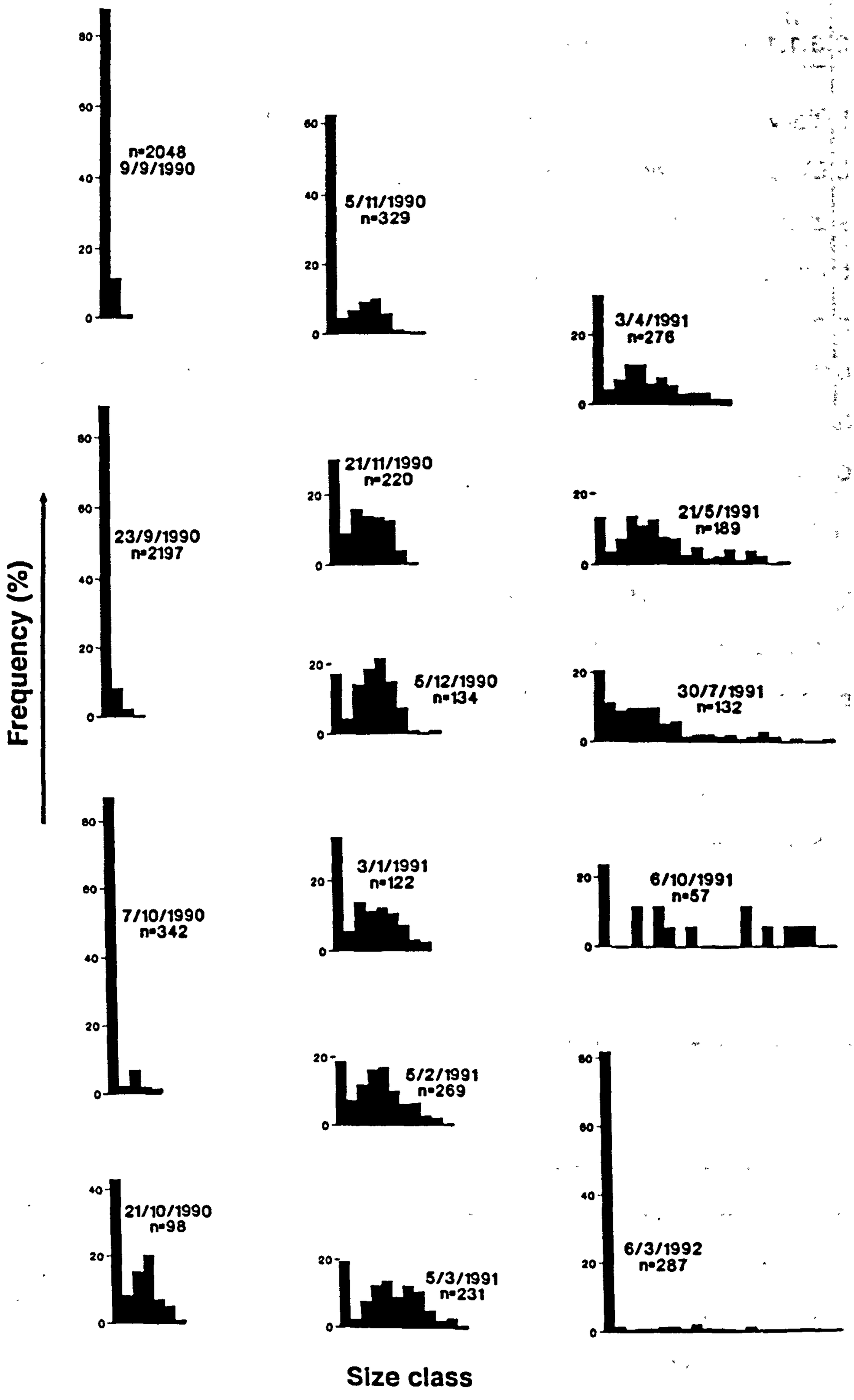


Figure 3.7 The variability of plant lengths in a population of *Fucus vesiculosus* over time (bars = ± 1SE). For 'corrected' data plants less than 10 mm were not included in calculations

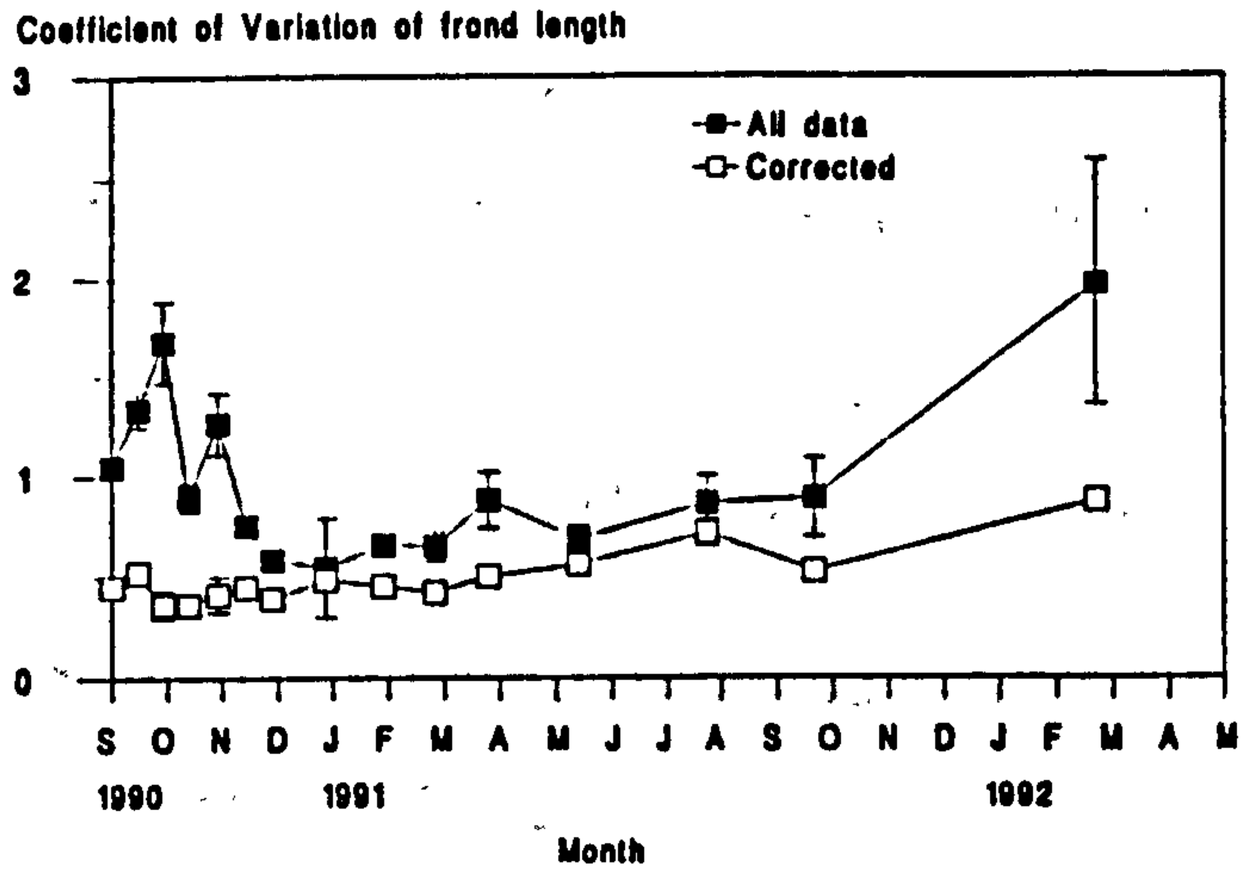


Figure 3.8 The equality of plant lengths in a population of *Fucus vesiculosus* over time (bars = ± 1SE). For 'corrected' data plants less than 10 mm were not included in calculations

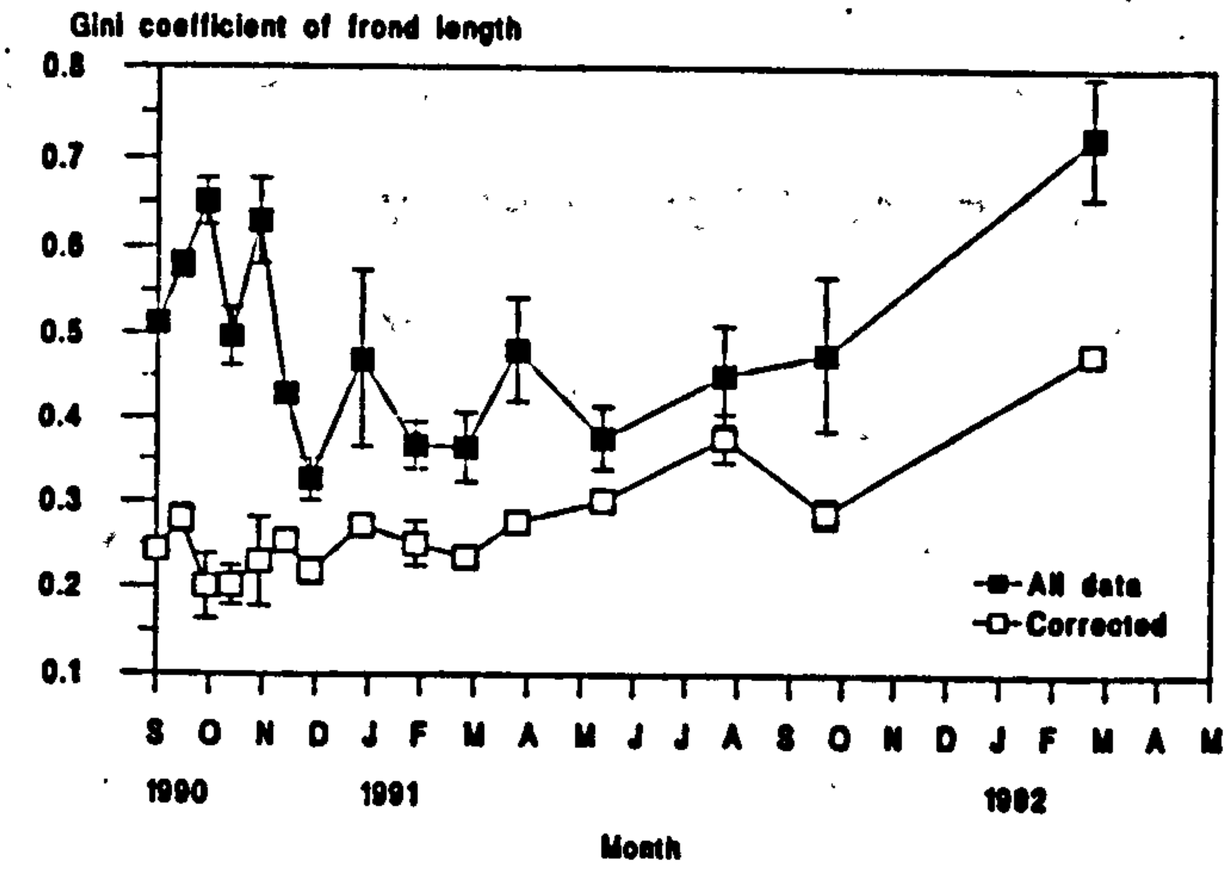
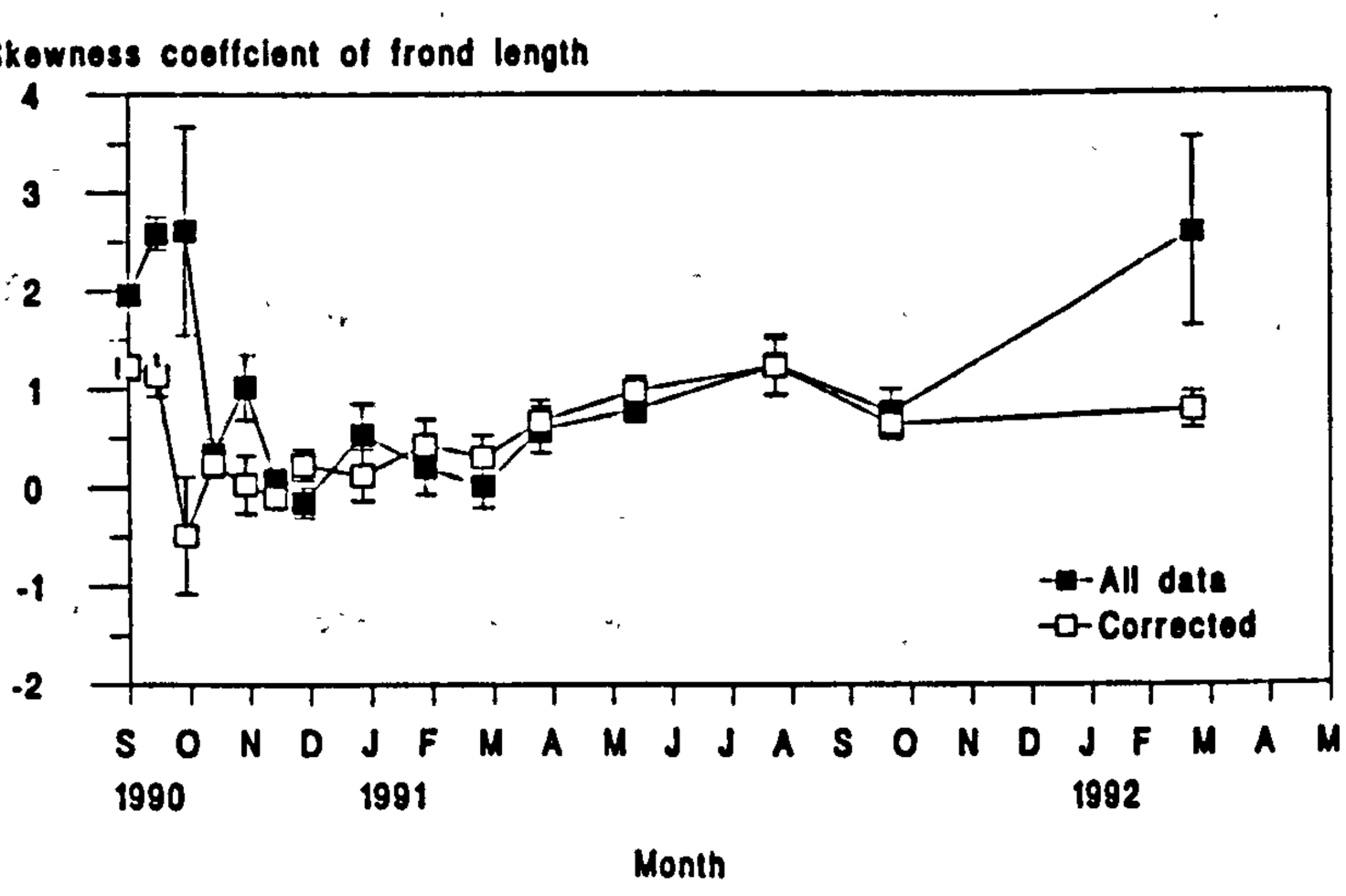


Figure 3.9 The skewness of plant lengths in a population of *Fucus vesiculosus* over time (bars = ± 1SE). For 'corrected' data plants less than 10 mm were not included in calculations



the winter, the population was no longer positively skewed and individuals within the population were distributed normally about the mean. Throughout 1991, the population gradually became more positively skewed, and by March 1992 had reached a similarly positive skew to what it had been at the start of the study.

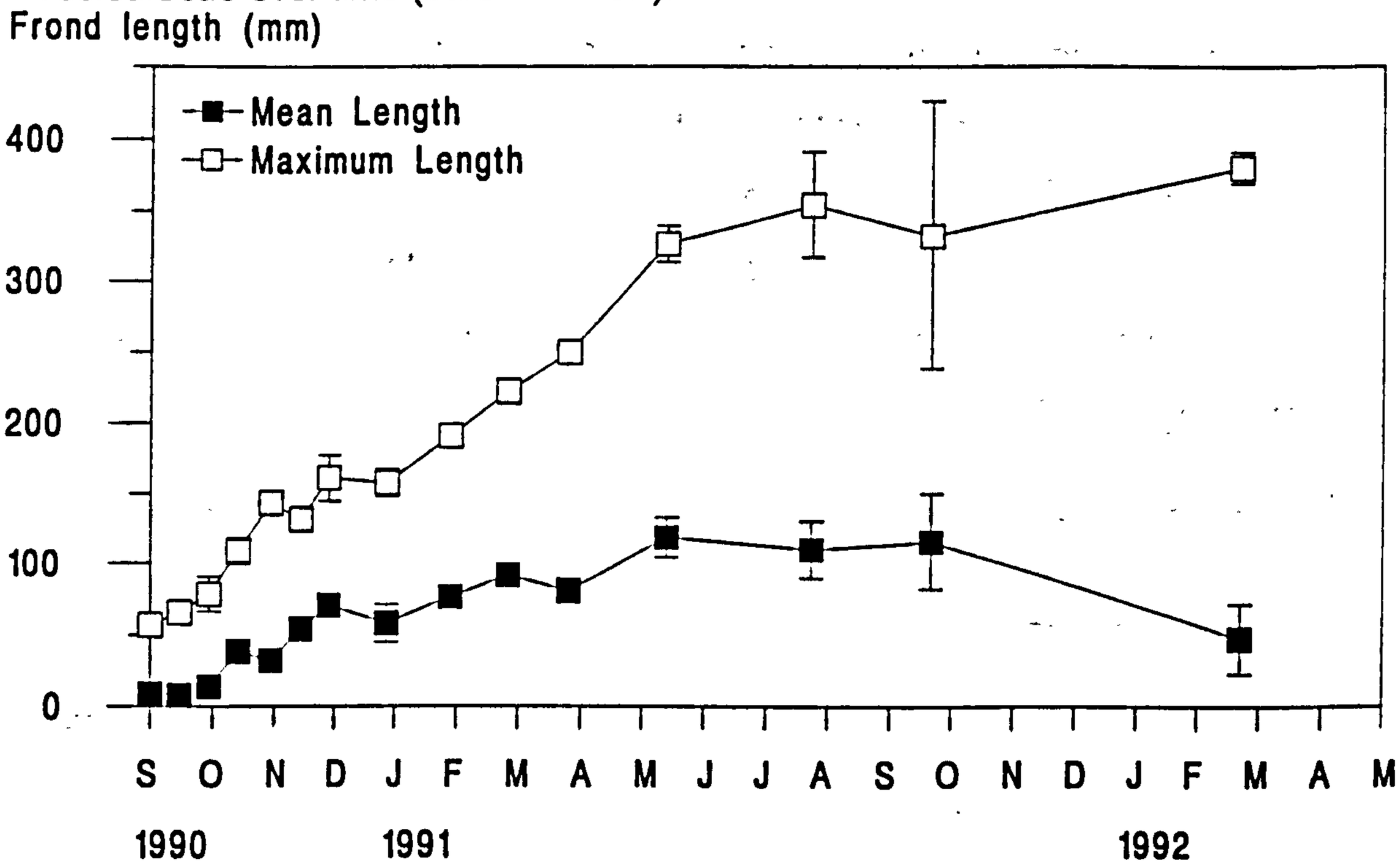
Analysis without first size class - 'corrected' data

It was abundantly clear that the population structure was being greatly affected by the smallest size class which was far greater than expected throughout most of the study (Figure 3.6). Though reasons for this will be discussed later, it was considered a valuable exercise to reanalyse these data without the first size class (frond lengths less than 10 mm). This 'corrected' data defined a much smoother transition over time than the original data with regard to the coefficient of variation (Figure 3.7). Within population variability was generally less in the corrected data being close to 0.5 for most of the period of study. There was a trend towards increased variability with time. The Gini coefficient was depressed by the exclusion of the first size class (Figure 3.8). Time to time variation was also lower and there was an increase in inequality with time. The skewness coefficient of the corrected data mirrored the original skewness coefficient (Figure 3.9). The only differences were to be detected at either end of the study period. Both at the beginning and the end of the study, corrected skewness coefficient values were lower than original coefficients.

3.3.1.2 Frond Length

Frond length was examined both as a function of mean frond length of all plants and mean frond length of the largest plant in each replicate sample at each time. The mean frond length for all plants increased until May 1991 (Figure 3.10). During this late winter and spring period plants on the shore appeared yellow, which may be indicative of fast growth. Between May and October 1991 there was no apparent increase in mean frond length and plants looked darker. During spring 1991 many of the plants started to produce receptacles, gamete

Figure 3.10 Mean and maximum frond length change in a population of *Fucus vesiculosus* over time (bars = ± 1SE).



release taking place during May and June, and receptacle necrosis occuring during autumn 1991. Mean frond length fell over the following winter (Figure 3.10). Maximum frond length was similar to the mean frond length, though less variable (Figure 3.10). The largest plants increased in size throughout the winter of 1990 and spring of 1991. After July 1991 there was no further increase in maximum frond length, though neither was there a decrease in maximum length as had been found in mean frond length.

3.3.1.3 Density and survivorship

The density declined from the start of the study (Figure 3.11). This decline was extreme over the first three months, though after this time was far more gradual. Minimum density was detected in October 1991. Survivorship was rather low, with most plants dying in the first few months (Figure 3.11).

3.3.1.4 Standing Crop

Biomass accumulation within the stand followed a three phase pattern similar to mean plant length (Figure 3.12). During the autumn and early winter there

was very little increase in standing crop. This was followed by a period of growth in which standing crop nearly tripled between January and May. Throughout the summer, autumn and winter of 1991 the standing crop decreased once more. Stepwise linear regression analysis of dry weight against mean and maximum frond length, number of reproductive plants, mean number of receptacles per reproductive plant and density explained some of the variation in standing crop. The best predictors were mean frond length:

$$\text{Standing Crop} = 161 + 8.92\,\text{Length}, n = 44, R^2 = 46.3\%, SD = 1.442, p < 0.001.$$

and maximum frond length:

$$\text{Standing Crop} = 75 + 3.32\,\text{Maximum Length}, n = 44, R^2 = 46.3\%, SD = 0.538, p < 0.001.$$

Figure 3.11 Density change in a population of *Fucus vesiculosus* over time (bars = ± 1SE).

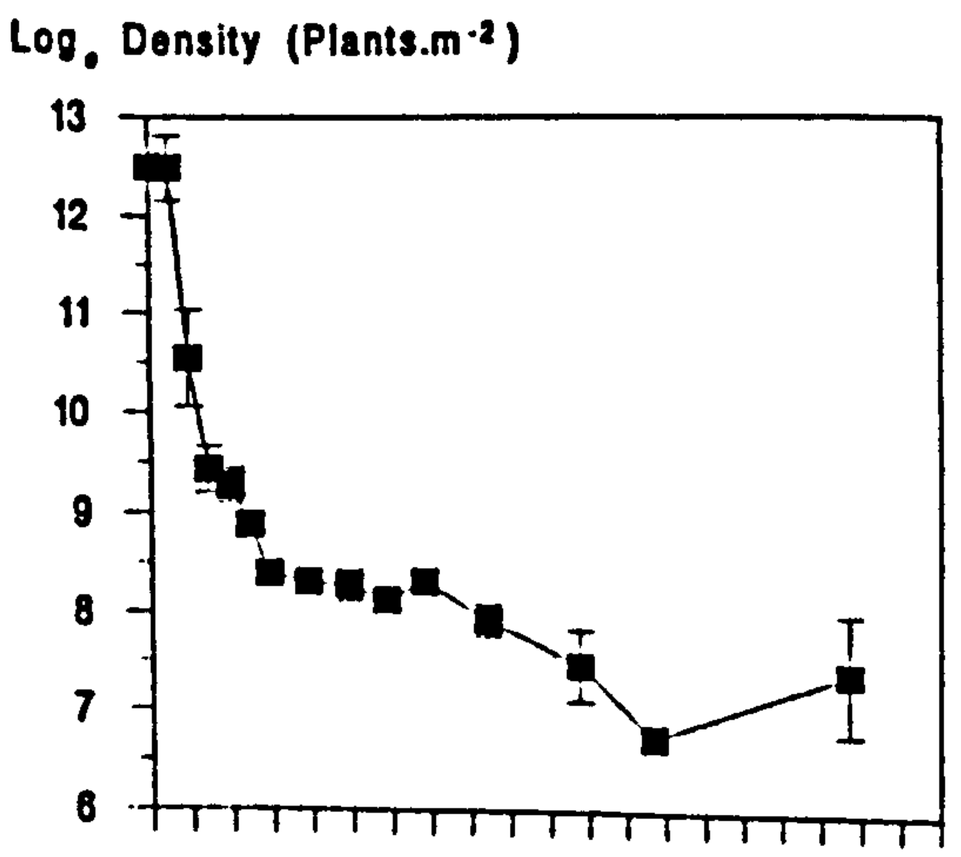
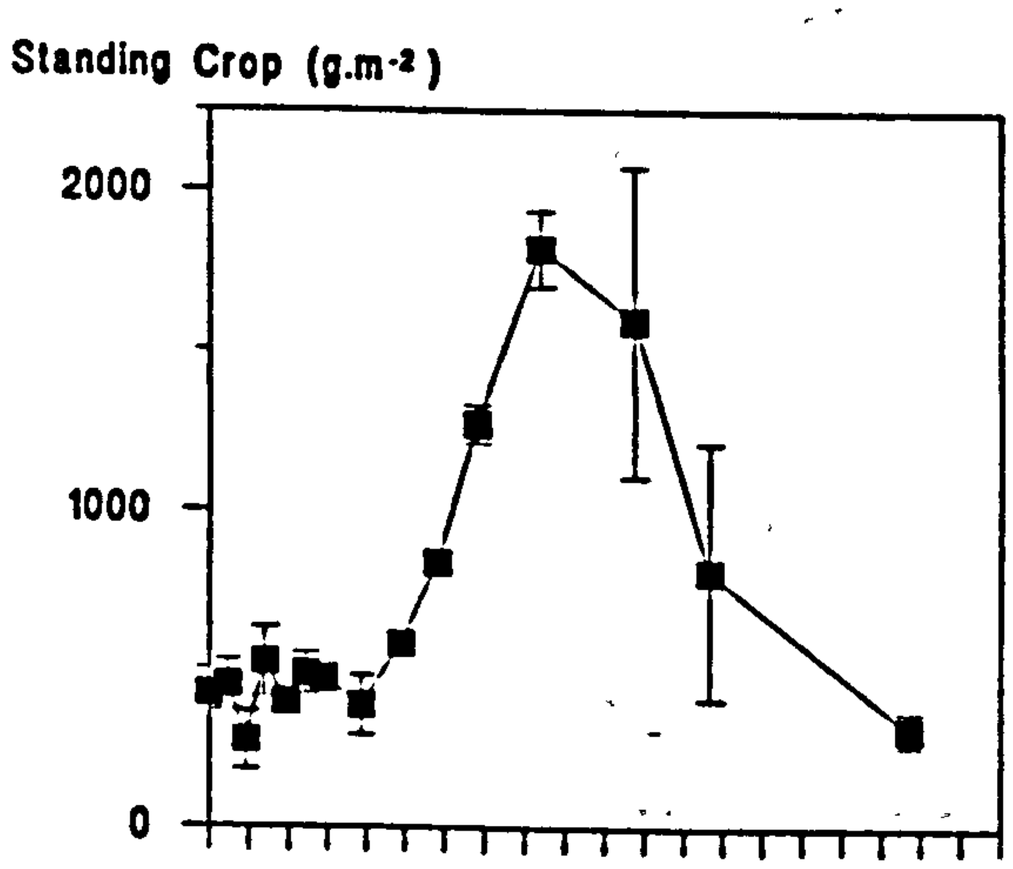


Figure 3.12 Standing crop in a population of *Fucus vesiculosus* over time (bars = ± 1SE).



3.3.1.5 Reproduction

The reproductive potential of the population was estimated by measurement of receptacle presence (both immature or mature). The reproductive output of the population was estimated by receptacle number per unit area of substratum, the percentage of plants which were reproductive and the dry weight attributable to reproductive parts (receptacles).

Plants first exhibited receptacles (immature) in March 1991. Throughout the spring the number of receptacles per unit area of substratum stayed constant, only diminishing in summer (Figure 3.13). During this time 35-55 % of the plants exhibited one or more receptacles (Figure 3.14). The receptacles accounted for 10-35 % of the total dry weight (standing crop) during this period (Figure 3.14). In the late summer and autumn receptacle necrosis had reduced to nothing reproductive output estimated by these measures.

Figure 3.13 Receptacle production in a population of *Fucus vesiculosus* over time (bars = ± 1SE).

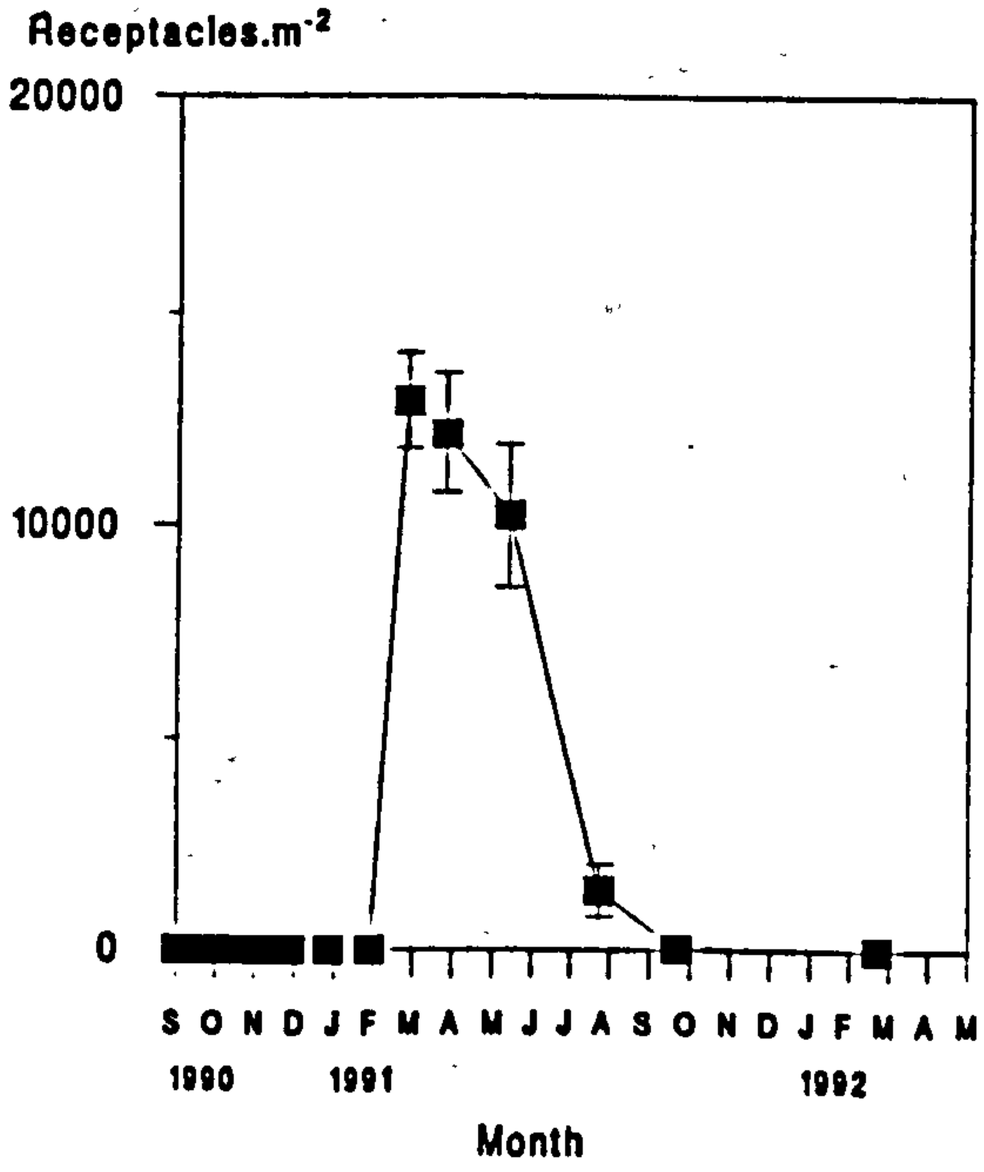
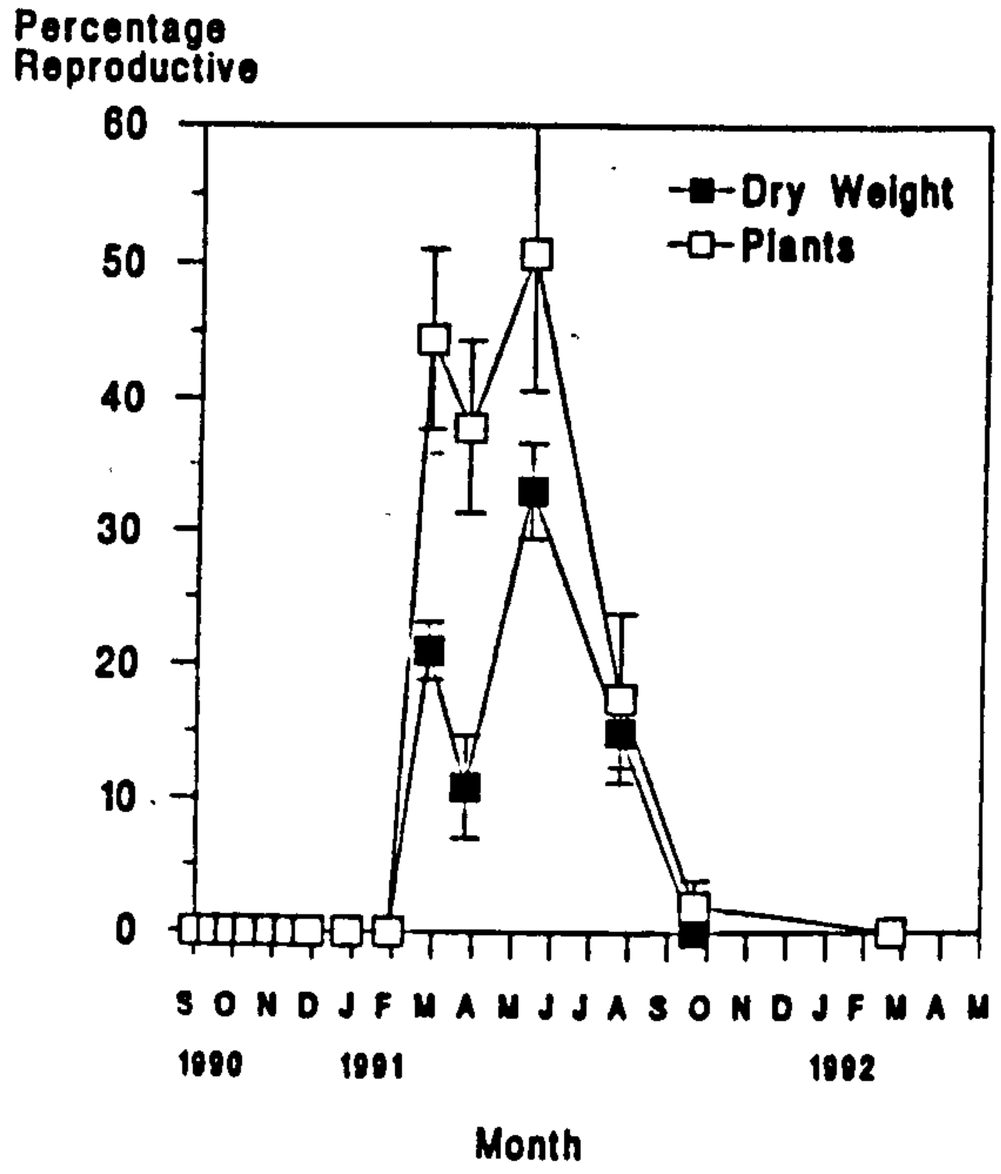


Figure 3.14 Percentage of reproductive plants and proportion of reproductive tissue in a population of *Fucus vesiculosus* over time (bars = ± 1SE).



There were, not surprisingly, strong positive correlations between the number of reproductive plants, the number of receptacles per unit area and the percentage of dry weight as reproductive material. Data on plant length and number of receptacles were pooled for the five times when receptacles were evident, and the observations below were based on these pooled data.

The smallest plant found to have receptacles was 73 mm long (Figure 3.15). The maximum number of receptacles on any plant was about 40 (Figure 3.15). No relationship between frond length and receptacle number was found (Figure 3.15). In relation to frond length, all of the largest plants had receptacles, though fewer had receptacles at intermediate sizes and none at all at smaller lengths (Figure 3.16). Of all receptacle bearing plants, the majority had few receptacles and the minority had many.

Figure 3.15 The number of receptacles related to plant size in a population of *Fucus vesiculosus*

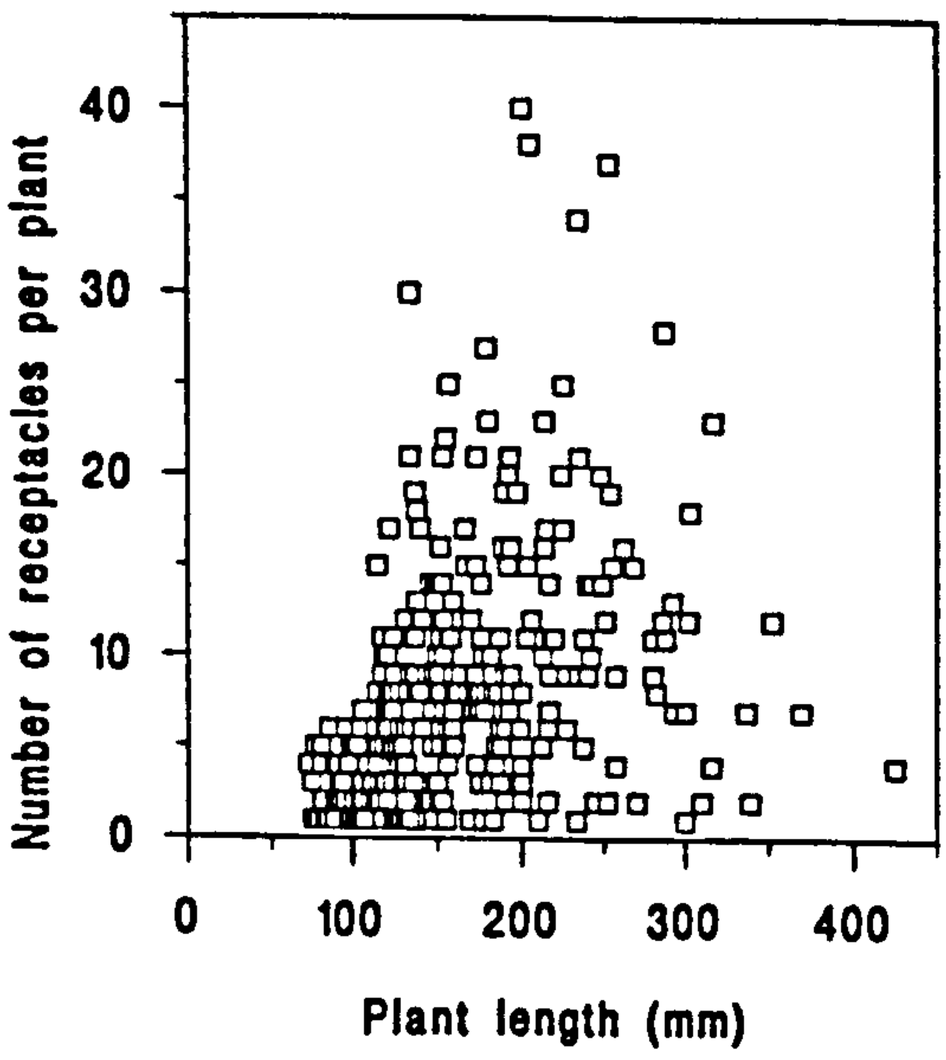
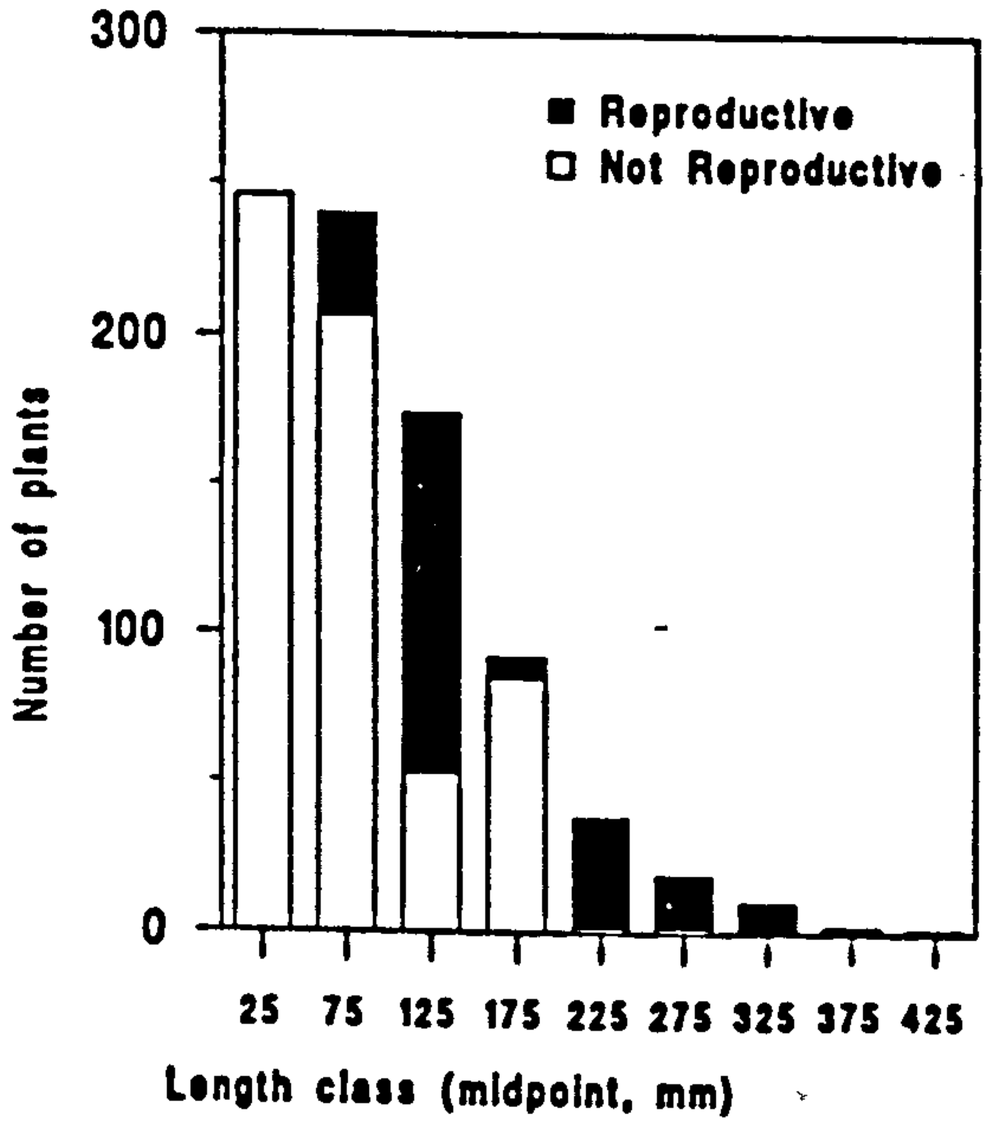


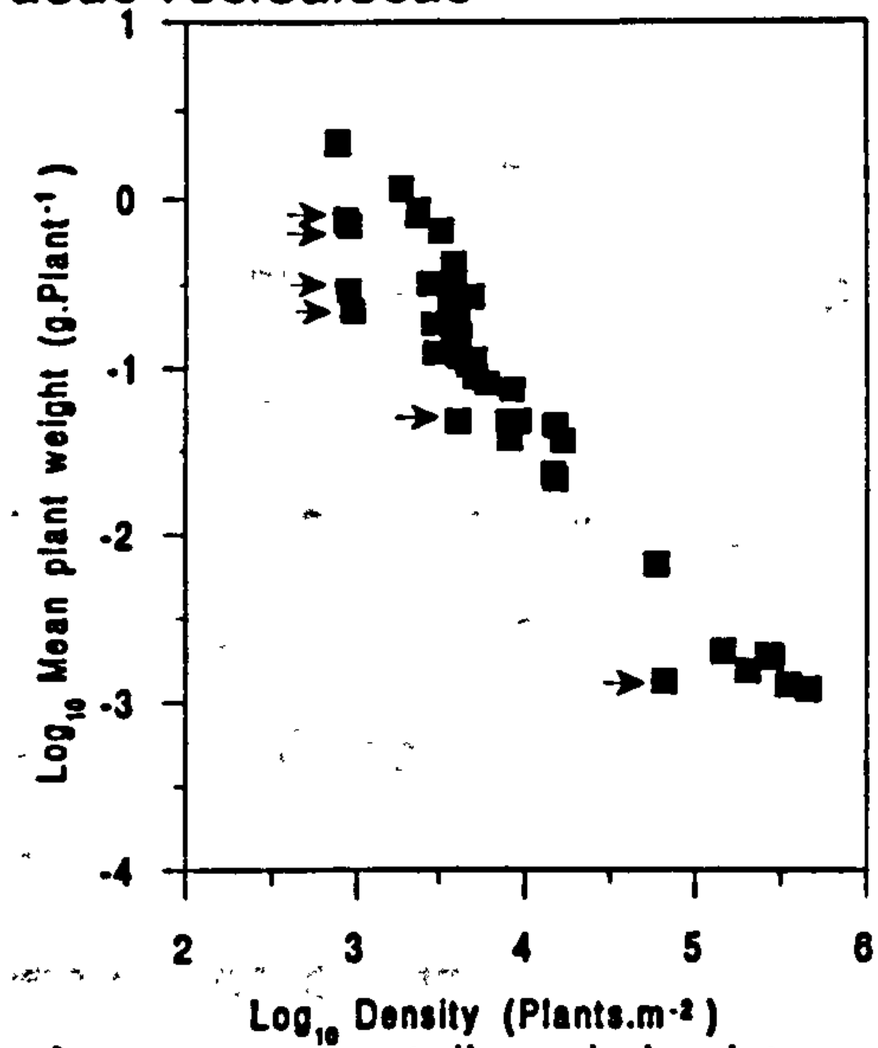
Figure 3.16 The proportion of reproductive plants in each size class in a population of *Fucus vesiculosus*



3.3.1.6 Density Biomass Relationships

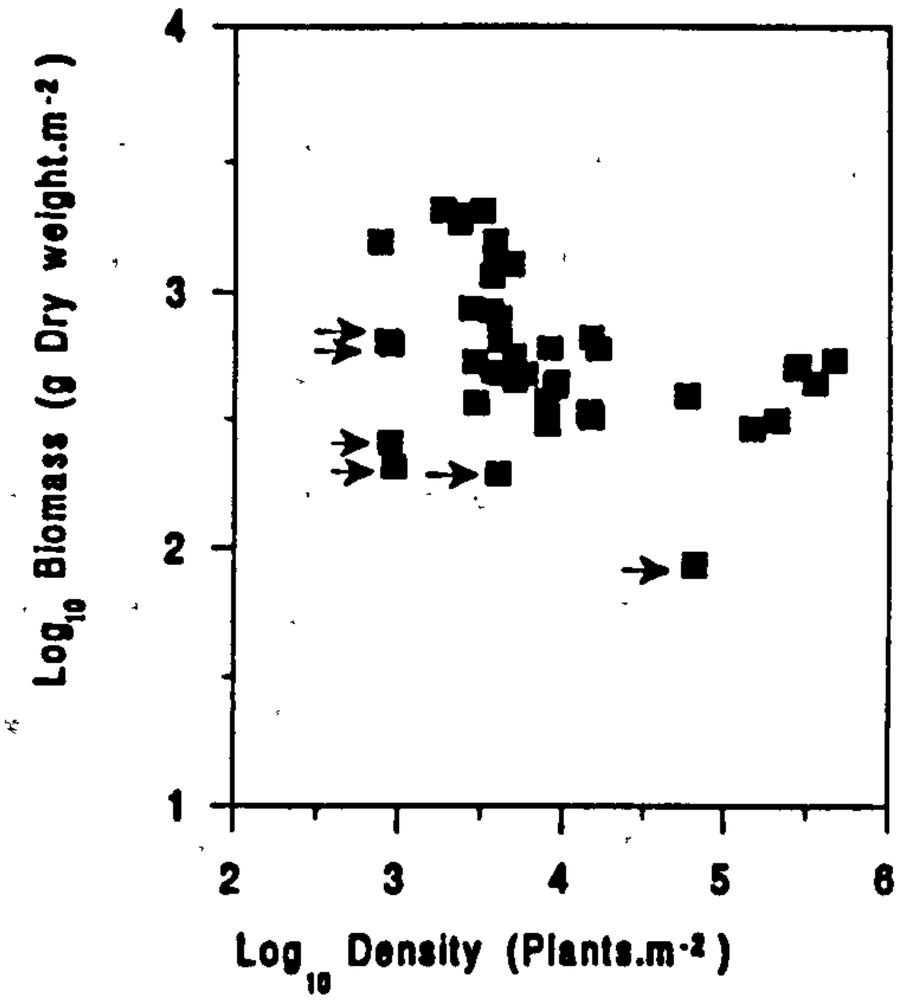
Data were log transformed. Log_{10} mean plant weight (log *m*) and log_{10} biomass(log *B*) were plotted against log_{10} density (log *N*). Six points were considered to be obviously below the suspected thinning lines and were removed from the data set before slope fitting (arrowed in Figure 3.17 and 3.18). Correlation revealed a significant relationship between log *N* and log *m* and between log *N* and log *B* (Table 3.5). Principal component analysis revealed slopes were significantly different from -1.5 for log *m* and -0.5 for log *B* expected from the self-thinning rule (Table 3.5).

Figure 3.17 Density and mean plant weight relationship in a population of *Fucus vesiculosus*



Arrows represent discarded points

Figure 3.18 Density biomass relationship in a population of *Fucus vesiculosus*



Arrows represent discarded points

Table 3.5 Slopes fitted by the PCA method relating density to biomass and mean plant weight in a population of *Fucus vesiculosus*

β	Constant	Confidence limits	Correlation coefficient	Different from expected
Log_{10} density log_{10} mean plant weight. Expected β = -1.5				
-1.238	3.75	-1.352, -1.134	-0.968	Yes
Log_{10} density log_{10} biomass. Expected β = -0.5				
-0.209	3.638	-0.328, -0.095	-0.523	Yes

3.3.2 Himanthalia elongata

3.3.2.1 Population structure

a) Photographed populations

At the start of the study in April the three populations were already quite closely packed. The population structures were remarkably similar for the three populations, (Figure 3.19). As the populations developed they became progressively less variable and more equal in size (Figures 3.20 and 3.21). The skewness of the plant sizes of the populations varied over time, but was always close to normal (Figure 3.22). There was some evidence of bimodality developing in all the populations later on (Figure 3.19).

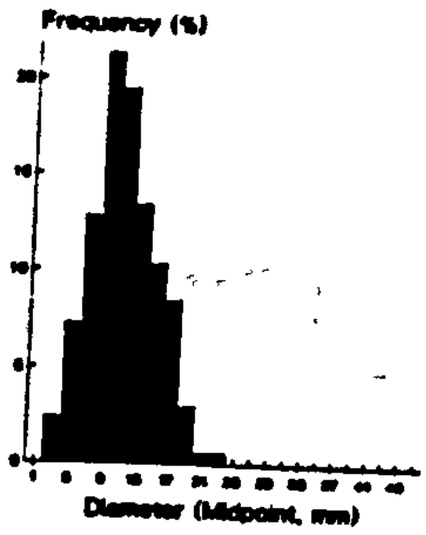
b) Harvested populations

Initially the population was skewed, with a predominance of smaller plants, though the smallest class was depressed in April 1991 (Figure 3.23). Subsequently the population became less variable or more equal in size (Figures 3.24 and 3.25) despite a slight bimodality (Figure 3.23) which had developed by August 1991. After this time and throughout the winter of 1991-1992 the smaller size classes became smaller so that in January 1992 an essentially normal population structure was evident (Figure 3.23 and 3.26). By this time thongs had started to be produced. The normal distribution appears to have been maintained in May 1992, though the small numbers of surviving plants broke up the button size frequency histograms in May 1991 and January 1992, and these are therefore somewhat unreliable (Figure 3.23).

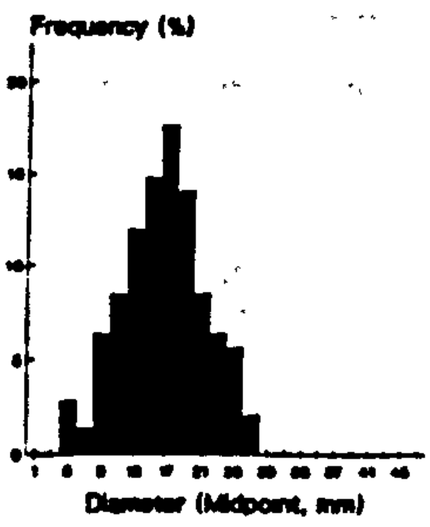
Figure 3.19 Button diameter frequency histograms of photographed populations of *Himanthalia elongata*.

Population 1

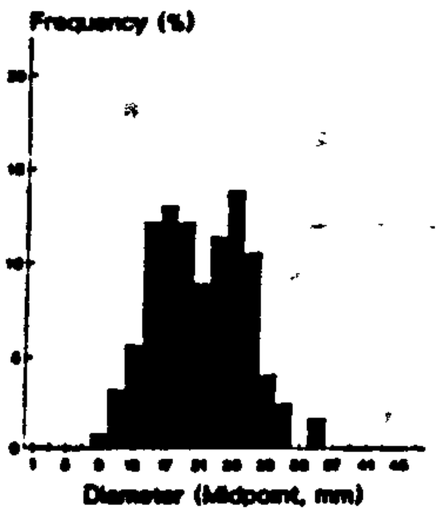
27th April
n=164



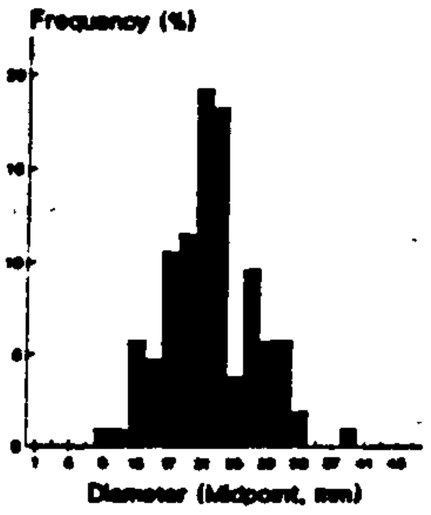
24th June
n=142



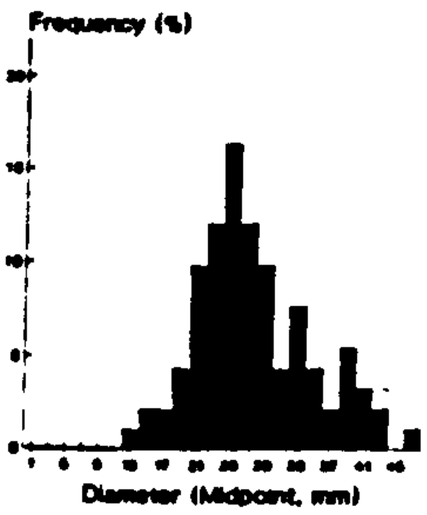
21st August
n=123



20th October
n=104

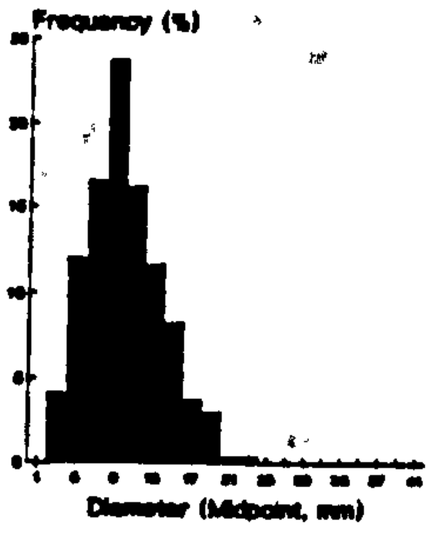


1st November
n=92

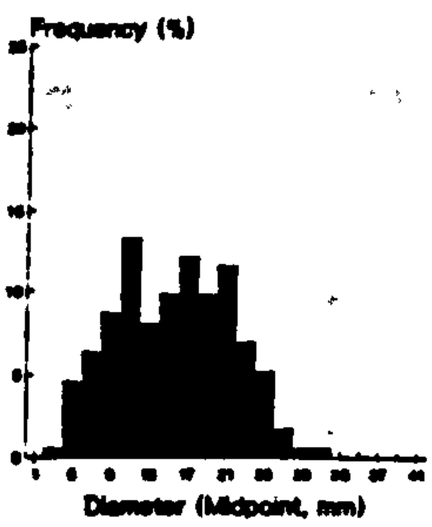


Population 2

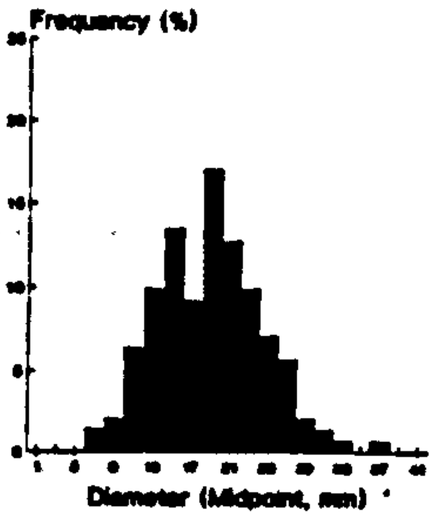
27th April
n=266



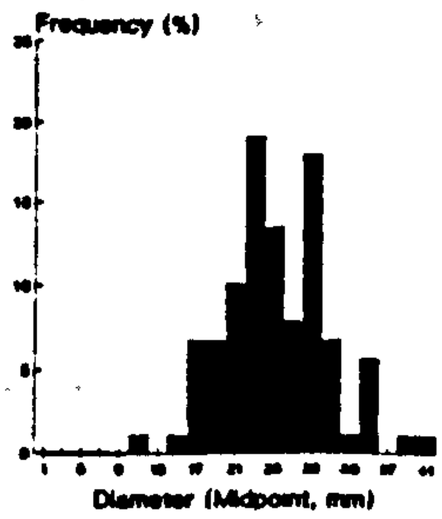
24th June
n=173



21st August
n=141

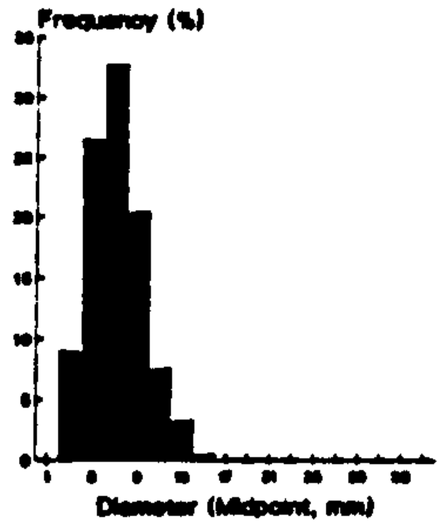


1st November
n=89

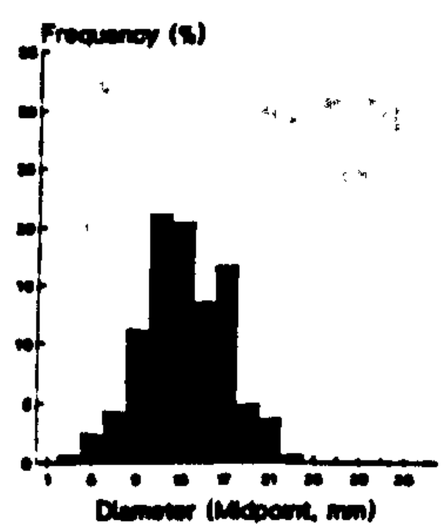


Population 3

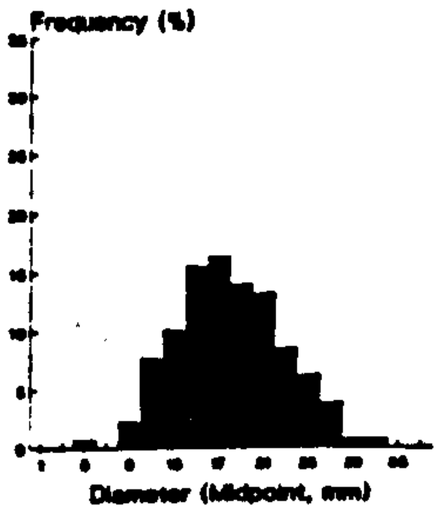
27th April
n=211



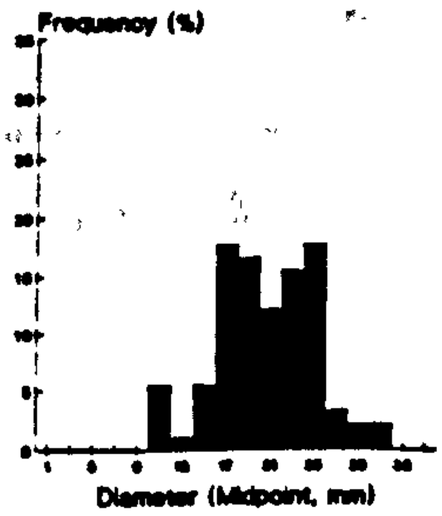
24th June
n=161



21st August
n=129



20th October
n=90



1st November
n=75

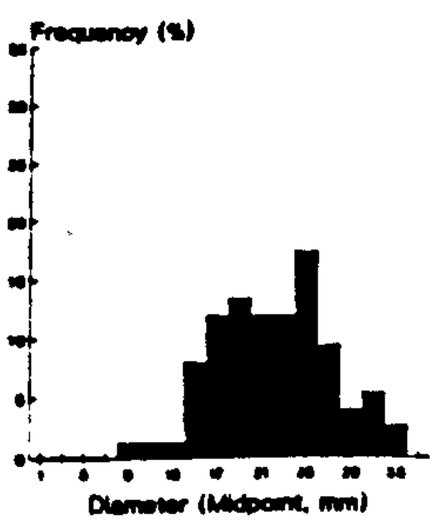


Figure 3.20 Variability of button diameters in photographed populations of *Himanthalia elongata*.

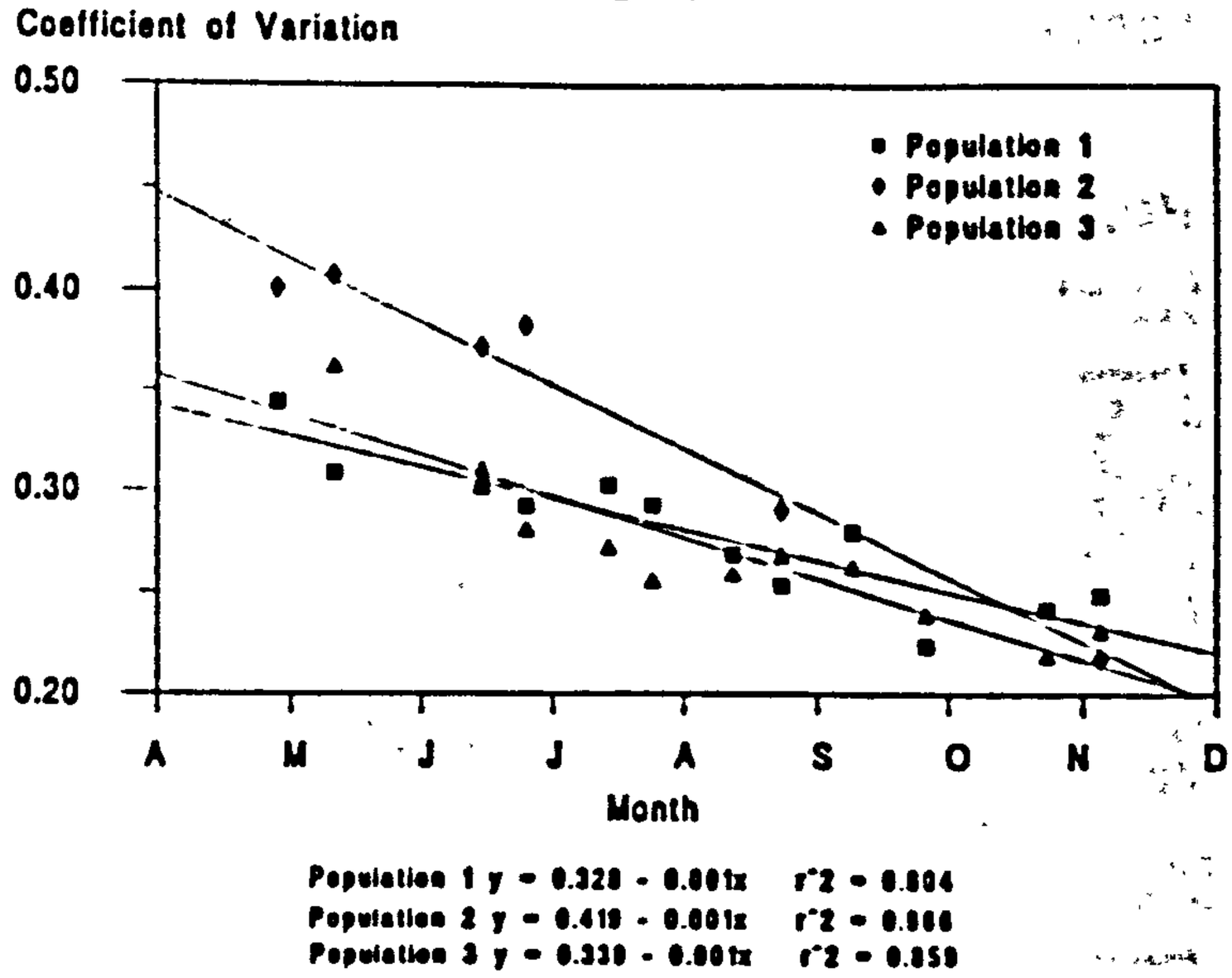


Figure 3.21 Inequality of button diameters in photographed populations of *Himanthalia elongata*.

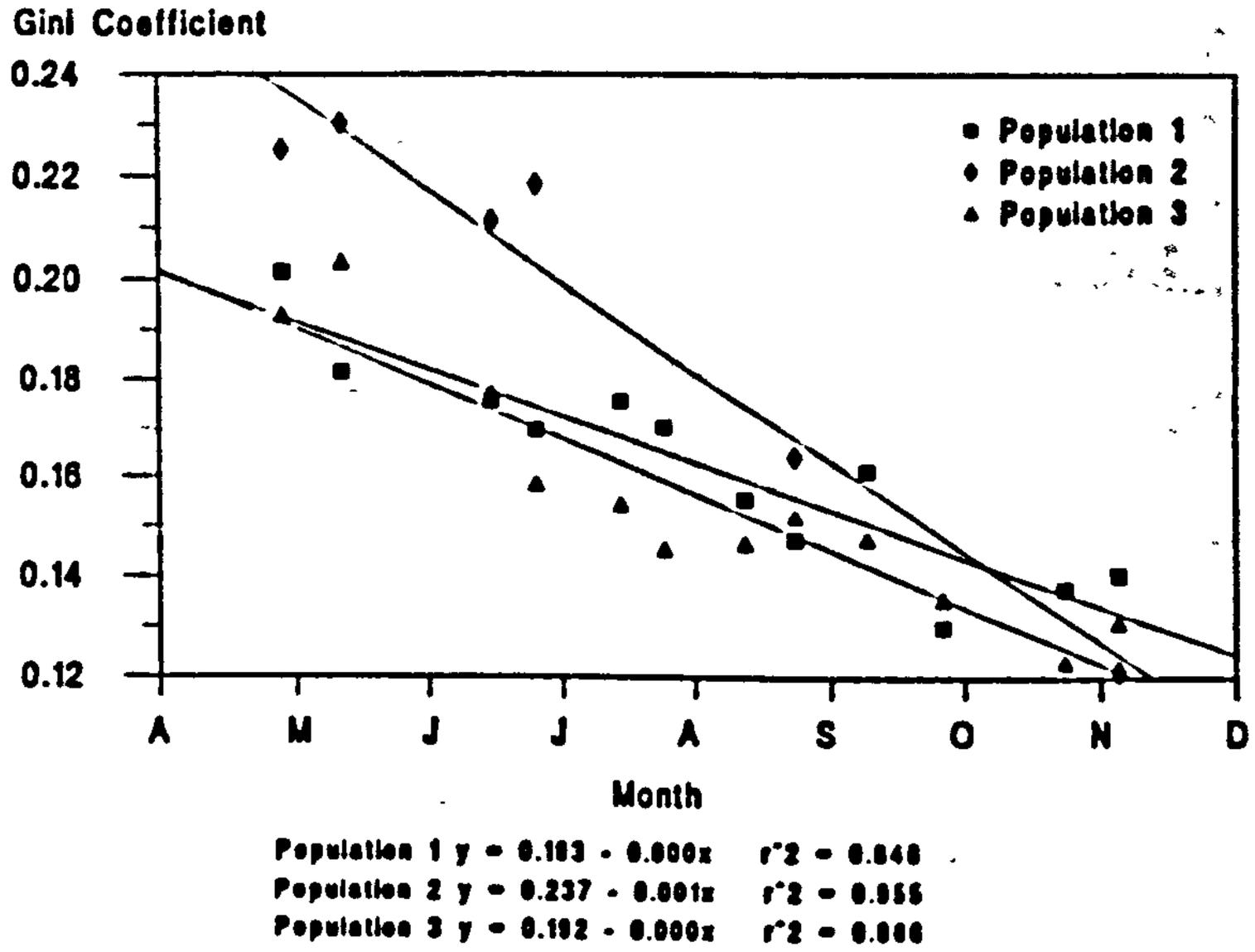


Figure 3.22 Skewness of button diameters in photographed populations of *Himanthalia elongata*.

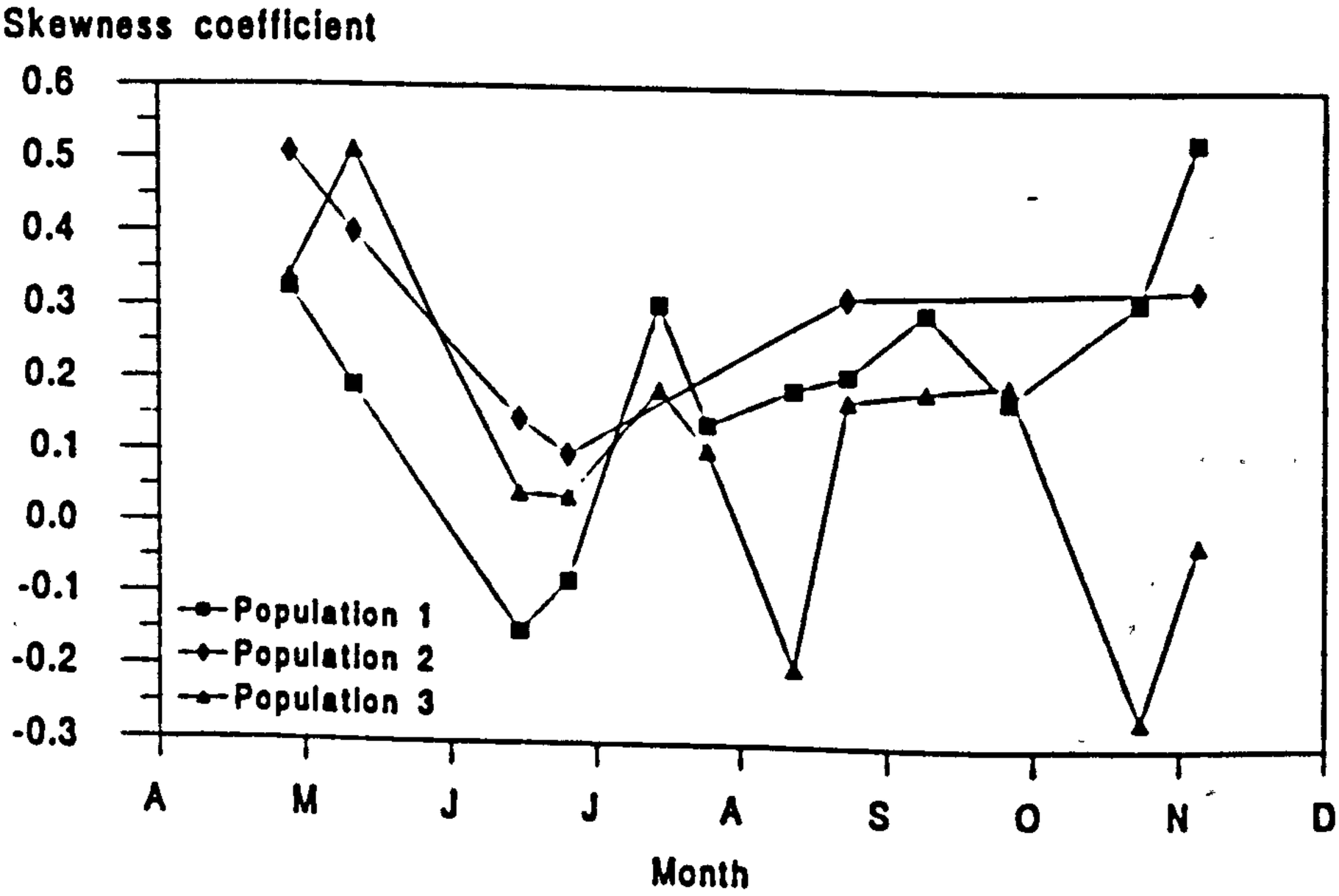


Figure 3.23 Button diameter frequency histograms of the harvested population of *Himanthalia elongata*.

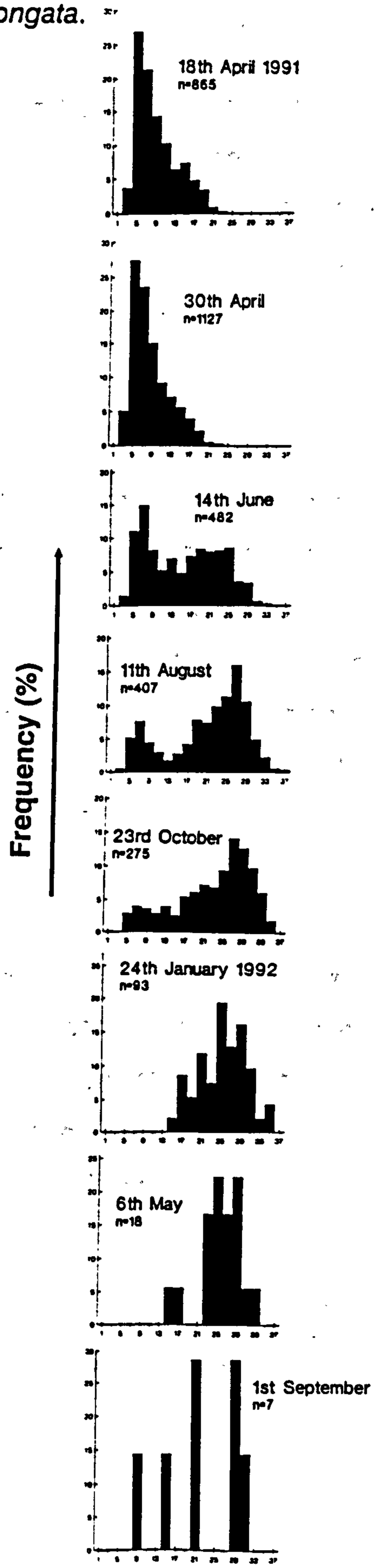


Figure 3.24 Variability of button diameters in the harvested population of *Himanthalia elongata* (bars = ±1.SE)

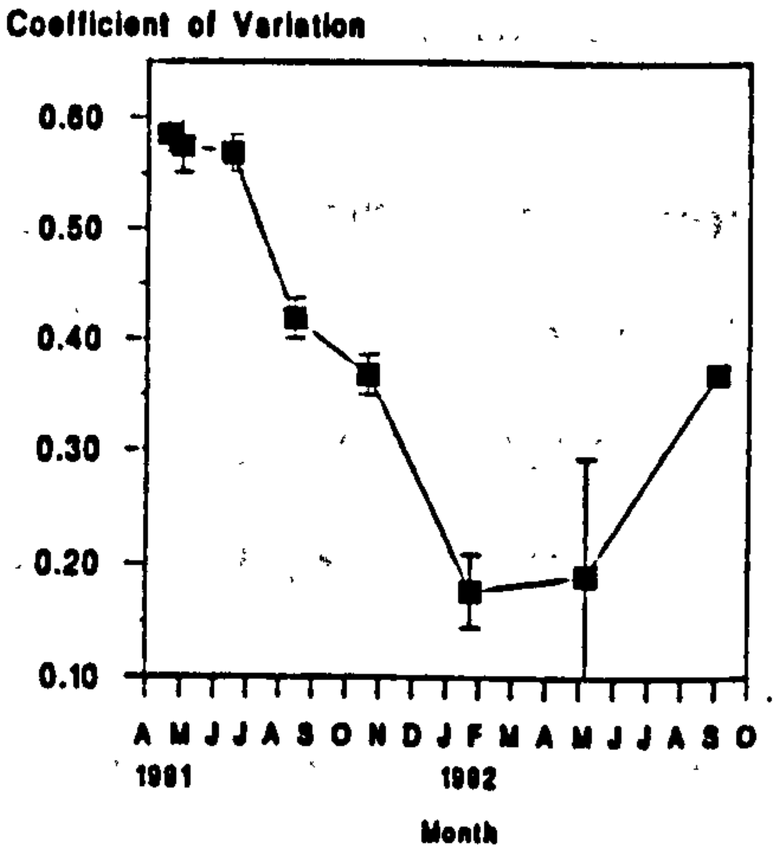


Figure 3.25 Inequality of button diameters in the harvested population of *Himanthalia elongata* (bars = ±1.SE)

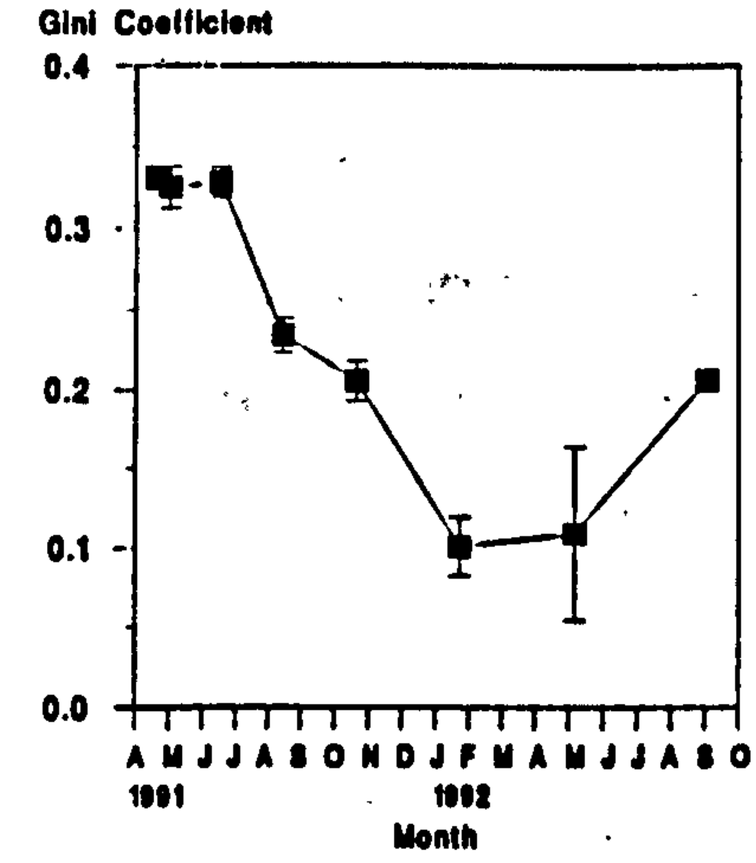
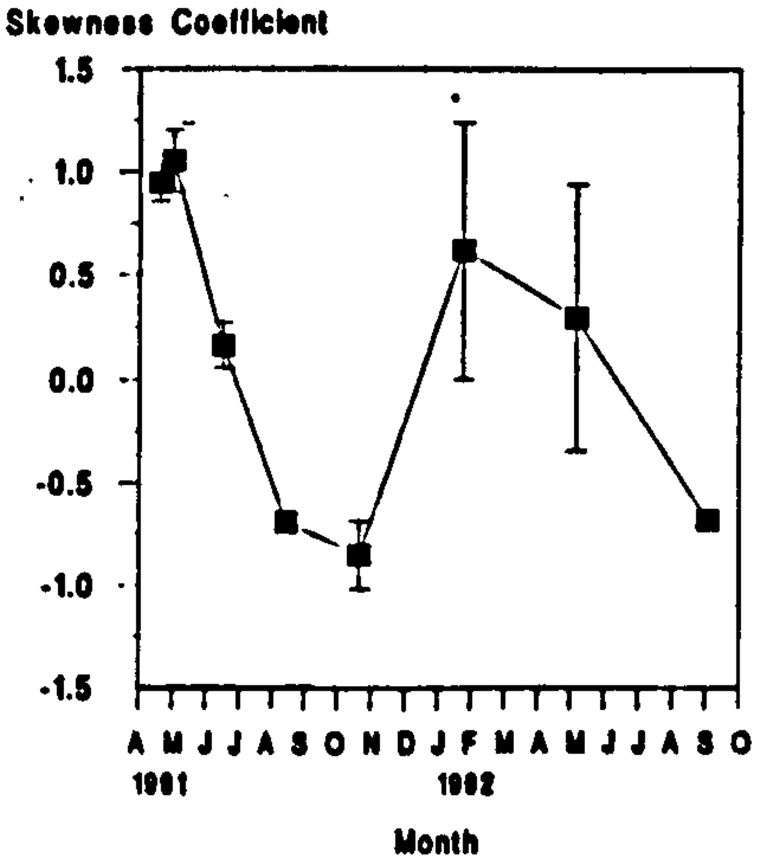


Figure 3.26 Skewness of button diameters in the harvested population of *Himanthalia elongata* (bars = ±1.SE)



3.3.2.2 Button diameter and thong length

a) Photographed populations

Mean button diameter increased steadily throughout the monitoring period. There was no obvious difference in the rate of button increase between the three populations. On average the buttons grew 0.439 mm in diameter per week (Figure 3.27). Monitoring was stopped before thongs developed.

b) Harvested populations

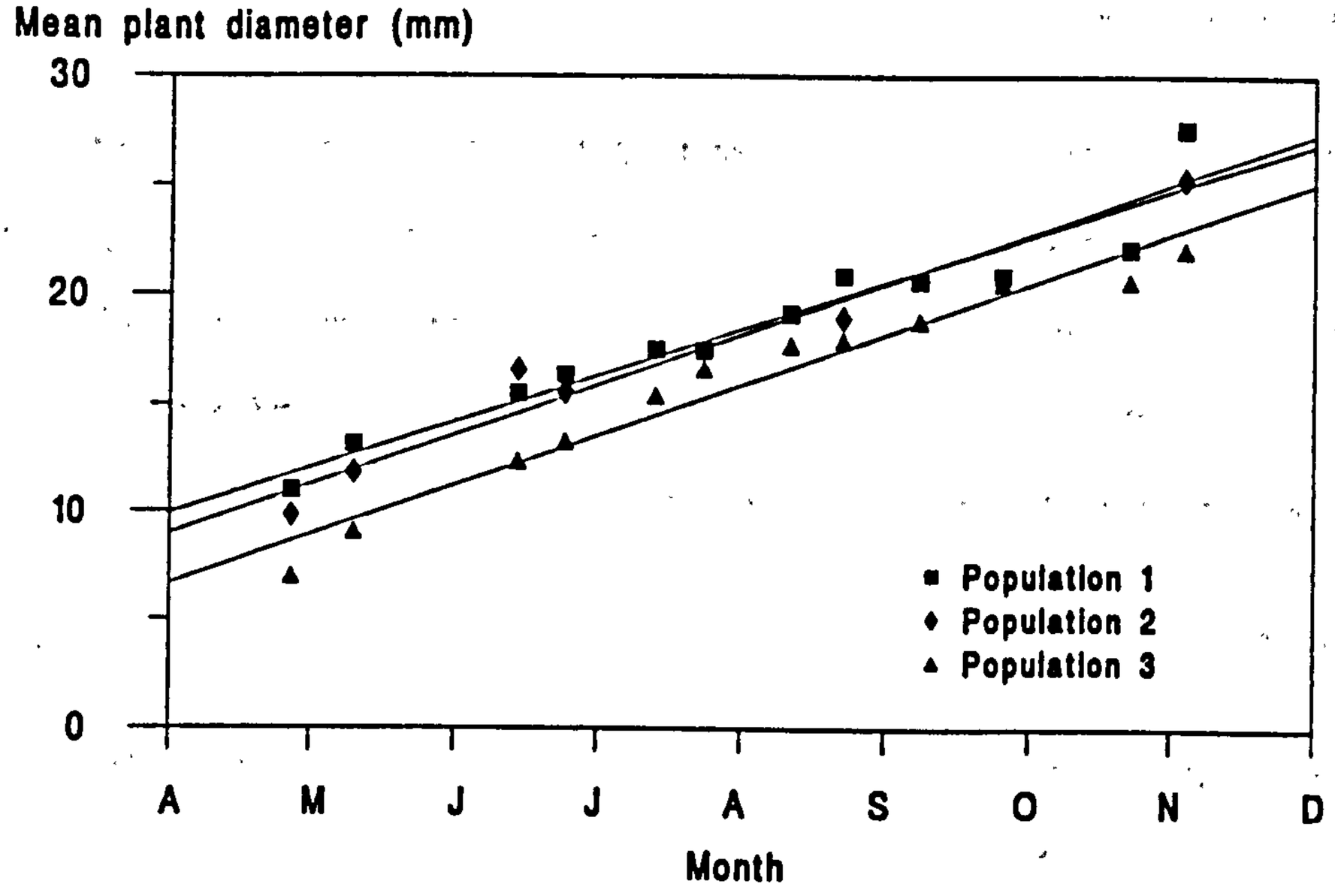
i) Button development

Mean and maximum button diameter exhibited similar trends over time. There was an increase in mean button diameter from the start of the study in spring 1991 until winter 1991-1992, after which mean button diameter decreased. Maximum button diameter increased until August 1991 and then stayed constant until the winter of 1991-1992. After this time maximum button diameter decreased. Absolute button growth rate over the first six sample times was 0.458 mm diameter per week (Figure 3.28).

ii) Thong development

Mean and maximum thong length behaved similarly (Figure 3.29). There was no thong initiation until January 1992 excluding a few abnormal plants (*sensu* Gibb, 1937) which were present in the August 1991 sample. Thong development was linear from August until the end of the study. Absolute mean thong growth rate over the last three sample periods was 3.1 cm per week.

Figure 3.27 Mean button diameter in photographed populations of *Himanthalia elongata* over time.



Population 1 y = 11.797 + 0.071x r^2 = 0.927
Population 2 y = 10.989 + 0.077x r^2 = 0.960
Population 3 y = 8.641 + 0.077x r^2 = 0.956

Figure 3.28 Mean and maximum button diameter in the harvested population of *Himanthalia elongata* over time (bars = ± 1SE).

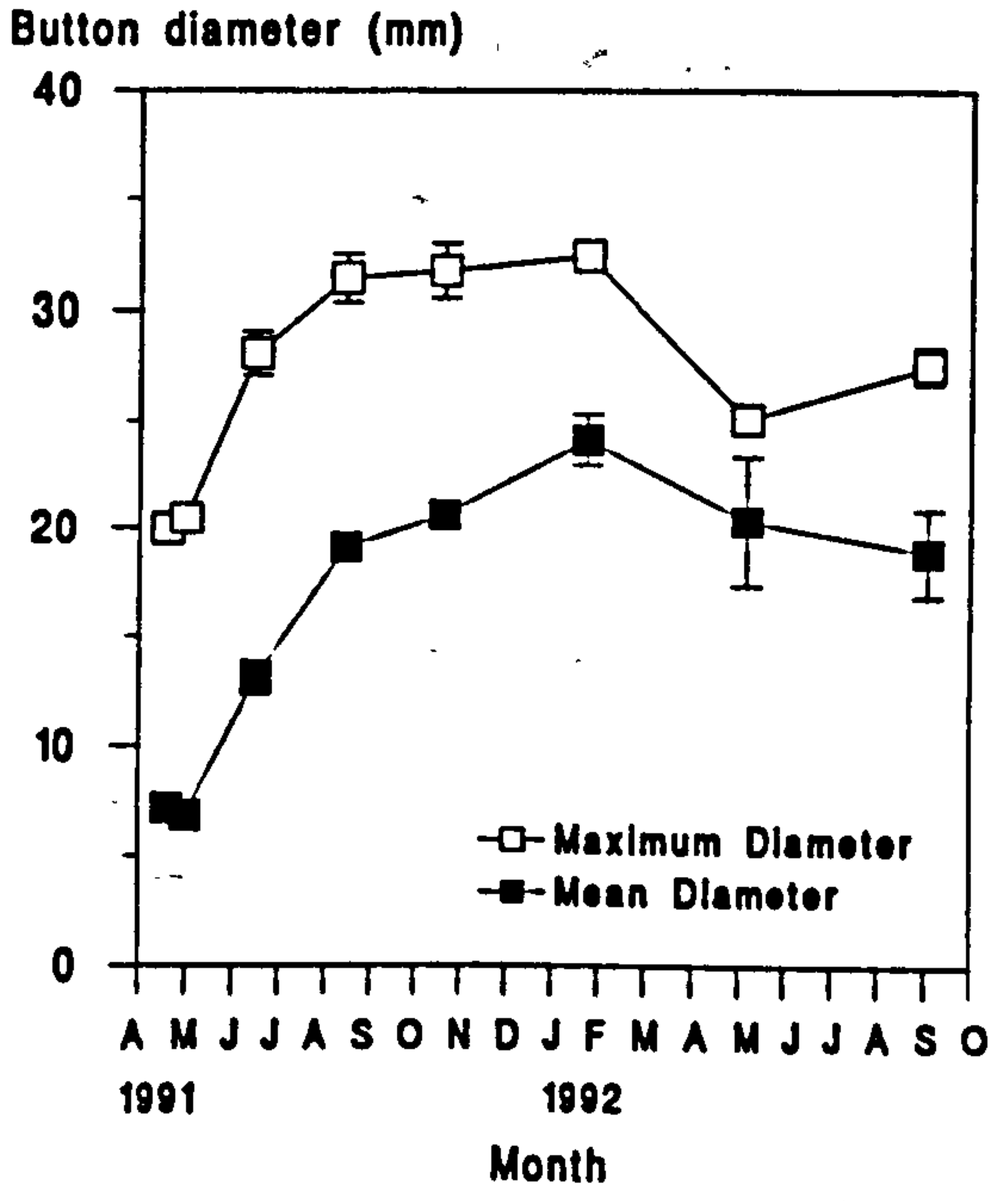
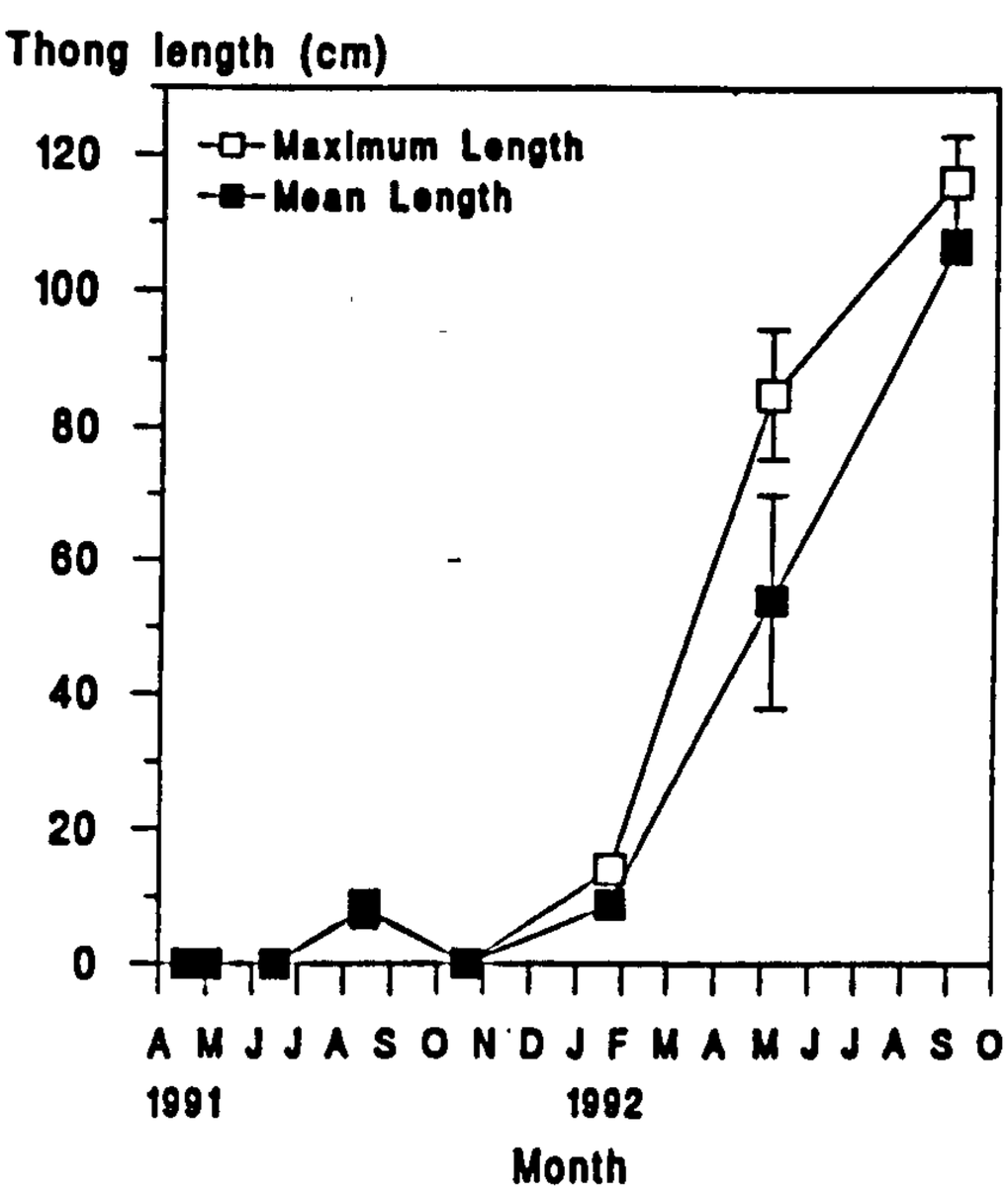


Figure 3.29 Mean and maximum thong length in the harvested population of *Himanthalia elongata* over time (bars = ± 1SE).



3.3.2.3 Density and survivorship

a) Photographed populations

In all three populations density decreased throughout the monitoring period (Figure 3.30). Density fell most in the first two months for all three populations, but mortality increased once more towards the end of the monitoring period (Figure 3.31). Initially different densities converged due to differential survivorship rates amongst the three populations (Figures 3.30 and 3.31).

b) Harvested populations

The density of plants fell steadily throughout the study (Figure 3.32). Most plants died within the first four months of the study.

Figure 3.30 Density in photographed populations of *Himanthalia elongata* over time.

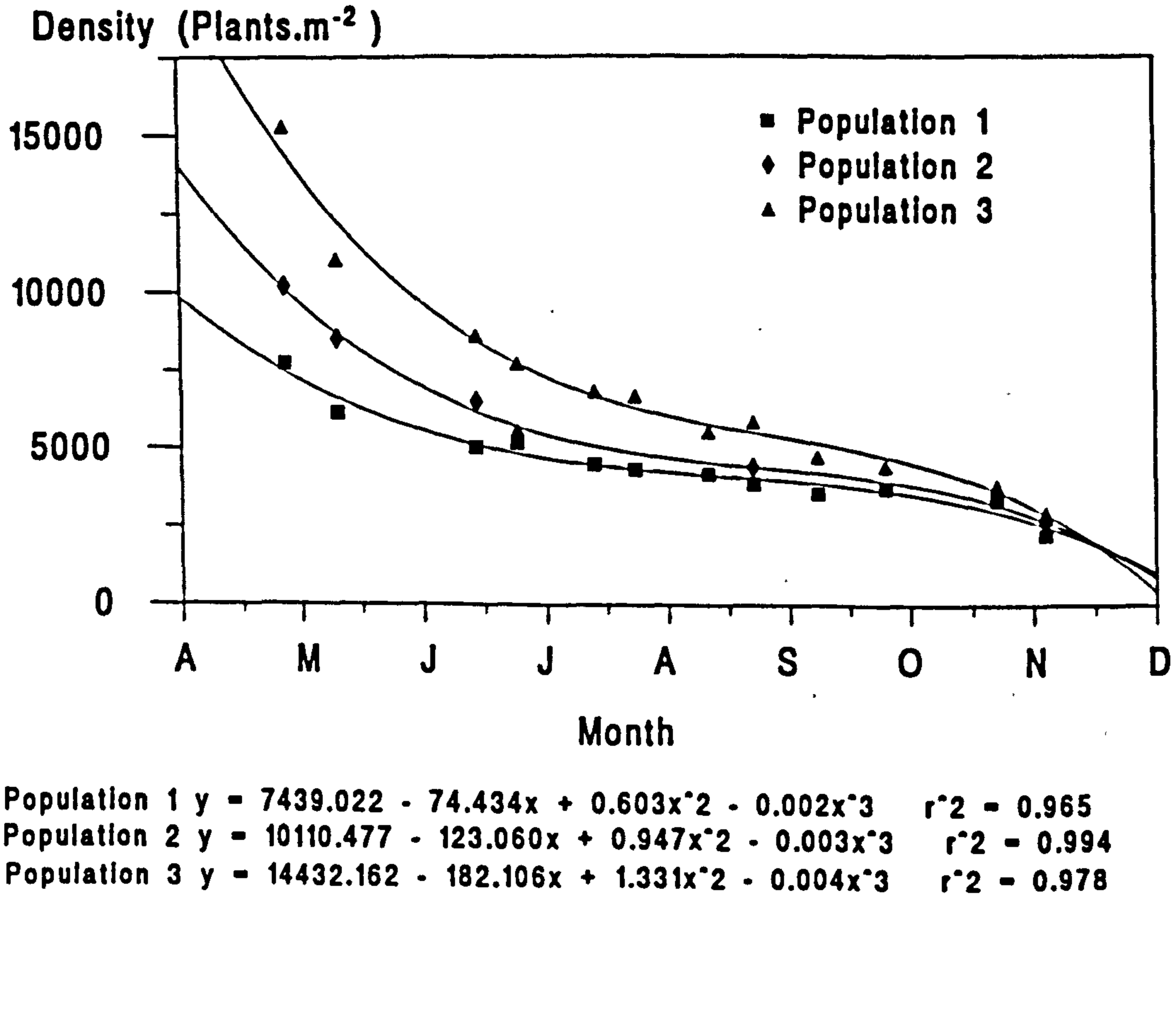


Figure 3.31 Percentage survivorship in photographed populations of *Himanthalia elongata* over time.

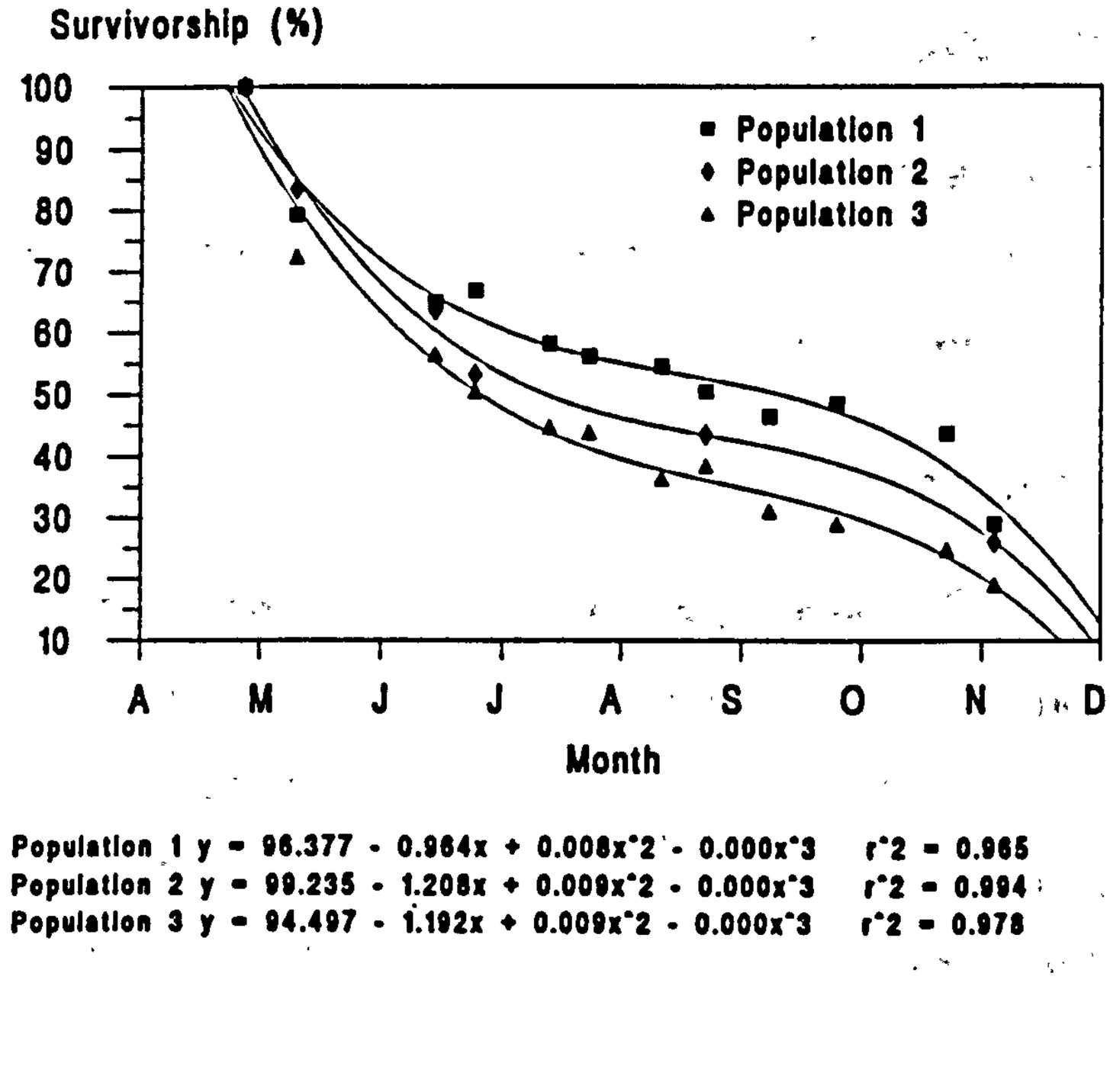
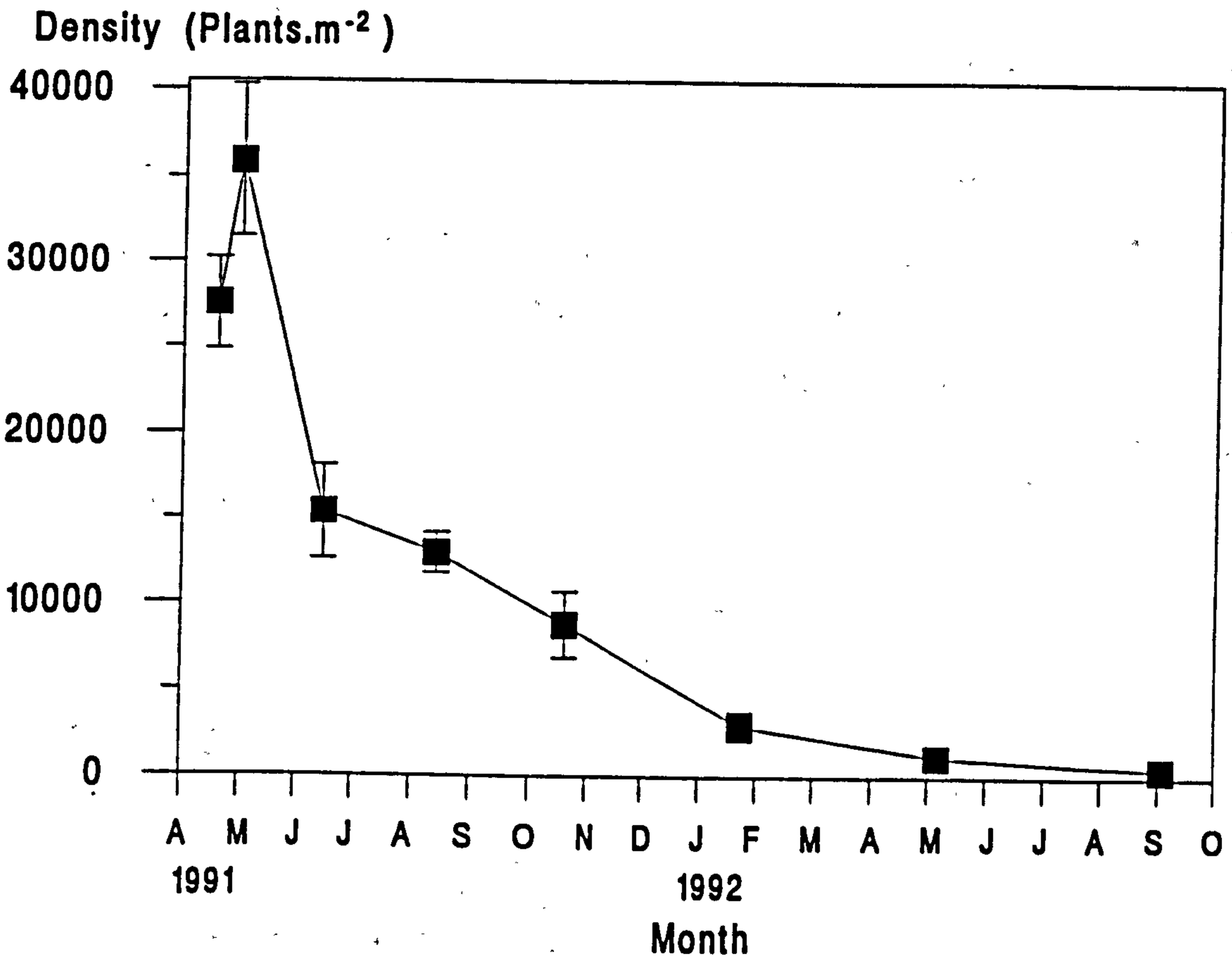


Figure 3.32 Mean density in the harvested population of *Himanthalia elongata* over time (bars = ± 1SE).



3.3.2.4 Standing crop

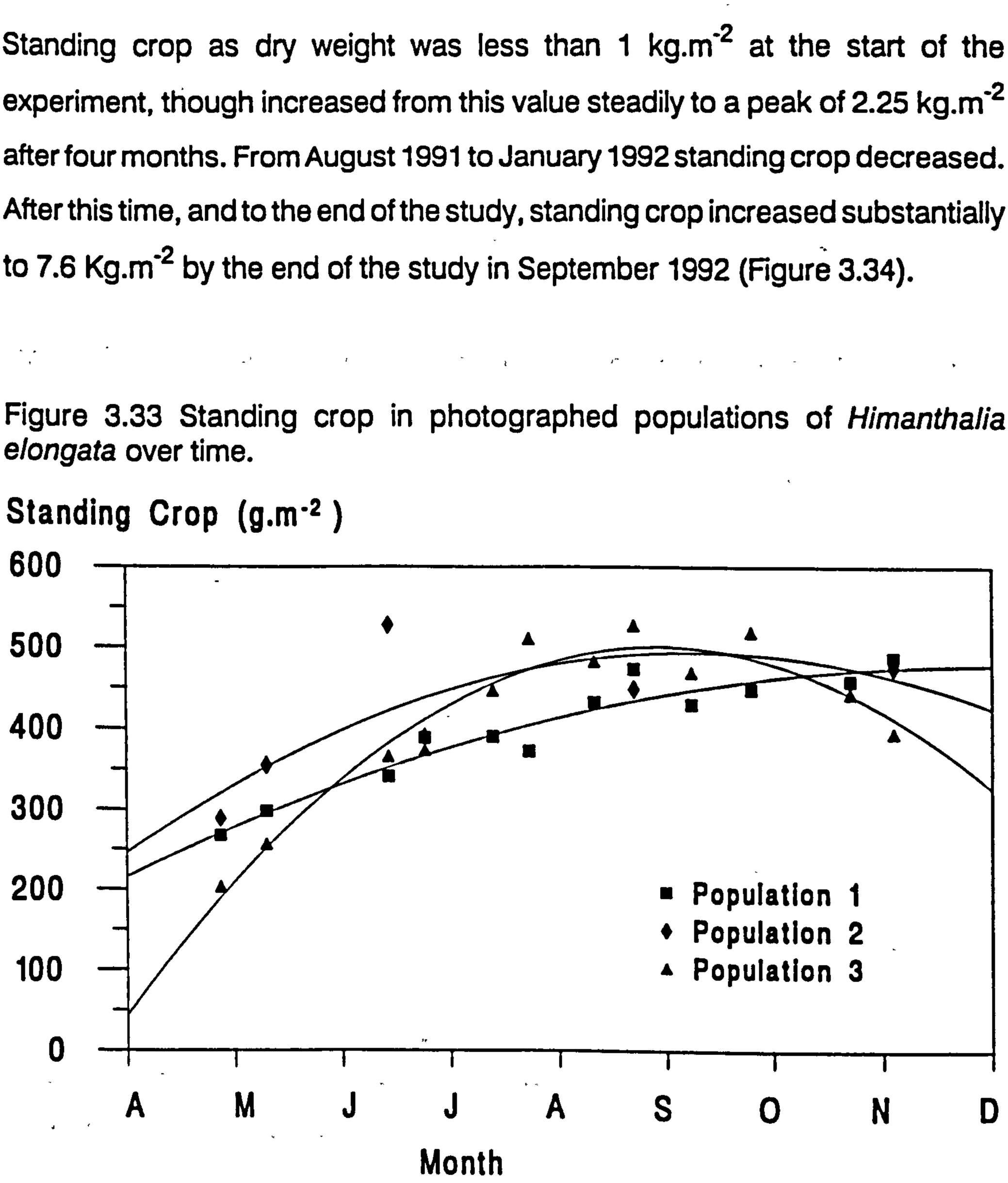
a) Photographed populations

While there was a general increase in estimated standing crop in all three of the populations, especially during the first four months of the study, there was some loss in standing crop later on (Figure 3.33).

b) Harvested populations

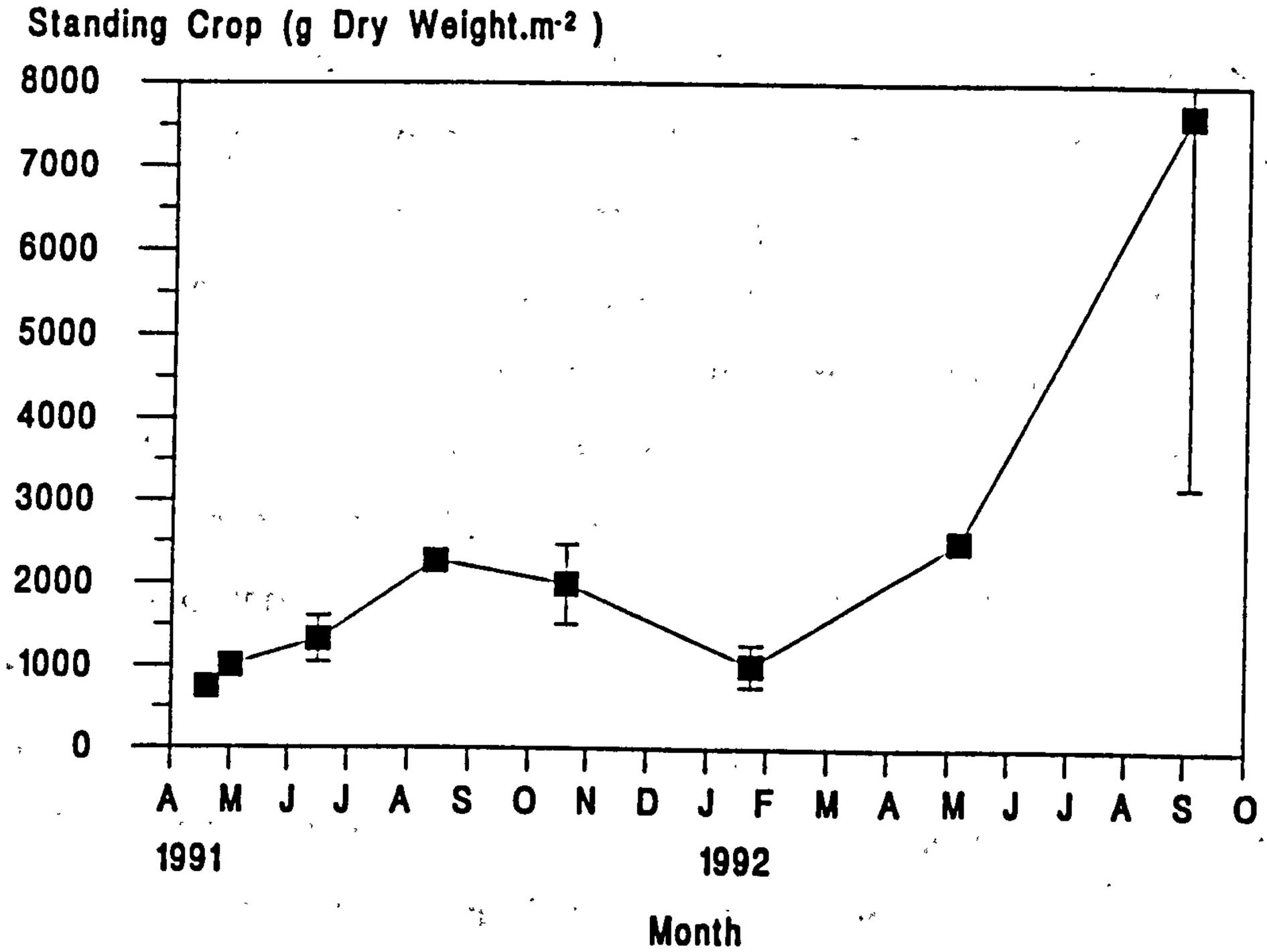
Standing crop as dry weight was less than 1 $kg.m^{-2}$ at the start of the experiment, though increased from this value steadily to a peak of 2.25 $kg.m^{-2}$ after four months. From August 1991 to January 1992 standing crop decreased. After this time, and to the end of the study, standing crop increased substantially to 7.6 $Kg.m^{-2}$ by the end of the study in September 1992 (Figure 3.34).

Figure 3.33 Standing crop in photographed populations of *Himanthalia elongata* over time.



Population 1 y = 270.235 + 1.984x - 0.005x^2 r^2 = 0.928
Population 2 y = 320.596 + 2.639x - 0.010x^2 r^2 = 0.572
Population 3 y = 189.586 + 5.087x - 0.021x^2 r^2 = 0.946

Figure 3.34 Standing crop in the harvested population of *Himanthalia elongata* over time (Bars = ± 1SE).



3.3.2.5 Density biomass relationships

a) Photographed populations

The $\log_{10}$ biomass (B) $\log_{10}$ density (N) relationship calculated by the principal component method from the data for all three of the populations pooled showed no difference from the expected -0.5 slope. Also the $\log_{10}$ mean plant weight (m) $\log_{10}N$ relationship was not significantly different from the expected -1.5 of the self-thinning rule (Table 3.6, Figures 3.35 and 3.36).

Table 3.6 Slopes fitted by the PCA method relating density to biomass and mean plant weight in photographed populations of *Himanthalia elongata*

β	Constant	Confidence limits	Correlation coefficient	Different from expected
$\log_{10}$ density $\log_{10}$ mean plant weight. Expected β = -1.5				
-1.44	4.24	-1.617, -1.289	-0.96	No
$\log_{10}$ density $\log_{10}$ biomass. Expected β = -0.5				
-0.421	4.17	-0.617, -0.249	-0.67	No

b) Harvested populations

Both $\log_{10} m$ and $\log_{10} B$ were plotted against $\log_{10} N$ (Figures 3.37 and 3.38). Three button stage samples and one thong stage sample were discarded from the data set subjectively as below the thinning line. It was clear from these plots that while the slopes of the different stages may not be different, the *y*-intercepts probably were, with the thong stage populations intercepting lower. As the thong stage populations had lower densities of plants, a slope fit to both stages together would have been artificially depressed. For this reason slopes were fit to the two stages seperately. The slope fit by principal component analysis to button stage populations was significantly more shallow than expected for both biomass and mean plant weight (Table 3.7). However, slopes fitted to thong stage populations were not significantly different from those expected. The slopes for the two stages were not significantly different from one another using 95% confidence limits (Table 3.7).

Table 3.7 Slopes fitted by the PCA method relating density to biomass and mean plant weight in harvested populations of *Himanthalia elongata*

β	Constant	Confidence limits	Correlation coefficient	Different from expected
Button stage				
$\log_{10}$ density $\log_{10}$ mean plant weight. Expected β = -1.5				
-1.85	6.810	-2.190, -1.586	-0.960	Yes
$\log_{10}$ density $\log_{10}$ biomass. Expected β =-0.5				
-0.87	6.910	-1.284, -0.581	-0.825	Yes
Thong stage				
$\log_{10}$ density $\log_{10}$ mean plant weight.Expected β = -1.5				
-1.67	5.482	-2.814, -1.103	-0.935	No
$\log_{10}$ density $\log_{10}$ biomass. Expected β =-0.5				
-0.68	5.515	-3.006, -0.052	-0.667	No

Figure 3.35 Density and mean plant weight relationship in the photographed populations of *Himanthalia elongata*.

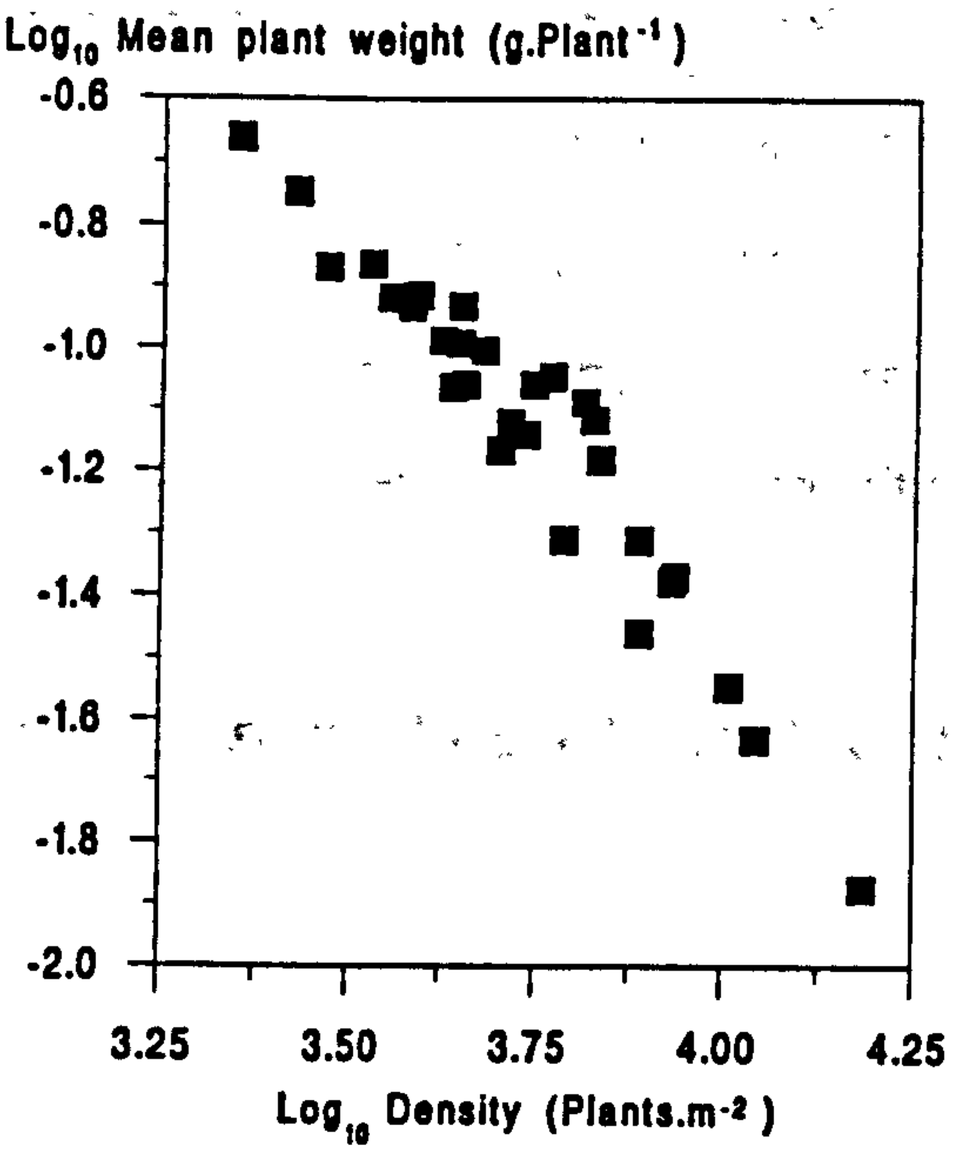


Figure 3.36 Density and biomass relationship in the photographed populations of *Himanthalia elongata*.

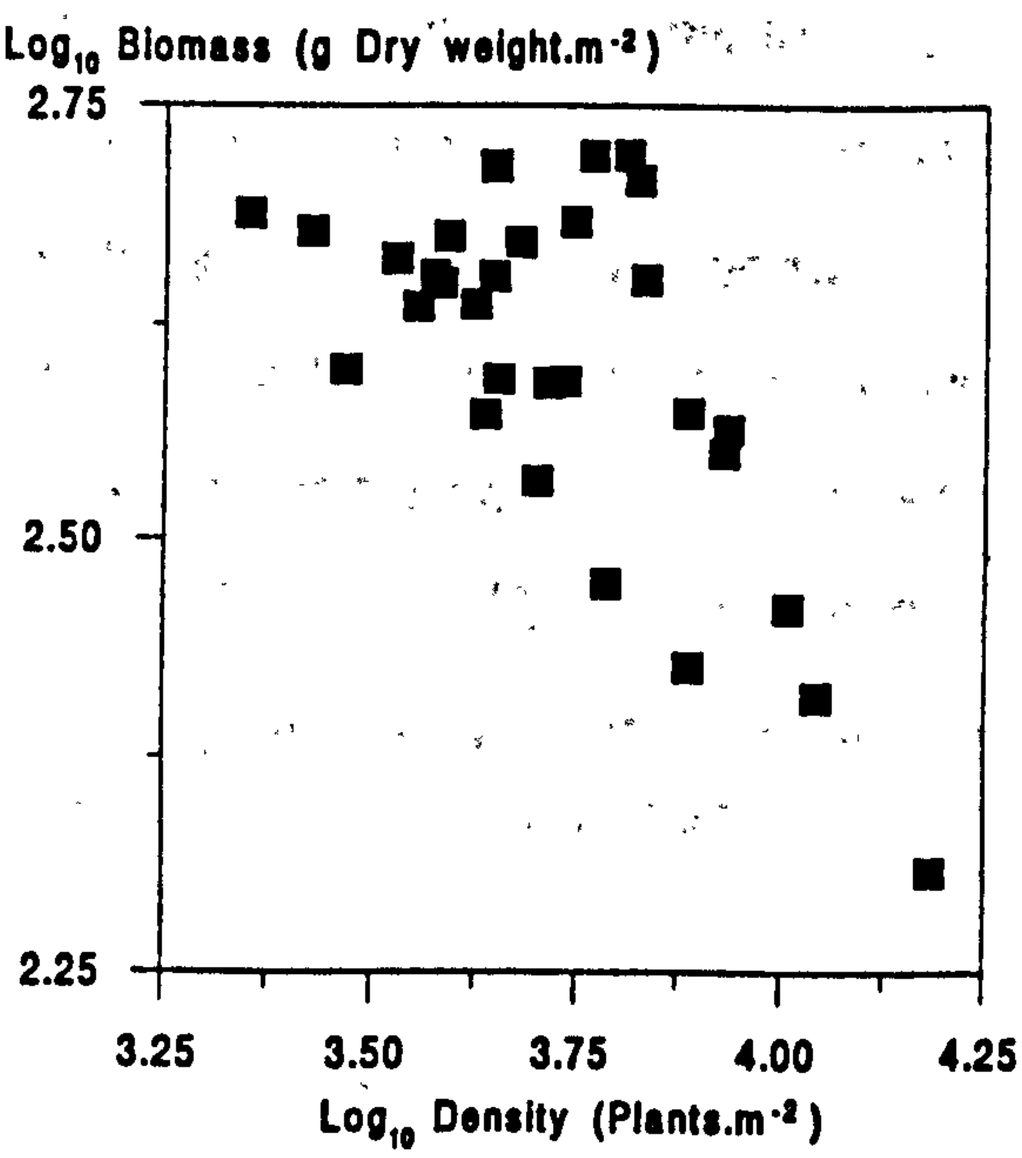


Figure 3.37 Density and mean plant weight relationship in the harvested populations of *Himanthalia elongata*. Arrows indicate discarded points.

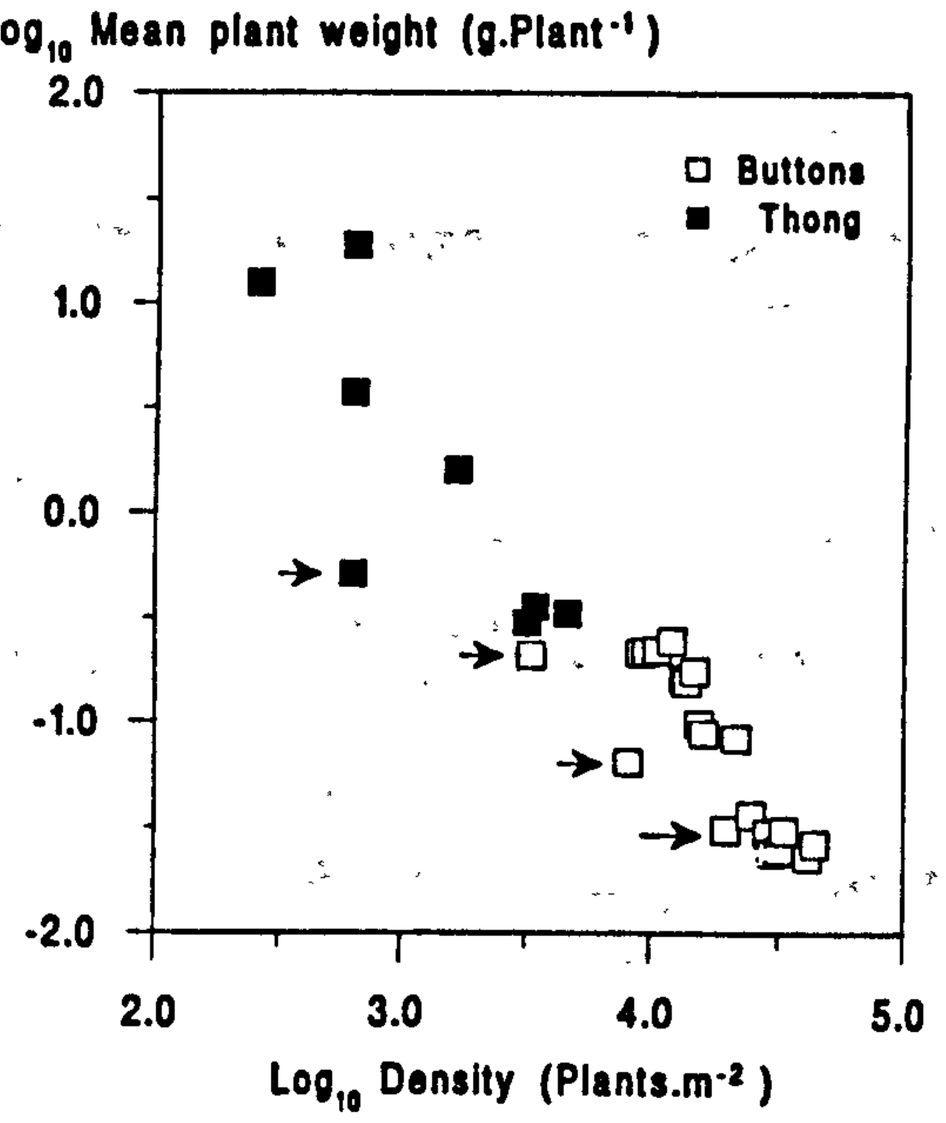
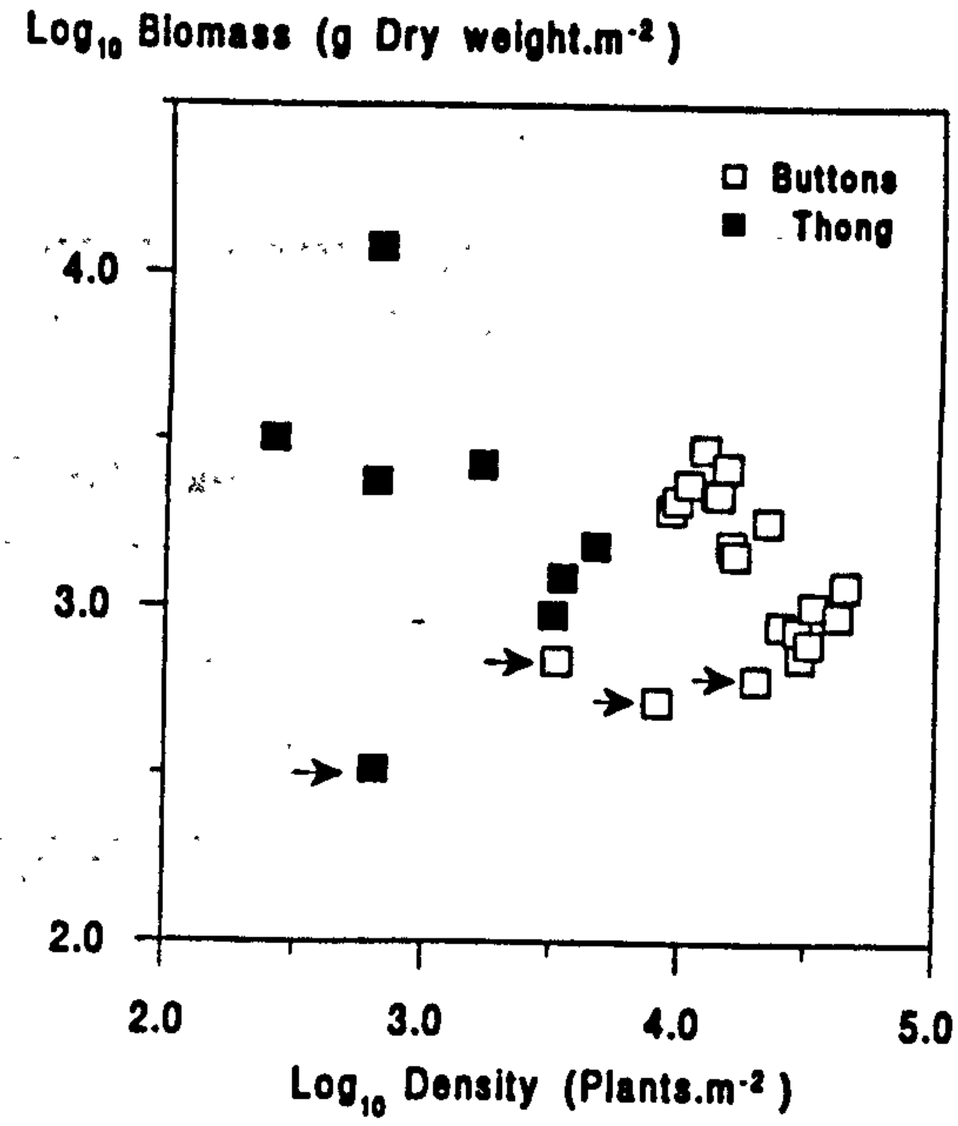


Figure 3.38 Density and biomass relationship in the harvested populations of *Himanthalia elongata*. Arrows indicate discarded points.



3.3.2.6 Relative growth rate

The relative growth rate of the three photographed populations started off quite high, but was subsequently very variable. Individually grown buttons generally had higher growth rates than buttons in populations (Figure 3.39) and larger plants had lower growth rates than smaller ones (Figure 3.40). Individually grown plants showed a different trend between initial size and relative growth rate, but regression slopes were not significantly different (H_0: B1 = B2 not rejected, Zar, 1984).

Figure 3.39 The mean relative growth rate of *Himanthalia elongata* buttons grown in populations and individually over time.

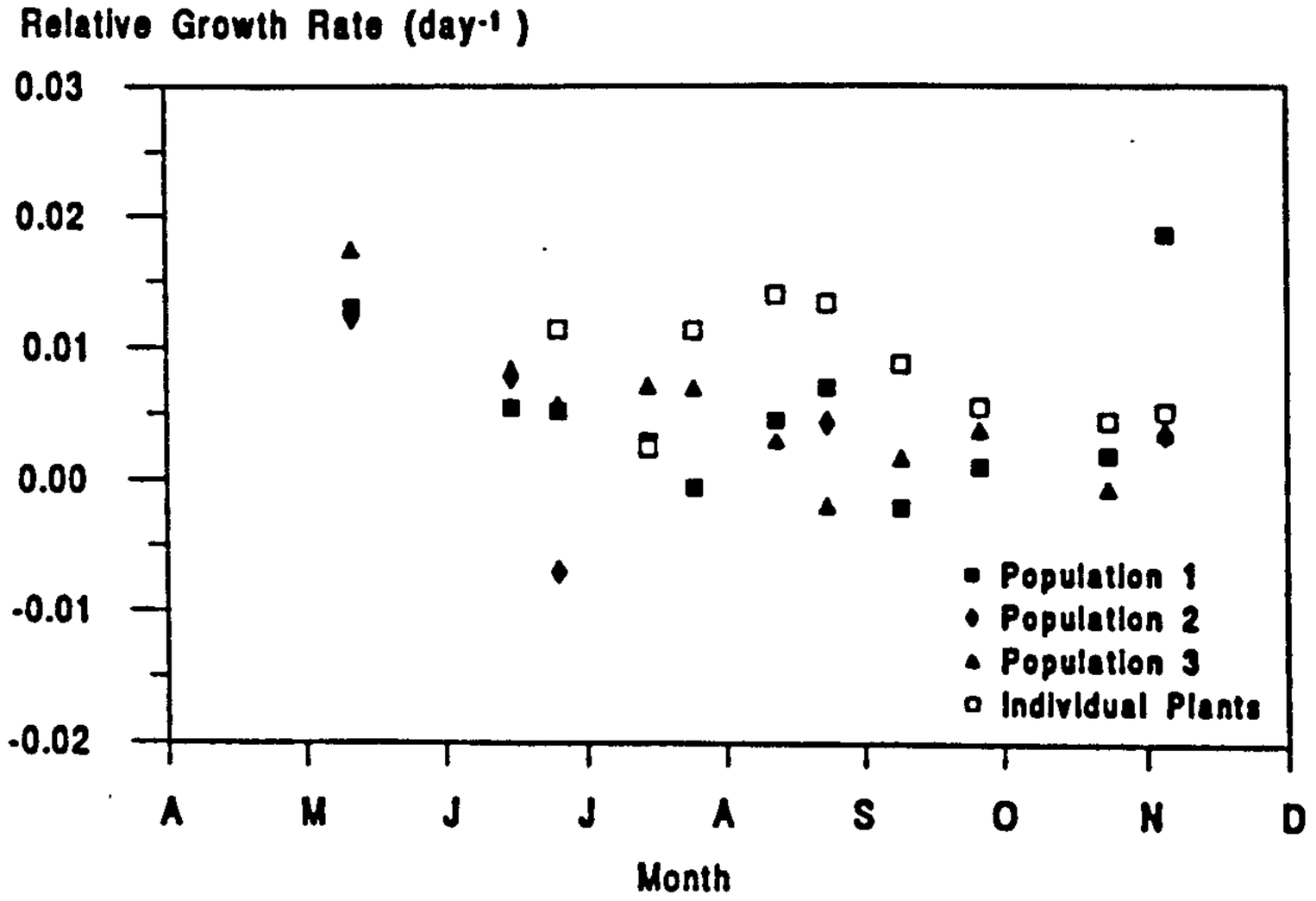
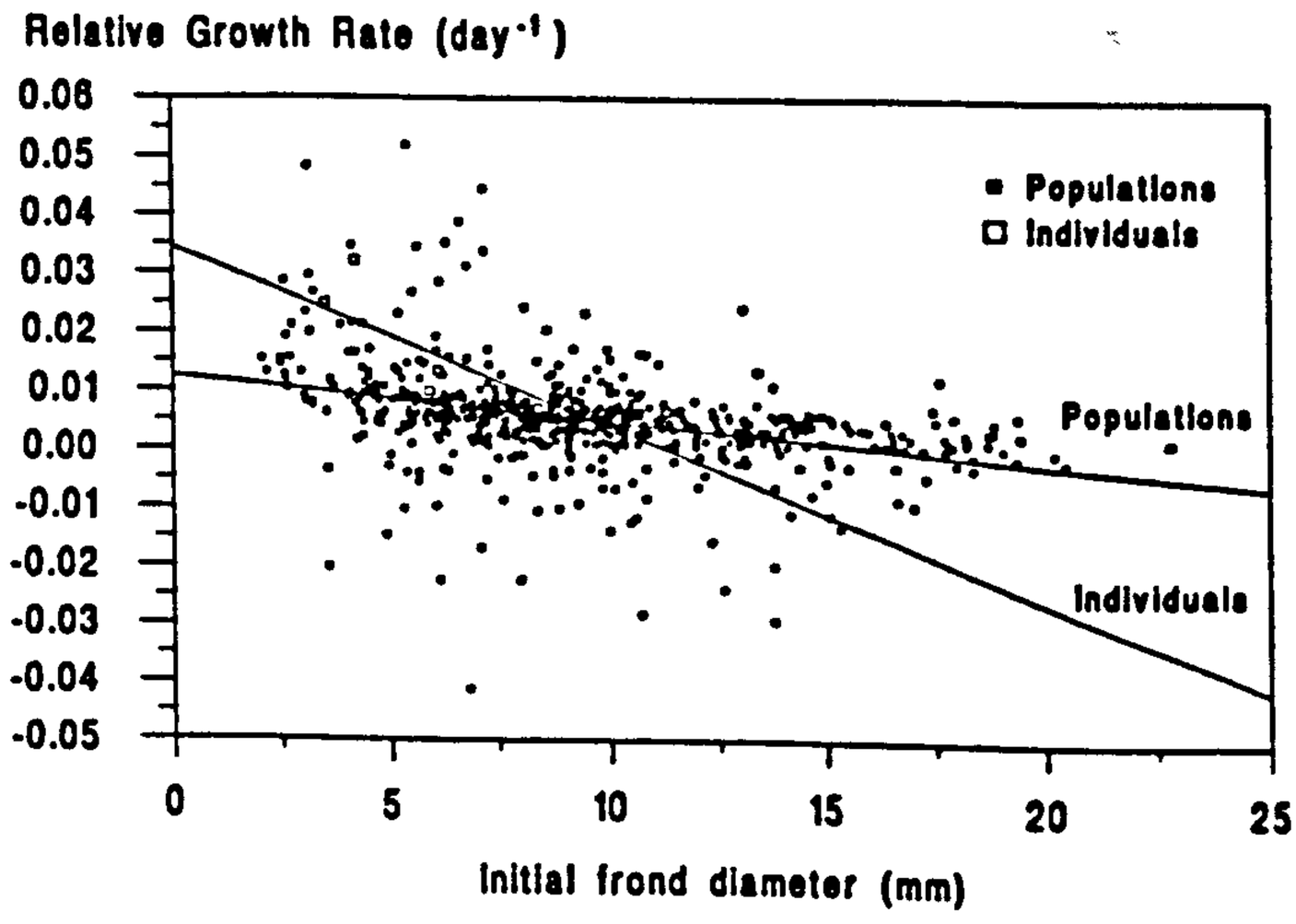


Figure 3.40 The relationship between initial plant size and mean relative growth rate in three populations of *Himanthalia elongata*.

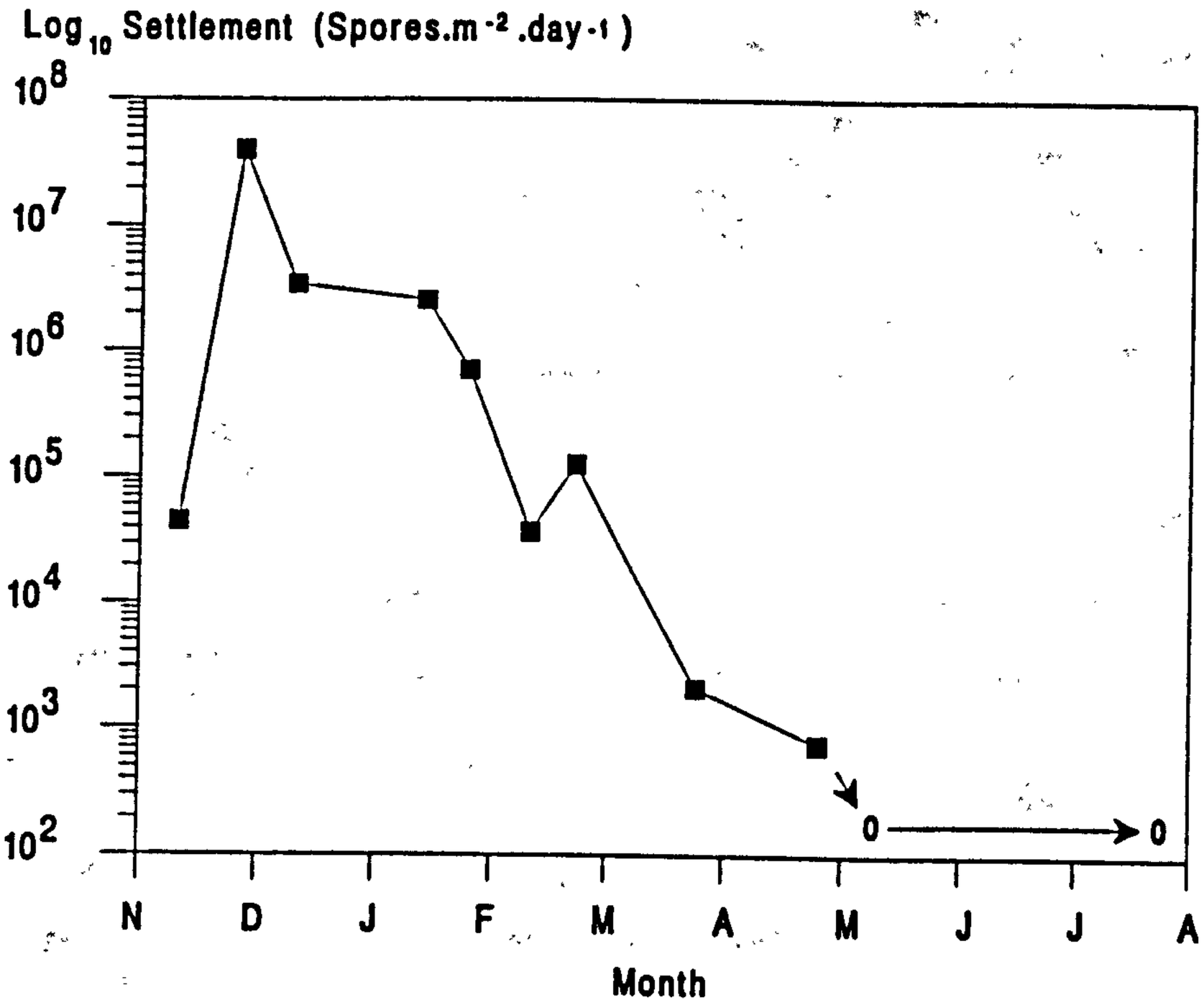


3.3.3 Fucus serratus

3.3.3.1 Settlement

Settlement was highest towards the end of November 1991 (Figure 3.41). After this time settlement rates decreased in a log linear fashion until May 1992, when there was no more settlement until the end of the experiment in July 1992.

Figure 3.41 The settlement of *Fucus serratus* propagules on artificial discs over time



3.3.3.2 Population structure

The populations started normally distributed, with rather low variability and inequality (Figure 3.42, Table 3.8). With time the populations became more positively skewed, more variable and more unequal as some plants grew substantially while many hardly grew at all (Figure 3.42, Table 3.8). The separately released oospore size distribution was normal, and the eggs were rather invariable and similarly sized (Figure 3.42, Table 3.8).

Figure 3.42 Length frequency histograms of artificially released *Fucus serratus* oospores and populations of propagules growing on artificial discs in the wild. Note the different scales.

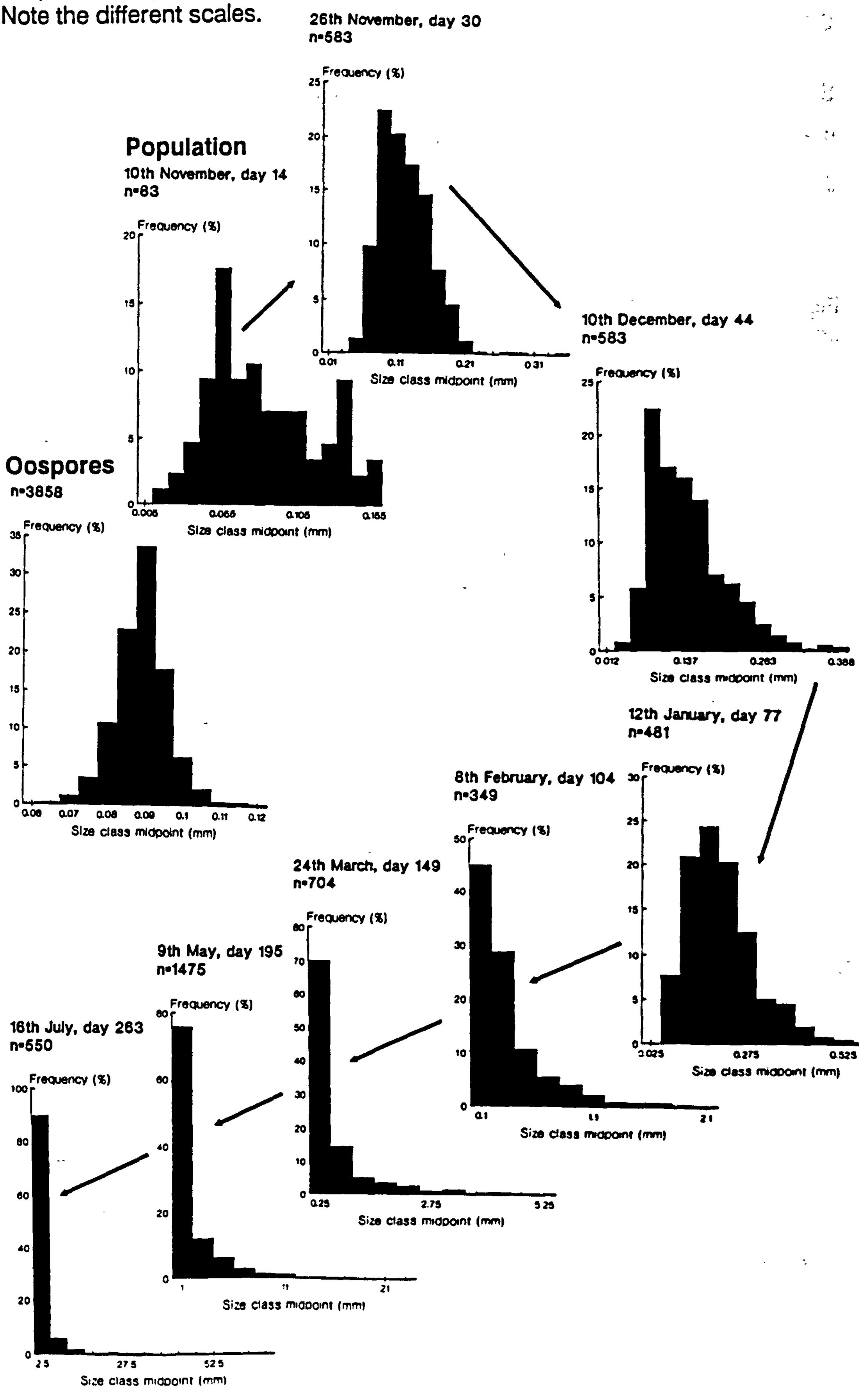


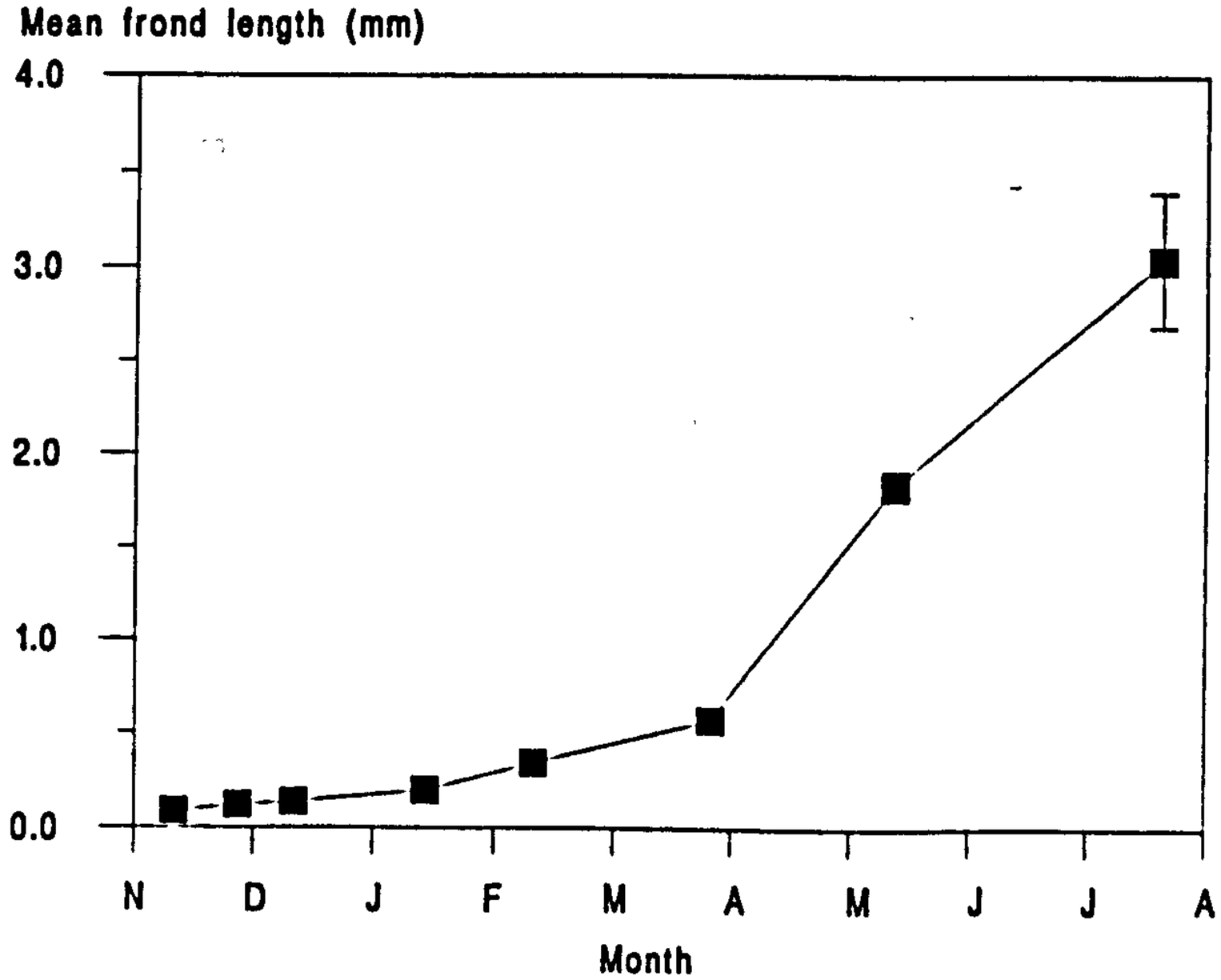
Table 3.8 Various population statistical measures of plant length of artificially released *Fucus serratus* oospores and populations of propagules growing on artificial discs in the wild.

	Coefficient of variation	**Gini coefficient**	**Skewness**
Oospores	0.081	0.045	0.259
Wild Embryos/Germlings			
10/11/1991	0.303	0.165	-0.045
26/11/1991	0.303	0.166	0.862
10/12/1991	0.383	0.203	1.197
12/01/1992	0.480	0.244	1.681
08/02/1992	0.851	0.403	2.140
24/03/1992	1.094	0.477	2.795
09/05/1992	1.346	0.544	3.296
16/07/1992	1.525	0.574	3.444

3.3.3.3 Frond length

Mean frond length increased gradually for the first three months of the study (Figure 3.43). However, after February 1992 there was a substantial increase in the rate of mean frond length increase until the end of the study in July.

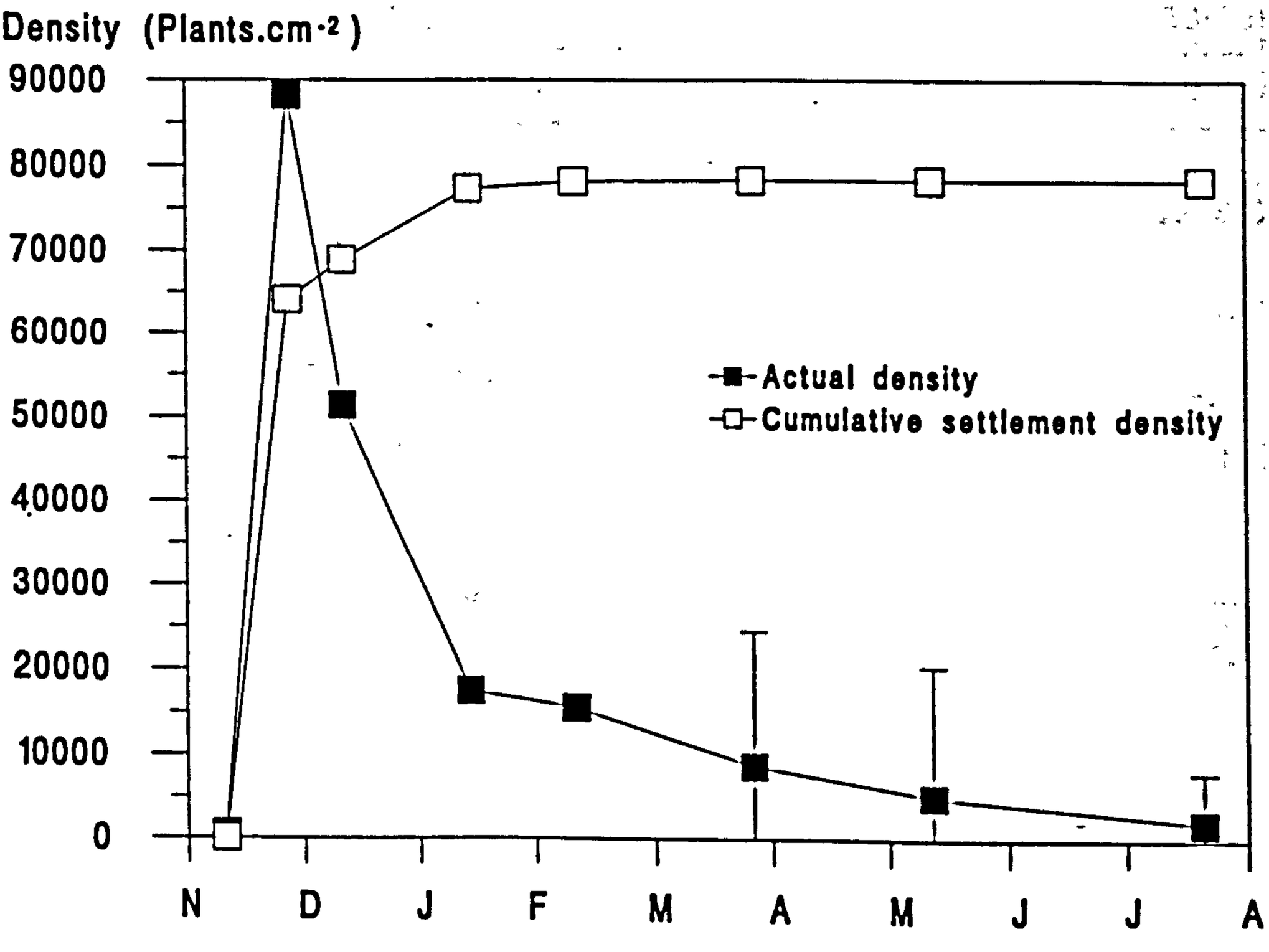
Figure 3.43 Mean frond length in a population of *Fucus serratus* growing on artificial discs (bars = ± 1 SE).



3.3.3.4 Density and survivorship

The density of propagules quickly became very high, and reached a peak in November 1991. After this time density decreased at every subsequent sample time (Figure 3.44). Massive mortality in the month after maximum density resulted in low survivorship early on. For comparison, cumulative settlement, derived from the data presented in Figure 3.41, and assuming no mortality, are also presented (Figure 3.44).

Figure 3.44 The density and cumulative settlement (see text) of *Fucus serratus* plants growing on artificial discs (bars = ± 1 SE)



3.4 Discussion

3.4.1 Population structure

The three species studied here demonstrated some interesting differences in population structure as they developed through time.

The predominance of the first size class in size-frequency histograms was the most outstanding feature of the population structural development of *Fucus vesiculosus*. This persistent feature of an oversized first size class is unusual and merits some consideration.

It is suspected that the feature of a dominant primary size class is related to a 'bank of microscopic forms' (*sensu* Chapman, 1986*b*) analogous to seed banks in terrestrial plants. In this study only plants of 1mm or greater were considered. If a bank of microscopic forms did exist in this population, two possible explanations could be put forward concerning the predominance of the first size class:

1. A 'bank of microscopic forms' is not strictly equivalent to a 'seed bank' as it results from the germination of zygotes and subsequent suspension of growth, while in terrestrial seeds germination has not taken place (Hoffman and Santelices, 1991). This is of course because marine algal zygotes are not storage propagules 'designed' for dormancy in the way that seeds are. It is possible that the first size class in this study consisted in part of the largest germlings able to survive but not grow *ie* the largest members of the 'seed bank'. This may explain why the second size class is smaller in comparison; there is no or little migration from the first size class to the second. In this case the 'seed bank' may include tiny macroscopic plants and 'a bank of microscopic forms' may be an unfortunate misnomer. A 'small-plant bank' may be more appropriate.

2. Microscopic individuals are constantly becoming macrorecruits (*sensu* Ang, 1991) and are able to penetrate the first size class level. However the growth

of larger plants maintains a competitively hostile environment which is constantly getting more hostile over time. Thus small-plant bank individuals may leave the bank but due to strongly competitive conditions die through competitive mortality whilst still in the first size class. In this case an interesting question is what physical factors encourage plants to leave the apparent relative security of the bank of microscopic forms.

Both these hypotheses rely on the fact that a small-plant bank does exist. Recent research confirms that they certainly exist in other macroalgal species. However, a recent review of the importance of algal 'seed' banks suggests that timescales for the survival of plants in 'seed' banks are low (only a few months, Hoffman and Santelices, 1991). That this conclusion is based almost entirely on data from laboratory experiments is excusable bearing in mind the difficulty of field experimentation with microrecruits (*sensu* Ang, 1991). However it is pertinent that the one field experiment considered in the review also exhibited the longest survival time of eight months. Species with discrete reproductive periods such as *F. vesiculosus* are useful in field studies of small-plant banks, while work on other species is made difficult by year round recruitment. The ability of *F. vesiculosus* sporelings to remain in a dormant phase has been noted before (Burrows and Lodge, 1950).

The persistence of first size class was also an important factor effecting the within population variation in plant size. The first size class was removed because of the probable existence of a seed bank. This was considered unimportant from the point of view of studying change in the rest of the population, though the removal of all plants from the first size class was a somewhat crude manipulation.

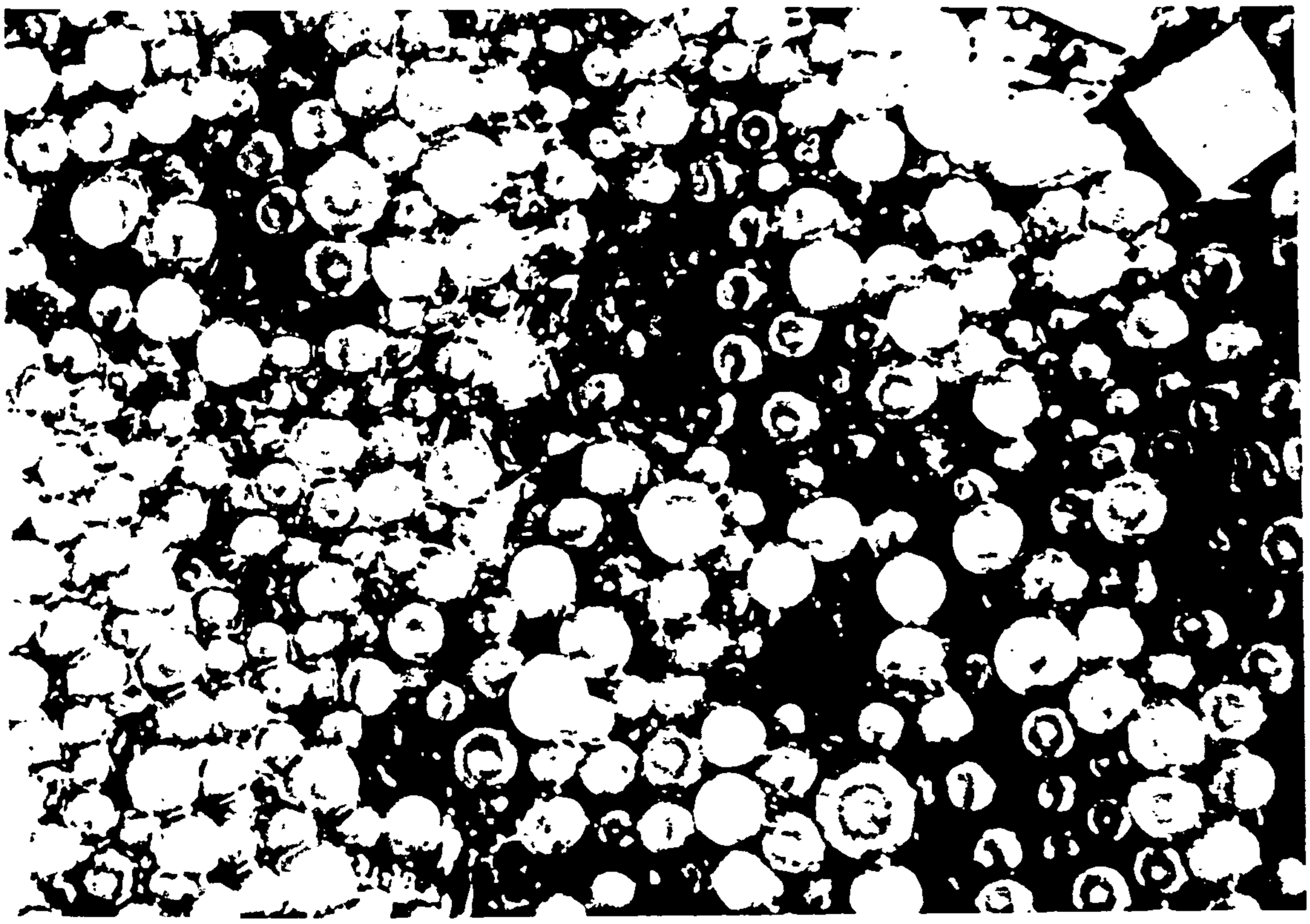
The removal of the first size class data resulted in far less plant to plant variation in the population. Ignoring the first two sample times (when removal of the first size class could have resulted in the removal of growing, non 'small-plant bank'

individuals, there was a general increase in variability in plant size with time in terms of the coefficient of variation and Gini coefficient.

Even in the absence of the first size class, the skewness coefficient revealed a transition from positive skew to normality to positive skew once more. This was interpreted as a move from a population already under the influence of intraspecific competition (and hence many small plants) to a population in which density dependent mortality was probably taking place.

Himanthalia elongata was a different kettle of fish. The population structure showed none of the positive skewness that was evident in *F. vesiculosus*. In fact, both button stage and thong stage populations became less variable and more equal in sizes of plants over time. Russell (1988, 1990) looked at the weight of vegetative thalli of *H. elongata* and found distinct positive skew in thallus weight in populations sampled from the same shore as this work. In his study however, Russell used random quadrats to sample multi-stage (and -age) populations rather than single staged populations, which explains the different results. The question still remains as to why the *H. elongata* populations behave quite differently to those of *F. vesiculosus*, at least at the button stage. While only experiments in which density has been manipulated will tell us whether intraspecific competition was taking place, the populations were very closely packed, often with no space between the tesselating thalli (Plate 3.1). Throughout the course of the experiments plants were disappearing under their conspecific neighbours never to return. Destructive harvests of these populations revealed no small plant bank. Plants 'losing' must die. It is probably very dark under the buttons of a *H. elongata* population where debris and silt usually collect. Silt has been found to be the major factor limiting *H. elongata*'s distribution as it cuts out light (Moss *et al.*, 1973). The speedy death of small unsuccessful plants may explain why plant sizes were less variable and less skewed in size. If this is the case then, two conclusions can be drawn about the *H. elongata* populations: they were subject to intense intraspecific competition and small plants were very susceptible to this competition. In *F. ves-*

Plate 3.1 Part of a typical cohort of *Himanthalia elongata* buttons



iculosus competition was probably less harsh and/or small plants could survive better.

The experimental monitoring of the *Fucus serratus* populations was designed to test a particular assumption widespread in plant demography that a population of seeds (or gametes/zygotes) starts with a normally distributed range of plant sizes which gets more variable as a plant heirachy develops (Koyama and Kira, 1956; Stern, 1965; Obeid *et al.*, 1967; Ogden, 1970; White and Harper, 1970; Ford, 1975; Mohler *et al.*, 1978; Turner and Rabinowitz, 1983; Higgins *et al.*, 1984; Weiner and Solbrig, 1984; Weiner, 1985; Schmitt *et al.*, 1986; Weiner and Thomas, 1986; Bonan, 1988; Bendel *et al.*, 1989). Unfortunately there seemed to be little evidence to support or refute this in microscopic seaweed populations as no population studies have been concerned with size distributions of gametes, newly settled zygotes or very small germlings/embryos. Furthermore, the *F. vesiculosus* and *H. elongata* populations studied here only

considered visible plants and were consequently pitched at a scale similar to the majority of investigations of seaweed demography.

The population structure of eggs of *F. serratus* was certainly normal. Furthermore as the populations of embryos/germlings developed, the sizes of plants became more variable, and a very strong positive skew had developed in plant sizes by the end of the experiment. Largescale settlement may have been periodic over the course of monitoring but a multi-modal size distribution which would be expected from such events was not found. Certainly the *F. serratus* populations fulfilled the assumption that plant sizes started normally distributed.

3.4.2 Density and survivorship

The maximum densities of *F. vesiculosus* found in this study were at least an order of magnitude greater than those found for the same species by other authors in the same area (Knight and Parke, 1950; Burrows and Lodge, 1950), and 6 times higher than those found in Maine (Kesser and Larson, 1984). The depletion of density was very marked in the first winter with approximately 10% of the original plants remaining after one month and 1 % after eight months. Kesser and Larson (1984) found that only 5 % of *F. vesiculosus* plants remained after seven months.

Density also fell in the *H. elongata* populations. Russell (1990) found densities of up to 10000 plants.m^{-2} on Manx shores, which was far lower than maximum densities found in both the photographed (15000 plants.m^{-2}) and destructively harvested (36000 plants.m^{-2}) of this study. The higher densities may be explained by the selection of sites in this study and the fact that populations of young buttons rather than multi-aged populations were being studied. Also, we both extrapolated to number per m^2. In terms of survivorship, in photographed populations approximately 30 % of plants died in the first month of the study, and 20-30% remained seven months later. In the harvested populations, over 50 % of plants died in the first two months of the study.

In *F. serratus* there was huge post settlement mortality of germlings. Large scale mortality has been predicted in microscopic populations because of a suite of factors (Santelices, 1990a and *b*; Vadas *et al.*, 1992). About 70 % of plants died within a month.

All three species studied exhibited Type III survivorship curves (*sensu* Deevey, 1947) for the periods studied, indicating extensive early mortality, with those plants that remain having a higher rate of survival subsequently (Begon *et al.*, 1986).

3.4.3 Increases in size of plants

Mean and maximum plant lengths in *F. vesiculosus* were related to season. Decreases were attributed to selective mortality of large plants and breakage (storms) and influxes of small plants.

In *H. elongata* there was a linear increase in mean plant diameter until thongs started to grow. It seemed that growth resources transfer from button enlargement to thong growth.

The growth rate of photographed *H. elongata* buttons was related to season and to plant size. There was no significant difference in the relationship of growth rate to initial plant diameter between the populations and individually grown plants. Had such a difference existed this would have been evidence for dominance and suppression (Schmitt *et al.*, 1987), though a lack of significant difference was probably due to the small number of individually grown plants in relation to those in populations, so the possibility of dominance and suppression should not be rejected.

In *F. serratus*, mean frond length increased in what seemed to be an exponential fashion, whith only small increases in the first five months, but then substantial increases after this time.

3.4.4 Standing Crop

Standing crop was also variable with season in *F. vesiculosus*, being at its maximum during the reproductive period (Knight and Parke, 1950). I obtained a maximum standing crop of about 1.8 $kg.m^{-2}$ dry weight. Dry weight is about 24 % of wet weight in *F. vesiculosus* (personal observation, DW = 0.0003 + 0.2433WW, $n = 20$, Std = 0.0064, $R^2 = 98.5\%$, $p < 0.001$) and using these values for conversion from wet weight Kesser and Larson (1981) found a maximum 2.11 $kg.m^{-2}$ and Knight and Parke (1950) found a maximum standing crop of 2.92 $kg.m^{-2}$.

H. elongata populations at the button stage had estimated maximum standing crops of 550 $g.m^{-2}$ in photographed populations and 2300 $g.m^{-2}$ in harvested populations. In the harvested populations maximum standing crop was at least 7.5 $kg.m^{-2}$, far higher than *F. vesiculosus* standing crop.

3.4.5 Reproduction in Fucus vesiculosus

In *F. vesiculosus* there was no relationship between frond length and number of receptacles though there was a minimum plant size for receptacle presence. It seemed that the minimum size requirement for reproductive development was about 7 cm. Knight and Parke (1950) found that *F. vesiculosus* plants were usually 15 - 20 cm long before becoming reproductive, and that 70 % of plants over 14 cm in length bore receptacles in the first year. In my study as much as 50 % of plants became reproductive in their first year. Ang (1991) found that most reproductive plants were at least 9.5 cm long in *F. distichus* with a probability of 55 - 80 % of being reproductive in the first year. Larger plants were more likely to possess receptacles than smaller ones, and most plants had small numbers of receptacles. In *F. distichus* about 35% of plants were reproductive in the first year (Ang, 1991), though this value was a little higher in my study of *F. vesiculosus*.

3.4.6 Self-thinning

Self-thinning relationships in the population of *F. vesiculosus* did not conform to the -1.5 or -0.5 rule. This population was probably subjected to the usual density independent mortality associated with natural seaweed populations as well as possible density dependent factors. The fitting of a thinning line is always subjective (Weller, 1987a) and this problem combined with the variability found in environmental field data makes relationships less distinct. Assuming the rule applies to seaweeds, then this population of *F. vesiculosus* was undermaximizing biomass per unit of density. The biomass was not as packed as it 'should' be. This is understandable if periodic events (eg storms) are removing large plants. The situation is further complicated by the possible presence of a small-plant bank, which may contribute to the density greatly, but the biomass very little. In real terms the population may have been even-aged but it was not even staged. Despite these various confounding factors, a thinning slope could be fitted to the data, which suggests that an underlying mechanism does exist which may be more exactly and conveniently studied in more controlled conditions.

The *H. elongata* populations that were photographed did conform to the expected self-thinning rule of -1.5 or -0.5. In the destructively harvested populations, the button stage populations had significantly steeper slopes than expected, while the thong stage slopes were as expected. The button stage populations may have been undermaximizing the biomass/plant weight for a given density at the beginning of monitoring and this may have steepened the slope. The steeper slope in the button populations resulted in a higher *y*-intercept than in the populations with thongs, while the *y*-intercept of photographed populations was lower still, maybe because of different growth conditions. Certainly the populations were in different sites, and probably at different heights on the shore. Gibb (1937) found quite substantial differences in the growth of *H. elongata* plants at different heights on the shore.

F. vesiculosus has been cited as conforming to the self-thinning rule using 4.3 as the *y*-intercept boundary condition (Cousens and Hutchings, 1983). Russell (1990) found a linear relationship between $\log_{10}$ mean plant weight and $\log_{10}$ density with a regression slope of -0.0108 and *y*-intercept of approximately 3.2, but stated the data were multi-aged and multi-specific. A comparison of interspecies differences in thinning trajectories will be considered later.

In summary, there is much evidence from the study of the three species here that suggests that populations of marine plants may behave similarly to terrestrial plant populations. Though we have found that important indicators of population dynamics may be distinctly different for different species, the underlying mechanisms which bring about those differences may be common to all seaweeds (or indeed to all plants and even some sedentary animals). There are many important factors acting on natural monospecific seaweed populations, and the following chapters aim to try to elucidate some of the mechanisms underlying seaweed population dynamics.

Chapter 4 The effect of density on the dynamics of natural seaweed populations

4.1 Introduction

We have seen in Chapter three that in naturally occurring seaweed populations population structure, reproductive output, density and biomass dynamically changed through time. The effect of density on natural seaweed populations will be considered in this chapter.

Density dependence and intraspecific competition are closely linked in both plant and animal populations (Begon and Mortimer, 1986). The manipulation of density is therefore a useful tool in the study of intraspecific competition within populations.

Natural seaweed populations have been subjected to numerous studies on the effect of density on intraspecific population development. A large body of evidence for the likelihood of intraspecific competitive action in seaweed populations comes from the ultimate density manipulation, total clearance of a mature plant canopy. Numerous authors have reported that in cleared areas conspecific juveniles arise, while under the canopy there is no such effect (*eg* Kain, 1963, 1976; Duggins, 1980; Schonbeck and Norton, 1980*a*; Kirkman, 1981; Dayton *et al.*, 1984; Schiel, 1985*a*; Chapman, 1989, 1990*b*). While canopy sweeping (*eg* Westermeier and Moller, 1990), reduced herbivore pressure (*eg* Kirkman, 1981), allelopathy (*eg* Dayton *et al.*, 1984) and nutrient limitation (*eg* Gerard and Mann, 1979) have been suggested as reasons for this response, light limitation by the canopy is most often cited (Rosenthal *et al.*, 1974; Dayton, 1975; Kain, 1976; Pearse and Hines, 1979; Keser and Larson, 1984; Reed and Foster, 1984; Santelices and Ojeda, 1984*a* and *b*; Druelh and Breen, 1986; Robertson, 1987). However, such all-or-nothing experiments often designed to

look at community interactions, are of little use in a detailed examination of density dependence.

Rather fewer experiments have concentrated on the manipulation of density by degrees and its subsequent effect on population dynamics. Unfortunately, because seaweed propagules are very small it has proved difficult to follow seaweed populations through their entire life. Consequently, studies have concentrated on density effects at germling (Ward, 1982; Reed, 1990*b*) or larger plant scales (Chapman and Goudey, 1983; Reed, 1987; Chapman, 1990a; Reed, 1990a; McCook and Chapman, 1991).

For studying small scale density effects laboratory culture (*eg* Russell and Fielding, 1974; Reed, 1990*b*; Reed *et al*., 1991) or outplanting (*eg* Schiel and Choat, 1980; Foster and Schiel, 1985; Reed, 1990a) have been used. Some populations of large plants have been studied by constructing them on artificial surfaces (Adams and Austin, 1979; Hurtado-Ponce, 1990). Other workers have experimentally thinned natural populations (Black, 1974; Chapman and Goudey, 1983; Reed, 1987; Chapman, 1990*b*; Reed, 1990a; McCook and Chapman, 1991), or used populations naturally occurring at different densities (Schiel and Choat, 1980; Schiel, 1985*b*).

Generally the results of such studies have demonstrated density dependence and intraspecific competition in the form of reduced growth rates (Black, 1974; Schiel, 1985*b*; Reed, 1990a), greater mortality (Chapman and Goudey, 1983; Reed 1990*b*), reduced recruitment (Black, 1974; Reed, 1990a) or reduced reproductive potential (Reed, 1987) in high density treatments.

Schiel and Choat (1980) however, found that plant lengths, mean plant weight, yield and reproductive output were higher at higher densities. Schiel (1985*b*) reported a positive relationship between plant size, reproductive potential and density. In both these studies high and low density populations were spatially discrete from the time of settlement, and differences in environmental and biological parameters may have existed between sites.

To my knowledge no authors have previously dedicated a demographic study to either *Fucus vesiculosus* or *Himanthalia elongata*. While the population dynamics of other fucoids have been studied in some detail (*Fucus distichus*, Thom, 1983; Keser and Larson, 1984; Ang, 1991; Ang and De Wreede, 1992; *Fucus spiralis*, Keser and Larson, 1984; Robertson, 1987; *Ascophyllum nodosum*, Keser *et al.*, 1981; Vadas *et al.*, 1982, 1990; Cousens, 1985, 1986), *H. elongata* and *F. vesiculosus* have received less attention.

In Knight and Parke's (1950) study of *F. vesiculosus*, various population parameters were measured, and cutting treatments (which may be equivalent to thinning) were made. Keser *et al.* (1981) also gave cutting treatments to *F. vesiculosus* stands in a study of harvesting regimes. Keser and Larson (1984) treated *F. vesiculosus* populations to canopy clearance and grazer exclusions to study colonisation and growth dynamics. McCook and Chapman (1991) treated *F. vesiculosus* canopy to total clearance or 75 % clearance in a multifactorial community level experiment.

Despite it being a common component of the flora of British shores (Gibb, 1937), the only studies relating directly to the population structure of *H. elongata* were carried out by Russell (1988, 1990).

Both *H. elongata* and *F. vesiculosus* occur in dense, monospecific, even-aged stands. Fucoid algae are useful subjects for such a study as they have a relatively simple life cycle compared to the kelps, without a prolonged haploid phase (Chapman, 1986*b*). Both species have discrete reproductive periods and are important components of the intertidal flora on semi-exposed Manx shores.

In this chapter two fucoid algal species were selected to clarify the importance of density-dependence in population development and reproductive potential. Specifically, my manipulations were designed to test whether theoretical self-thinning relationships could explain seaweed population development in nature.

Thinning treatments were carried out on the macroscopic portion of these two species to investigate the effect of density on various population parameters.

4.2 Materials and Methods

4.2.1 Fucus vesiculosus

An area of shore at The Ledges, Port St. Mary, Isle of Man had previously been selected and manipulated to study the population dynamics of a population of *F. vesiculosus* (Chapters 2 and 3). This experimental area was created in August 1990, and regular sampling of the population was carried out for the next five months (Chapter 3). In January 1991 part of the area was used for a study of the effect of artificial thinning on this population. Sixteen 0.25 m^2 permanent quadrats were marked within the area as four blocks of four quadrats, each with a 30cm buffer zone around it which received the same manipulations, but was not sampled. Care was taken to avoid bare patches (which limpets had previously occupied), and only areas with 100 % barnacle cover were included. A map was made of the quadrat location, and numbers were assigned to the quadrats.

Within each block of four permanent quadrats, each quadrat was randomly assigned a treatment. To facilitate treatment each permanent quadrat and associated buffer area was divided into contiguous square 100 cm^2 areas. Each of these sub-areas was considered a unit area on which treatment could be effected (Figure 4.1). The aim of thinning manipulations was not only to reduce pre-existing densities by differing amounts, but also to preserve the population structure during this process. The population had been sampled a few days before (Chapter 3), and the density found to be 40 plants per 100 cm^2. Also, the population structure had been determined, and was simplified into four size classes, 1-40 mm, 41-80 mm, 81-120 mm and >120 mm, and the relative proportions of plants in each size class calculated (Figure 4.2). This ratio of plant sizes was used to remove selectively proportions of different sized plants.

All the permanent quadrats in all the blocks were treated in this way over a period of five days (ten low tides), with the removal of 15, 25 or 35 of the 40 plants per 100 cm^2 area, which resulted in the removal of 0, 38, 63 or 88 % of plants.

At each sample time sub-samples were taken from each treatment in each block. The position of the sub-sample within each permanent quadrat was determined randomly. Sample details may be found in Table 4.1. Samples were collected and analysed as in Chapter 3.

4.2.2 Himanthalia elongata

During the winter storms of 1990-1991 an area of the Ledges, Port St. Mary was naturally cleared of most reproductive *H. elongata* plants by wave action, exposing a large area of small dense *H. elongata* 'buttons' (see Chapters 2 and 3 for study site details).

Populations were standardised using the 'roundrat' method detailed in Chapter 3. They were then subjected to artificial thinning treatments. The roundrat was divided into small (2 x 2 cm) squares using fishing wire (Figure 4.3). To reduce plant density (thin), a pair of open forceps was inserted into each square of the roundrat and down amongst the plants, closed, and pulled up. In this way a number of plants were randomly plucked from the population. Treatments consisted of 0, 2, 4 or 8 plucks from each square of the roundrat.

To ease relocation, the rock to the top left of each population was marked with brass screws and fluorescent plastic tape, and a map of the populations was drawn with reference to the string grid to facilitate relocation. Populations were numbered and random numbers generated to select populations for sampling at different times.

Whole populations (usually four) were sampled on each occasion (Table 4.2). These were brought back to the laboratory in plastic bags for subsequent measurement.

Maximum button width was measured to 0.1 mm using callipers and, where appropriate, maximum thong length was measured to 1mm using a ruler. Whole populations were then oven dried (as above) and population dry weight measured.

Table 4.1 Sampling details for the *Fucus vesiculosus* experiment

Sample Number	**Sample date**	**Days from thinning**	**Replicates: Thinned (Unthinned)**
1	5/2/91	0	4(3)
2	5/3/91	28	(3)
3	3/4/91	56	4(3)
4	21/5/91	105	4(3)
5	30/7/91	175	4(3)
6	6/10/91	242	2(2)
7	6/3/92	393	2(2)

Table 4.2 Sampling details for the *Himanthalia elongata* experiment

Sample Number	**Sample date**	**Days from thinning**	**Replicates**
1	18/4/91	0	4
2	30/4/91	12	4
3	14/6/91	57	4
4	11/8/91	115	4
5	23/10/91	181	4
6	24/1/92	274	4
7	6/5/92	377	2
8	1/9/92	494	2

Figure 4.1 Schematic diagram showing the experimental design and thinning treatments in the *Himanthalia elongata* experiment

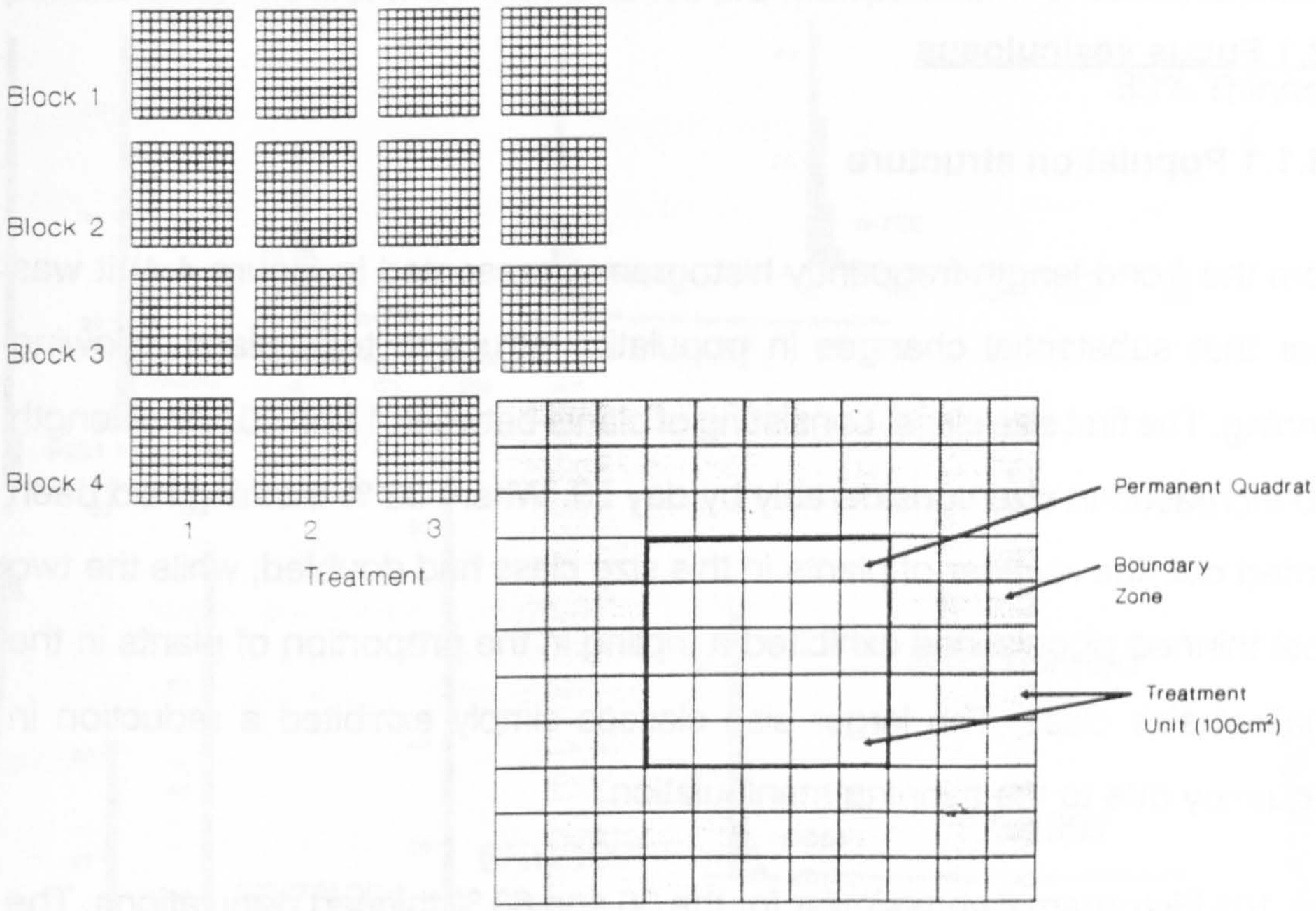


Figure 4.2 Size frequencies used for the thinning treatments in *Himanthalia elongata*

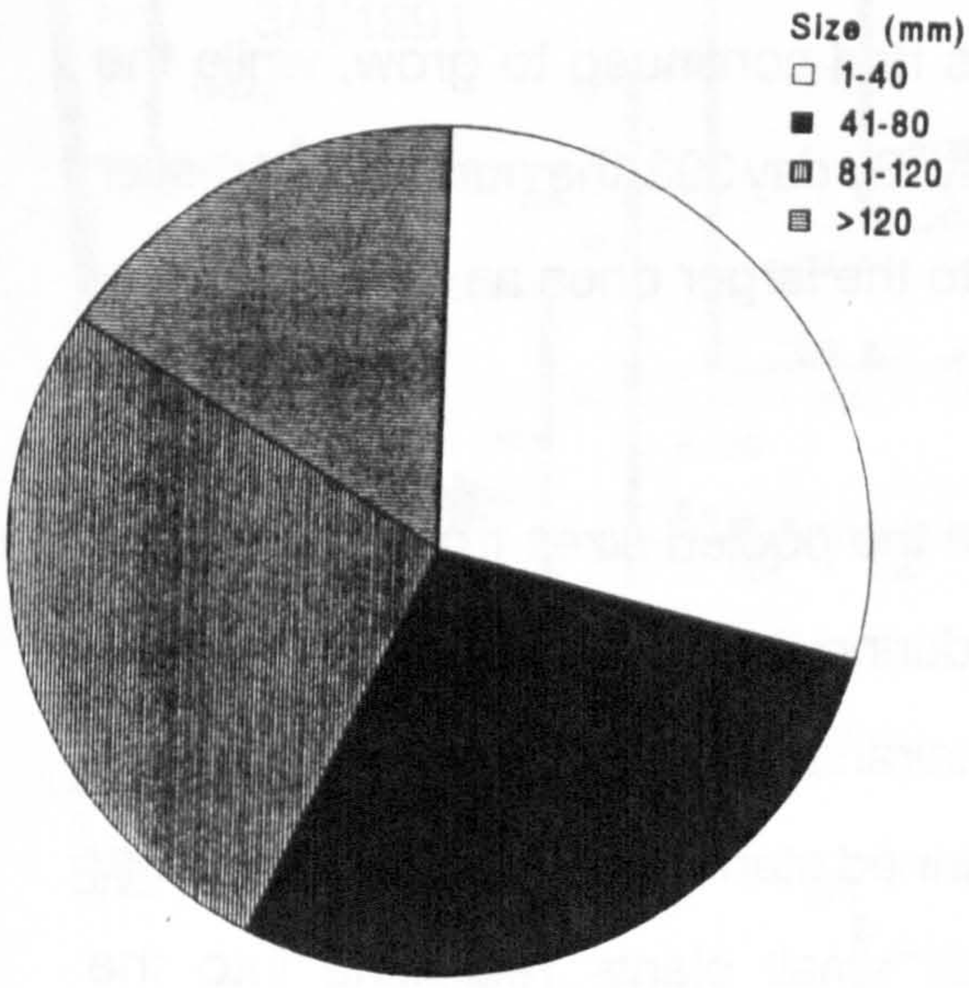
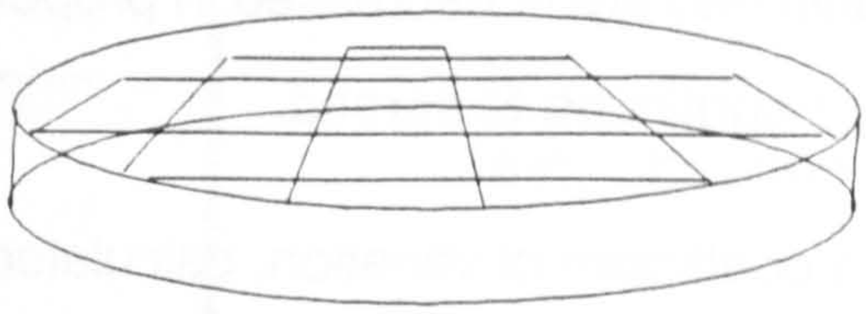


Figure 4.3 Diagram of the 'roundrat' used for treating *Himanthalia elongata* populations to thinning manipulations



4.3. Results

4.3.1 Fucus vesiculosus

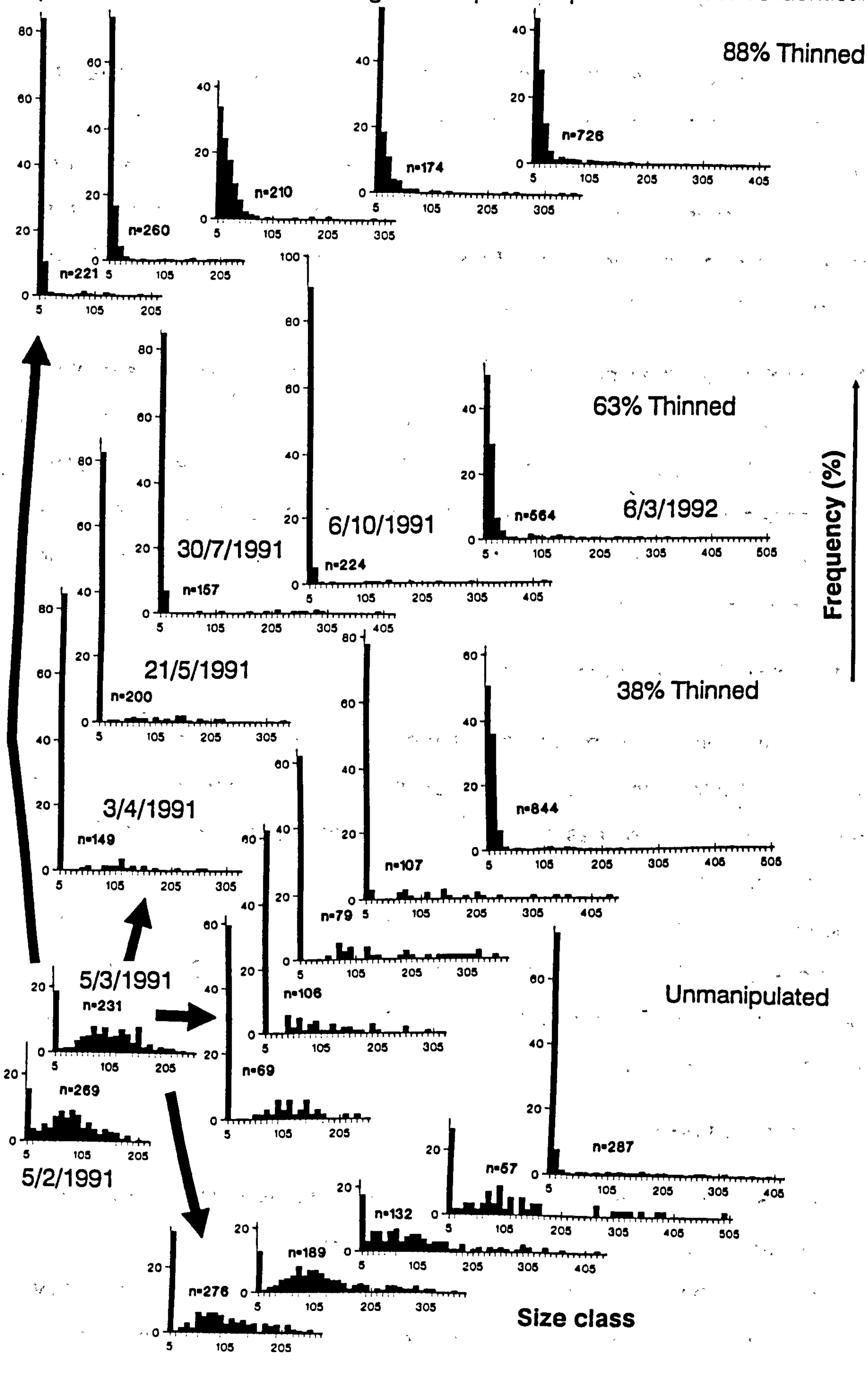
4.3.1.1 Population structure

From the frond length-frequency histograms (presented in Figure 4.4) it was clear that substantial changes in population structure took place following thinning. The first size class, consisting of plants between 1 and 10 mm in length had increased in size considerably by day 56. Where 38 % thinning had been carried out, the number of plants in this size class had doubled, while the two most thinned populations exhibited a tripling in the proportion of plants in the smallest size class. The larger size classes simply exhibited a reduction in frequency due to the thinning manipulation.

Day 105 histograms were similar for the 38 and 63 % thinned populations. The population frequency of the smallest plants fell in the 88 % thinned populations, as the size variation increased and plants moved into the next classes. This trend continued to day 175, where growth of the new small plants into larger size classes became even more obvious in the most thinned population, and plants between 1 and 10 mm comprised only 33 % of the population. By day 242, in all manipulations, the largest plants had continued to grow, while the number of small plants had increased slightly. By day 393 the number of smaller plants had again decreased in proportion to the larger ones as all the populations continued to spread.

The coefficient of variation, calculated from the pooled sizes from all replicate samples, increased in all the populations during the study, indicating that the populations were becoming increasingly heirarchical (Figure 4.5). The rate of increase was substantial in the two most thinned stands in the first 60 days after manipulation, and was due to numerous small plants recruiting into the measureable size range, 1 mm (Figure 4.5). Initially there was a trend of increased variability with increased artificial thinning, though the two most

Figure 4.4. Percentage frond length frequency histograms for the four manipulations of *Fucus vesiculosus* over time. Percentages are calculated from pooled data. The first two histogams are pre-manipulation. All scales identical.



thinned stands subsequently became less variable in sizes of plants, and by the end of the study all the stands had similarly variable plant sizes.

The Gini coefficient generally behaved similarly to the coefficient of variation, and was thus characterised by an increase in plant size inequality in all stands during the course of the study (Figure 4.6). Size inequality increased most quickly in the most thinned stands though subsequently stayed rather constant, resulting in rather similar Gini coefficient values by the end of the study for all the stands (Figure 4.6).

As expected from the length frequency histograms, positive skewness of plant lengths was a feature common to all the manipulated stands (Figure 4.7). However, the more a stand was thinned, the faster and greater positive skewness became. While increasing skewness was maintained over time in the two least thinned stands, the skewness became stable, or decreased in the two most thinned stands (Figure 4.7).

4.3.1.2 Density and survivorship

Obviously mean frond density was initially lowest in the most thinned population and highest in the unmanipulated population (Figure 4.8). However, density (of measurable plants) increased in the three thinned stands, while the density decreased throughout the study in the unthinned stands. The greater the degree of thinning, the greater and more quickly density increased as new plants entered the visible stand (Figure 4.8). Two-way ANOVA revealed a significant difference in density between thinning levels, time and the interaction of the two (Table 4.3).

4.3.1.3 Frond length

Mean frond length increased in the unthinned stands until 240 days after manipulation, but after this time fell to levels similar to the three thinned stands (Figure 4.9). The three thinned stands' mean frond lengths decreased quickly, almost certainly because the large number of 'new' small plants decreased the

Figure 4.5 Coefficient of variation in four density manipulated populations of *Fucus vesiculosus* over time, calculated from plant lengths pooled from replicates.

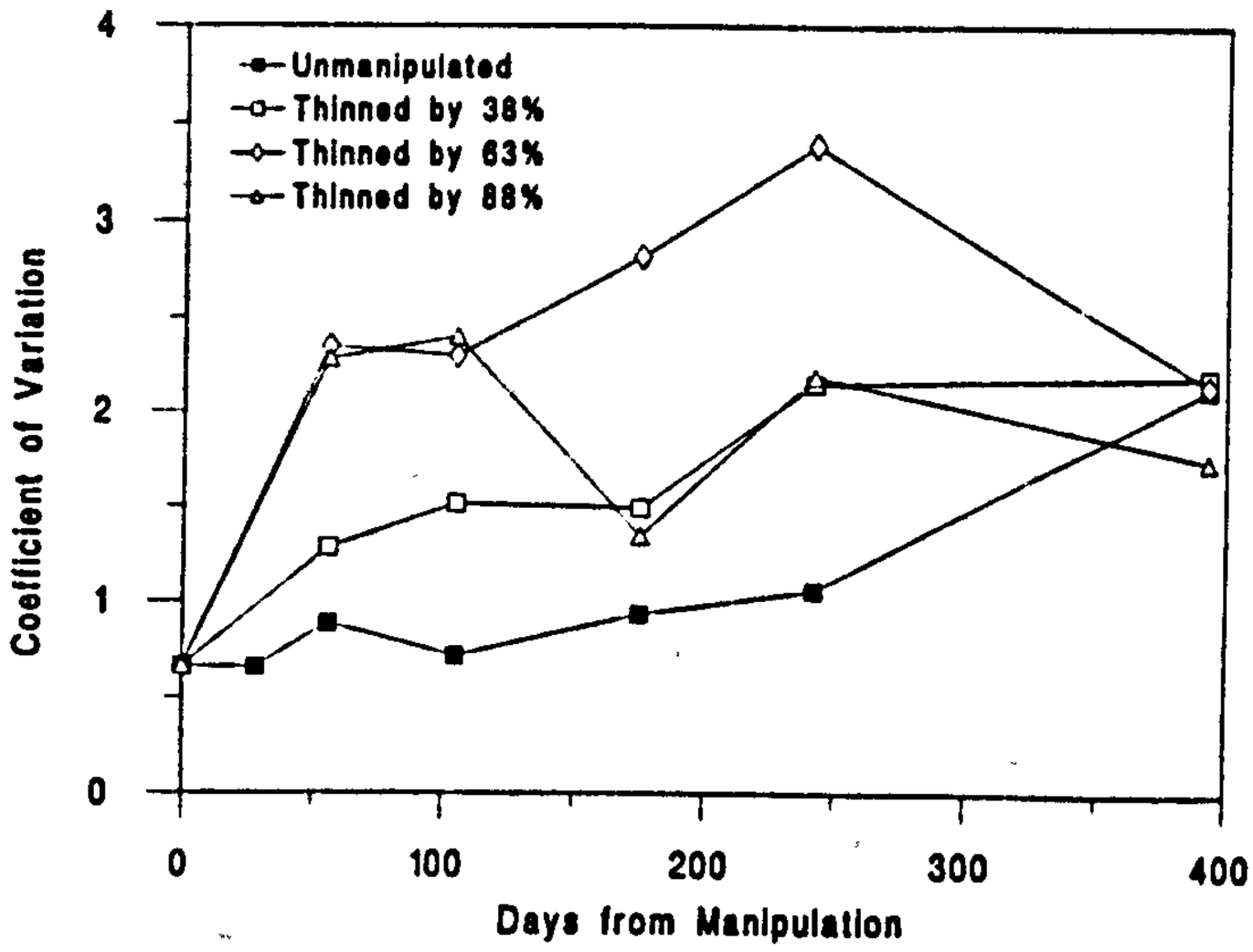


Figure 4.6 Gini coefficients in four density manipulated populations of *Fucus vesiculosus* over time, calculated from plant lengths pooled from replicates.

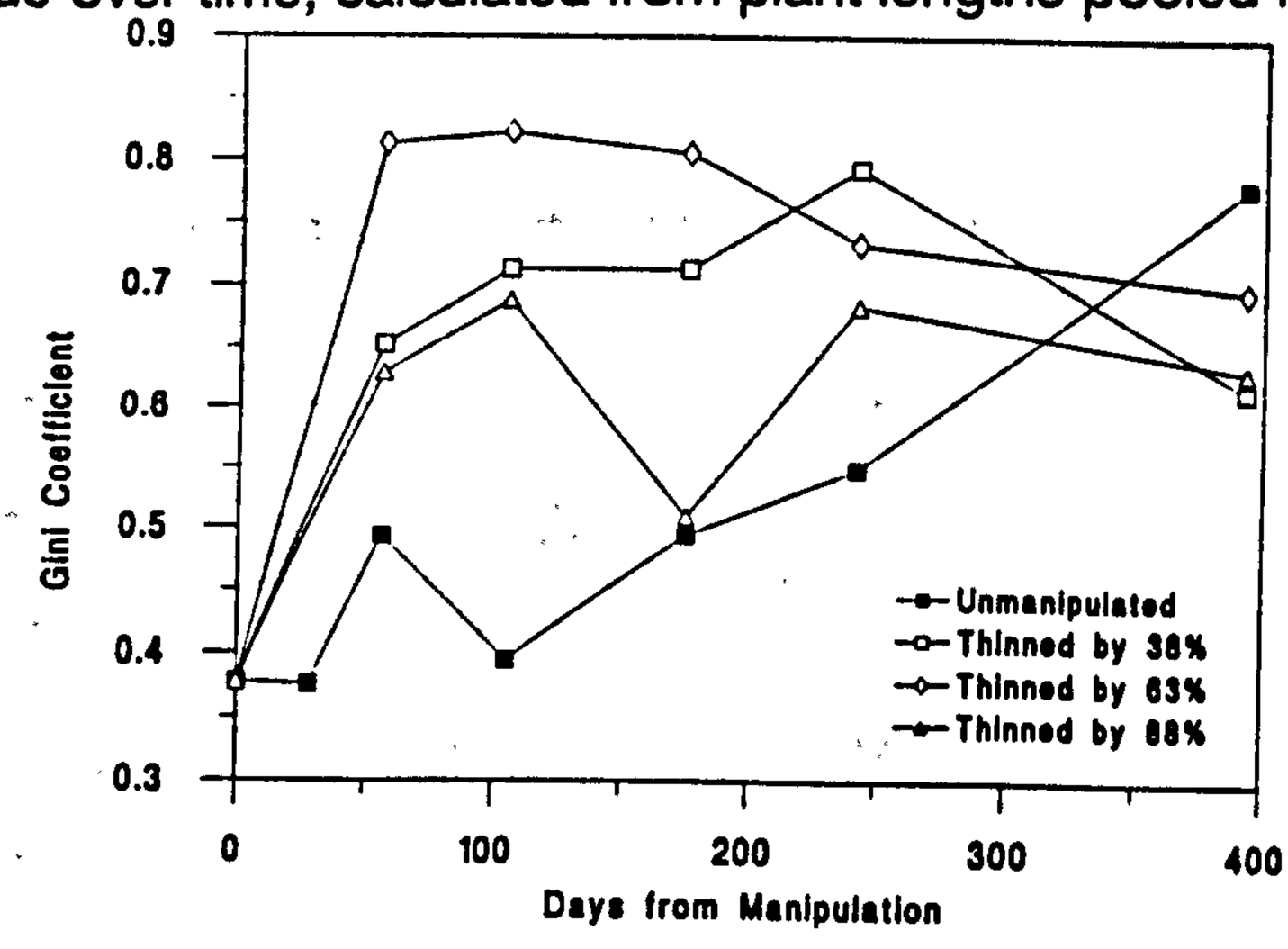


Figure 4.7 Skewness coefficient in four density manipulated populations of *Fucus vesiculosus* over time, calculated from plant lengths pooled from replicates.

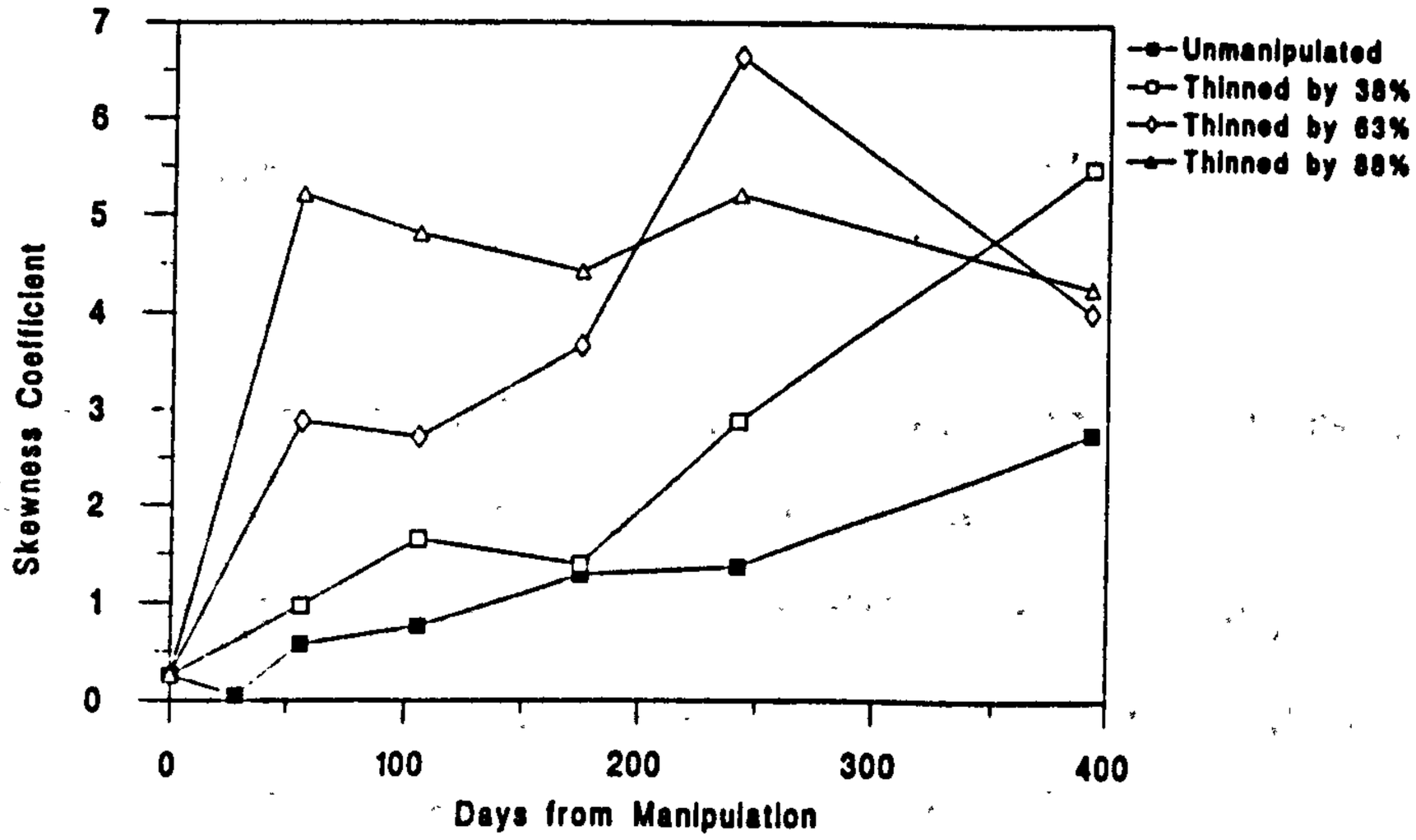


Figure 4.8 Density variation over time in four thinned populations of *Fucus vesiculosus*. n = 4 for all thinned populations, *n* = 3 for unthinned population, n = 2 for last two samples for all populations (bars = ±1S.E.).

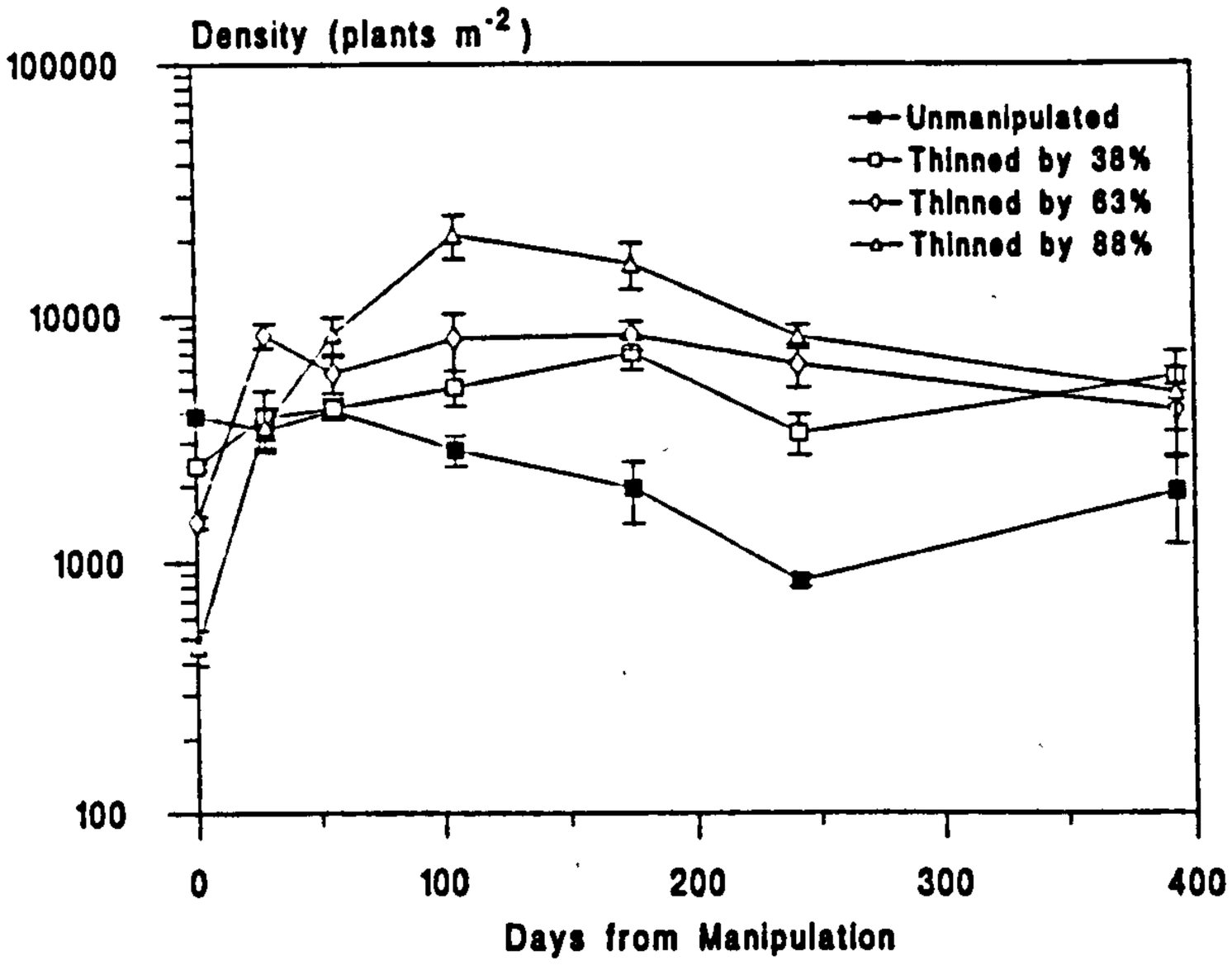


Table 4.3 Analysis of variance of time and initial artificial thinning effects on density in *Fucus vesiculosus*.

Source of Variation	D.F.	M.S.	F.	p value
Time (A)	5	2591275520	8.19	<0.001
Thinning (B)	3	5066054656	16.01	<0.001
A x B	15	1075392384	3.40	<0.001
Residuals	59	316365152		

mean frond length. Thinning had a significant effect on mean frond length (Table 4.4)

Mean maximum frond length was calculated as the mean of the five largest plants in order to compare the effects of density on the growth of largest plants. There was no significant difference (ANOVA F=0.82, *p*=0.498) between manipulations in maximum frond length when all times were considered together (Table 4.4). However, maximum frond length increased in all the

manipulations over time, except the unmanipulated populations which exhibited an initial increase in maximum length followed by a decrease (Figure 4.10). There was no correlation between mean and maximum frond length during the study (Pearson product moment correlation coefficient = 0.021, critical value for $n = 24$ was 0.388), which indicated that the largest plants were not effected by the thinning treatments, while mean plant size was.

Figure 4.9 Mean frond length (pooled replicates) in *Fucus vesiculosus* stands subjected to differing artificial thinning treatments.

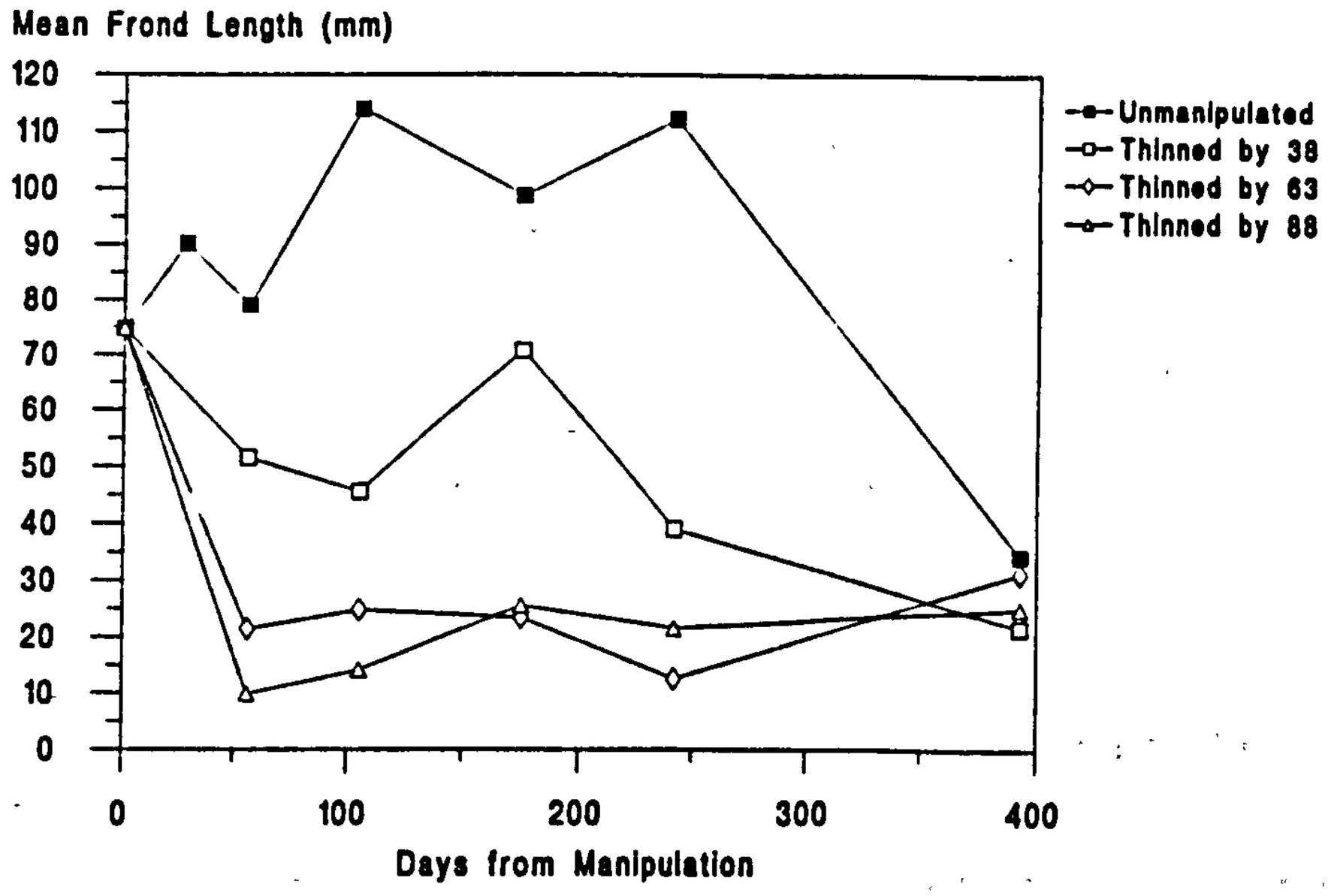
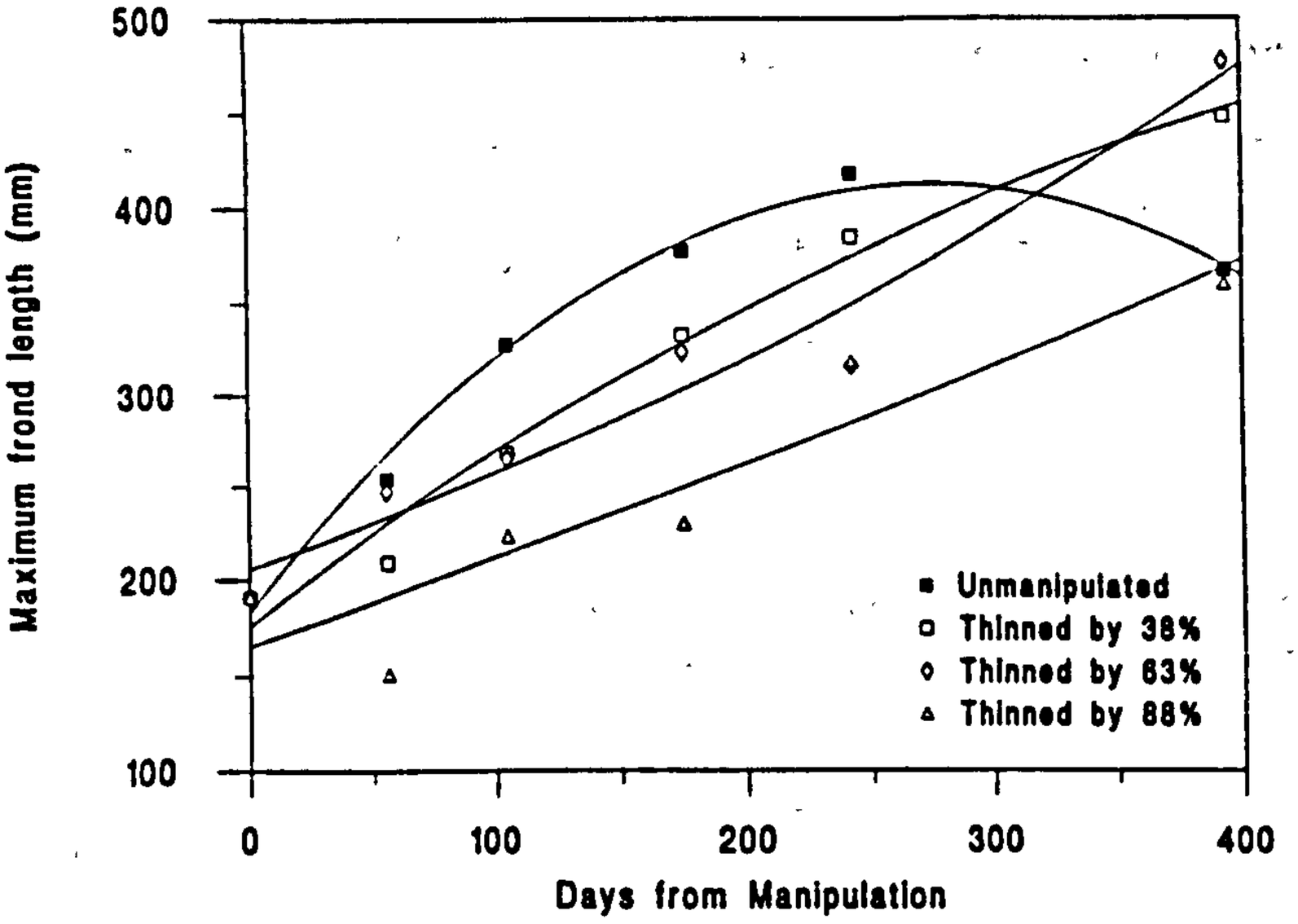


Table 4.4 Analysis of variance of initial artificial thinning on mean and maximum frond lengths in *Fucus vesiculosus*

Source of Variation	D.F.	M.S.	F.	p value
Mean frond length				
Thinning manipulation	3	4128	7.07	0.002
Residual	20	584		
Maximum frond length				
Thinning manipulation	3	6813	0.82	0.498
Residual	20	8315		

Figure 4.10 Maximum frond length (pooled replicates) in *Fucus vesiculosus* stands subjected to differing artificial thinning treatments. Maximum frond length was calculated from three largest plants



Curves fit by second order polynomial regression equations:-

Unmanipulated $y = 183 + 1.67x - 0.00305x^2$,r^2 0.99

38% thinned $y = 176 + 1.01x - 0.00078x^2$,r^2 0.98

63% thinned $y = 205 + 0.47x + 0.00052x^2$,r^2 0.96

88% thinned $y = 165 + 0.45x + 0.00017x^2$,r^2 0.87

4.3.1.4 Standing crop

Standing crop remained significantly different for the four manipulations until 175 days after thinning (Table 4.5, Figure 4.11). ANOVA revealed that time and initial density interacted (Table 4.5). After 175 days there was no significant difference in standing crop between treatments. The unthinned populations reached a maximum standing crop of 1817 g dry weight.m^{-2} after 175 days, while the three thinned populations achieved maximum standing crop later (Figure 4.11).

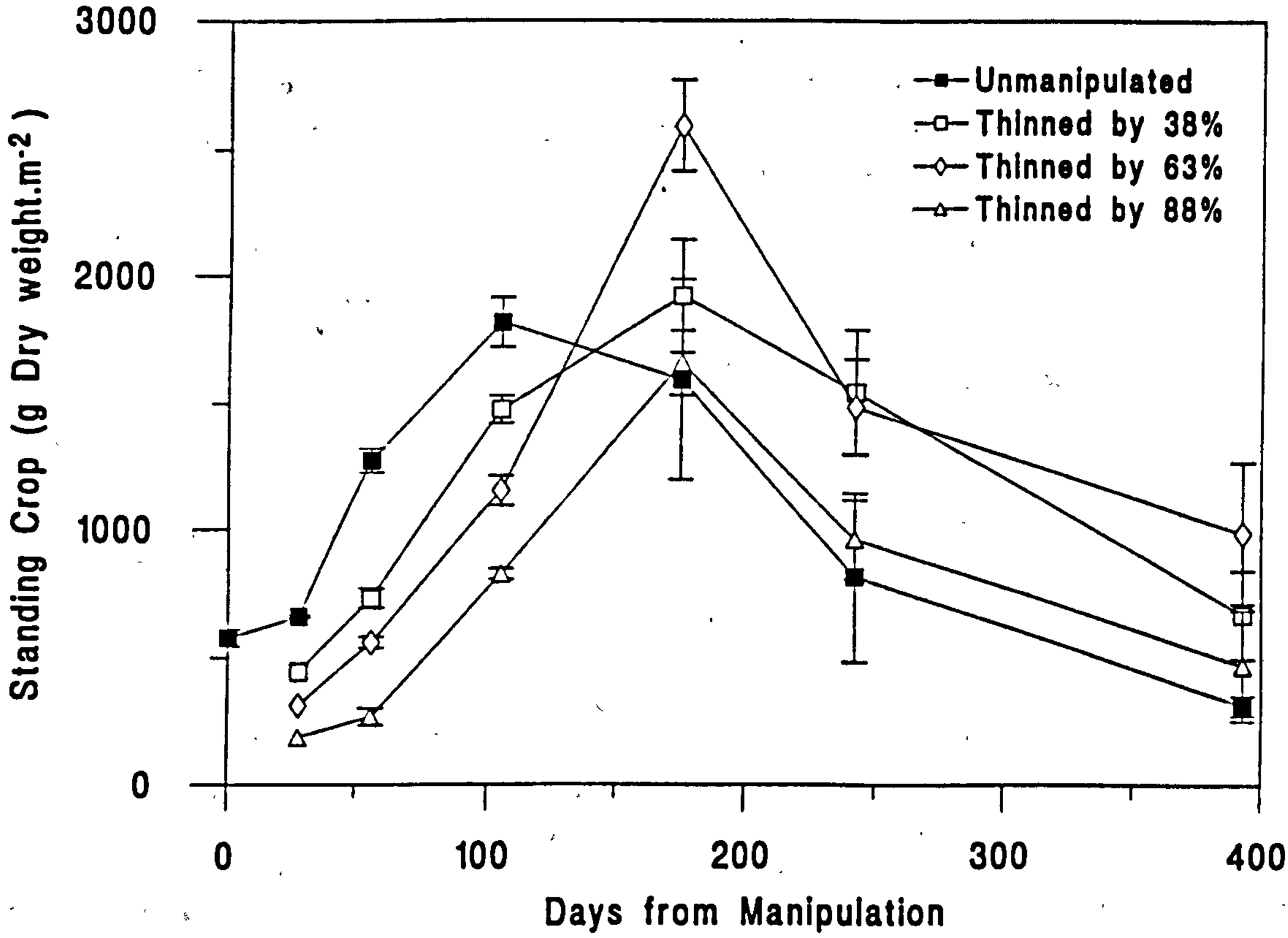
4.3.1.5 Reproduction

Reproductive output as mean number of receptacles per plant (Figure 4.12) and percentage of plants with reproductive tissue (Figure 4.13) was similar. The

Table 4.5 Analysis of variance of initial artificial thinning on standing crop in *Fucus vesiculosus*

Source of Variation	D.F.	M.S.	F.	p value
Time (A)	5	4509452	30.77	<0.001
Density (B)	3	865373	5.90	0.001
A x B	15	371631	2.54	0.006
Residuals	59	146571		

Figure 4.11 Standing crop in *Fucus vesiculosus* stands subjected to differing artificial thinning treatments. Bars = ±1S.E.



more thinned the stand, the fewer receptacles per plant and reproductive plants there were. 51% of plants had reproductive tissue in May 1991.

In terms of the percentage of biomass as reproductive tissue ANOVA on arcsine transformed data revealed that though there was a significant difference through time there was no significant difference between thinning levels and no interactions (Table 4.6, Figure 4.14).

Figure 4.12 Mean number of receptacles per plant in artificially thinned populations of *Fucus vesiculosus*. Bars = ±1S.E.

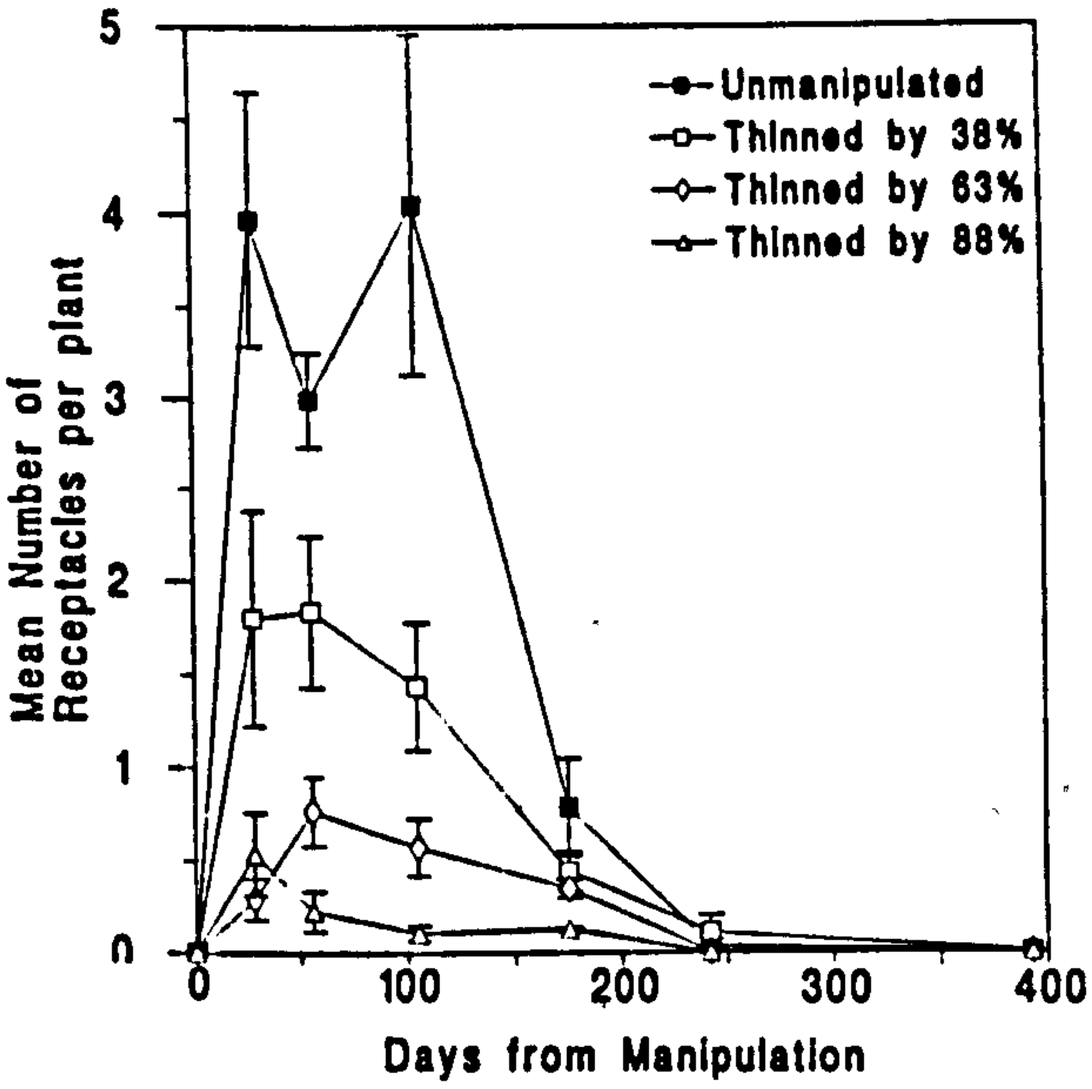


Figure 4.13 Percentage of plants with reproductive tissue in artificially thinned populations of *Fucus vesiculosus*. Bars = ±1S.E.

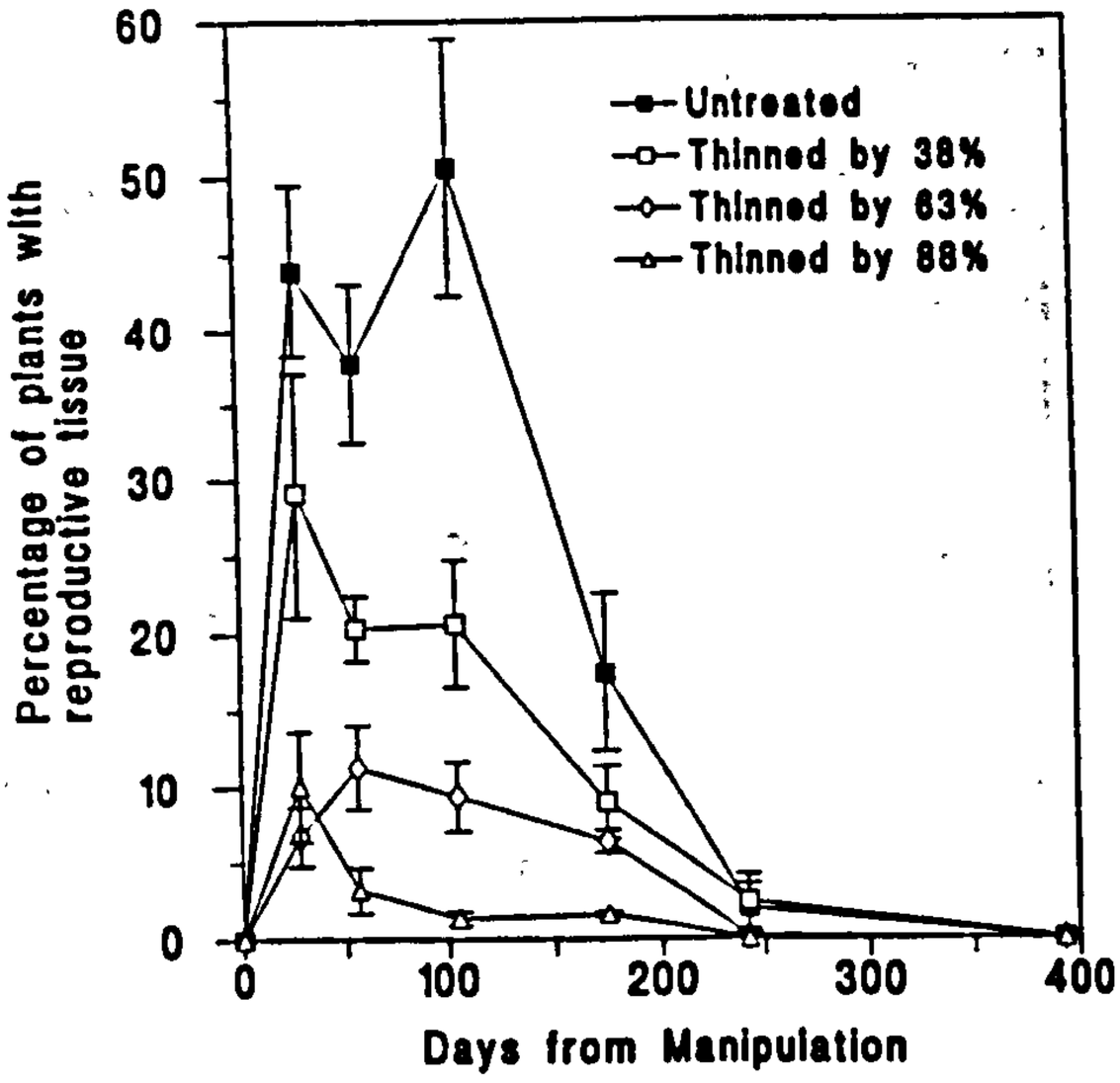


Figure 4.14 Percentage of dry weight as reproductive tissue in artificially thinned populations of *Fucus vesiculosus*. Bars = ±1S.E.

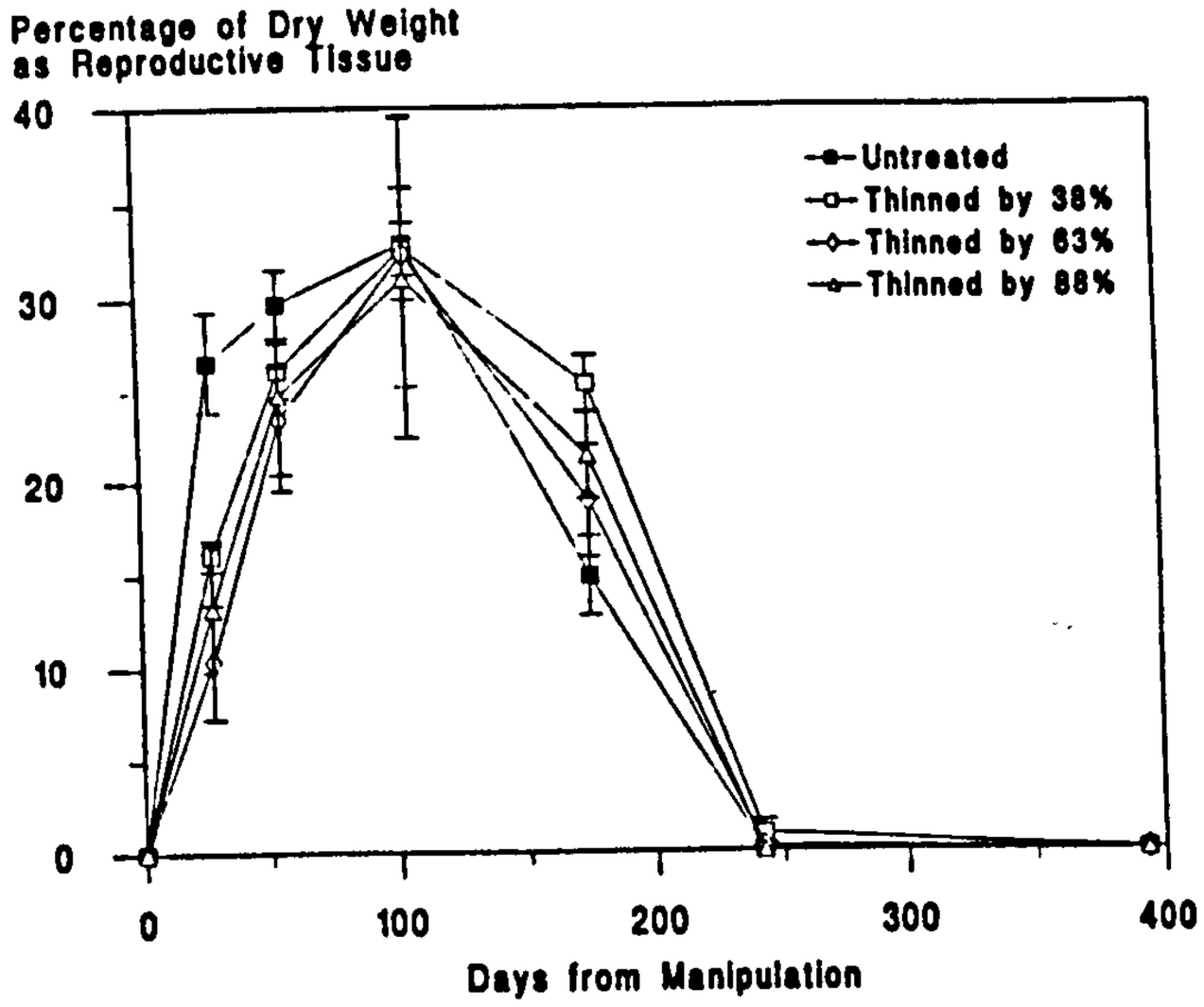


Table 4.6 Analysis of variance of time and artificial thinning treatments on percentage dry weight as reproductive tissue in *Fucus vesiculosus* stands. Data are arcsine transformed.

Source of Variation	D.F.	M.S.	F.	p value
Time (A)	5	0.82864	83.38	<0.001
Density (B)	3	0.01066	1.07	0.368
A x B	15	0.00767	0.77	0.702
Residuals	59	0.0094		

4.3.1.6 Density biomass relationships

As large numbers of small plants joined the populations soon after thinning had been carried out, there was little point in a statistical analysis of thinning trajectories.

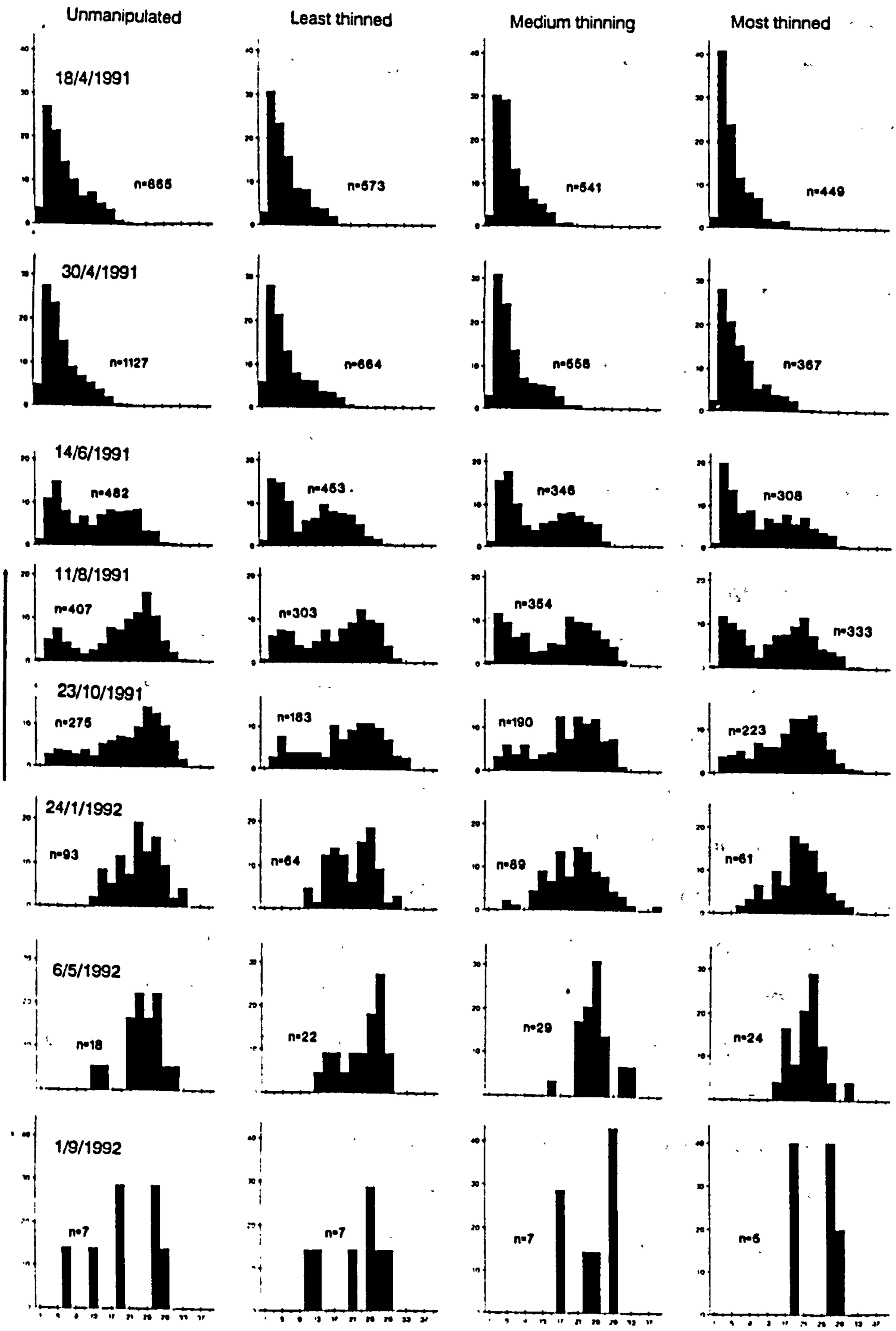
4. 3. 2 Himanthalia elongata

4.3.2.1 Population structure

After manipulation, diameter-frequency histograms for the four manipulations were rather similar, characterised by a small first size class (0-2 mm diameter) of 2-3 %, a maximum second size class (2-4 mm diameter) of 30-40 % and a subsequent fall in proportion of plants in the subsequent diameter size classes (Figure 4.15). This shape indicated a positive skew to the larger button sizes. Two months after thinning the spread of plant sizes had increased substantially with the largest plants 26-30 mm in diameter. It was also evident that a distinct bimodality was developing in all the manipulations. One mode of smaller plants occurred between 2 and 8 mm diameter, and was narrower than the less peaked second mode between 12 and 28 mm diameter. This bimodality was conserved throughout the next four months in all the manipulations while the populations spread and the largest plants got larger. The mode of small plants reduced in size during this period, with a concurrent increase in the proportion of plants in the mode of larger plants until day 181, when the populations became negatively skewed. However, by day 274 most of the small plants had disappeared from the populations, and normality of size distribution was restored, centred on a peak between 20-26 mm which comprised 14-20 % of the population.

The measures of variability and equality of population structure behaved very similarly (Figures 4.16 and 4.17). Both the Gini coefficient (*G*) and coefficients

Figure 4.15 Population structure as diameter frequency histograms for buttons of *Himanthalia elongata*. All scales are identical.



of variation (*CV*) at the start of the experiment were similar for all manipulations (*G* 0.30-0.34, *CV* 0.54-0.61). Over the next month these increased slightly in all manipulations except the most thinned which exhibited a slight fall in both *CV* and *G*. Over the rest of the experiment both *CV* and *G* values fell at a rather constant rate which signified that the sizes of plants were getting less variable in all the populations. There was a tendency for the most thinned population to have the most equal (Figure 4.17) or least variable (Figure 4.16) and the unmanipulated population to have the most unequal/most variable distribution of frond sizes.

Initially all manipulations were positively skewed, with highest skewness exhibited in the unmanipulated populations (1.6) and lowest skewness in the most thinned manipulation (0.9, Figure 4.18). Subsequently skewness coefficients became similar for all manipulations as a result of a slight increase in positive skew in the most thinned populations and decrease in positive skew in the unmanipulated populations. All manipulations exhibited a decrease in positive skewness to normality and subsequently to negative skewness through time (Figure 4.18), though while the three thinned populations moved more quickly to normality then negative skew, the unmanipulated populations did not become negatively skewed so quickly. After reaching maximum negative skewness the skewness coefficient increased slightly in all the manipulations, while by the end of the experiment skewness became very variable between manipulations due to the small number of plants (Figure 4.18).

4.3.2.2 Density and survivorship

After the initial difference in density brought about by the thinning treatments, the density decreased over the next two months in all treatments, and density differences were reduced (Figure 4.19). After 115 days there was no significant difference between densities until the end of the experiment. Twoway ANOVA revealed that there was a significant difference in subsequent density through time, between manipulations, and the significant interaction indicated that

Figure 4.16 Coefficient of variation of button diameter in artificially thinned stands of *Himanthalia elongata* as they develop through time (bars = ± 1S.E.)

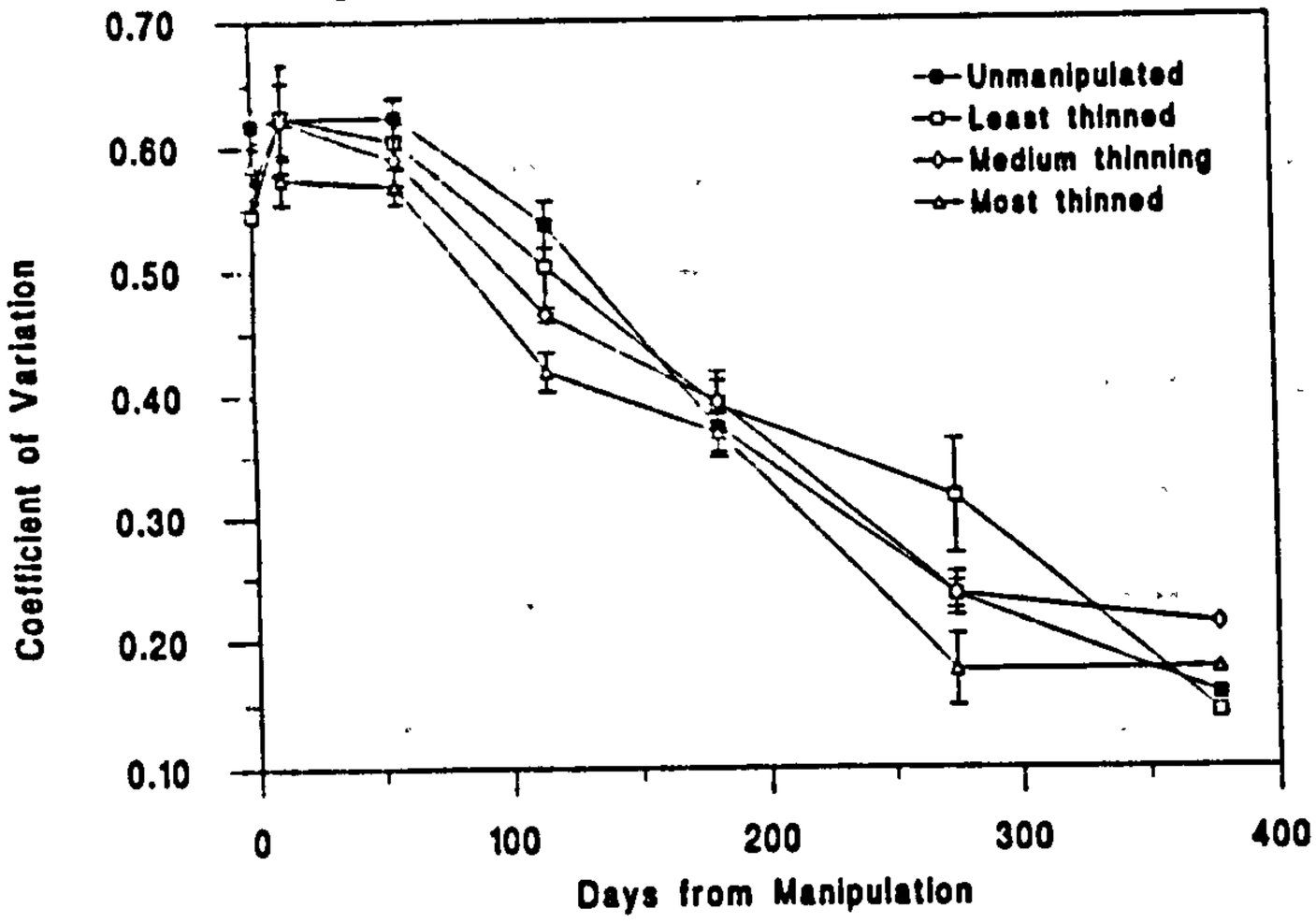


Figure 4.17 Gini coefficient of button diameter in artificially thinned stands of *Himanthalia elongata* as they develop through time (bars = ± 1S.E.)

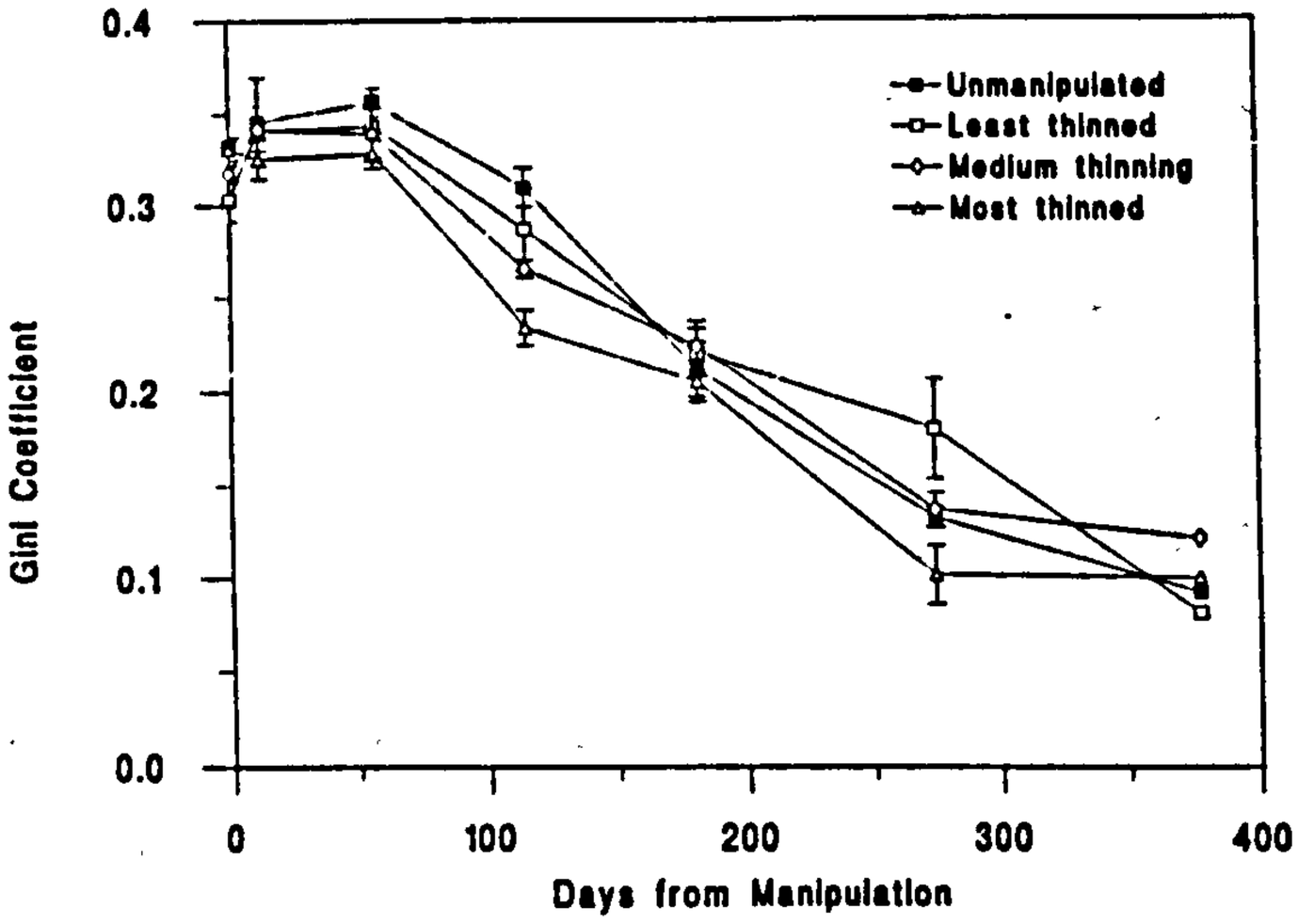
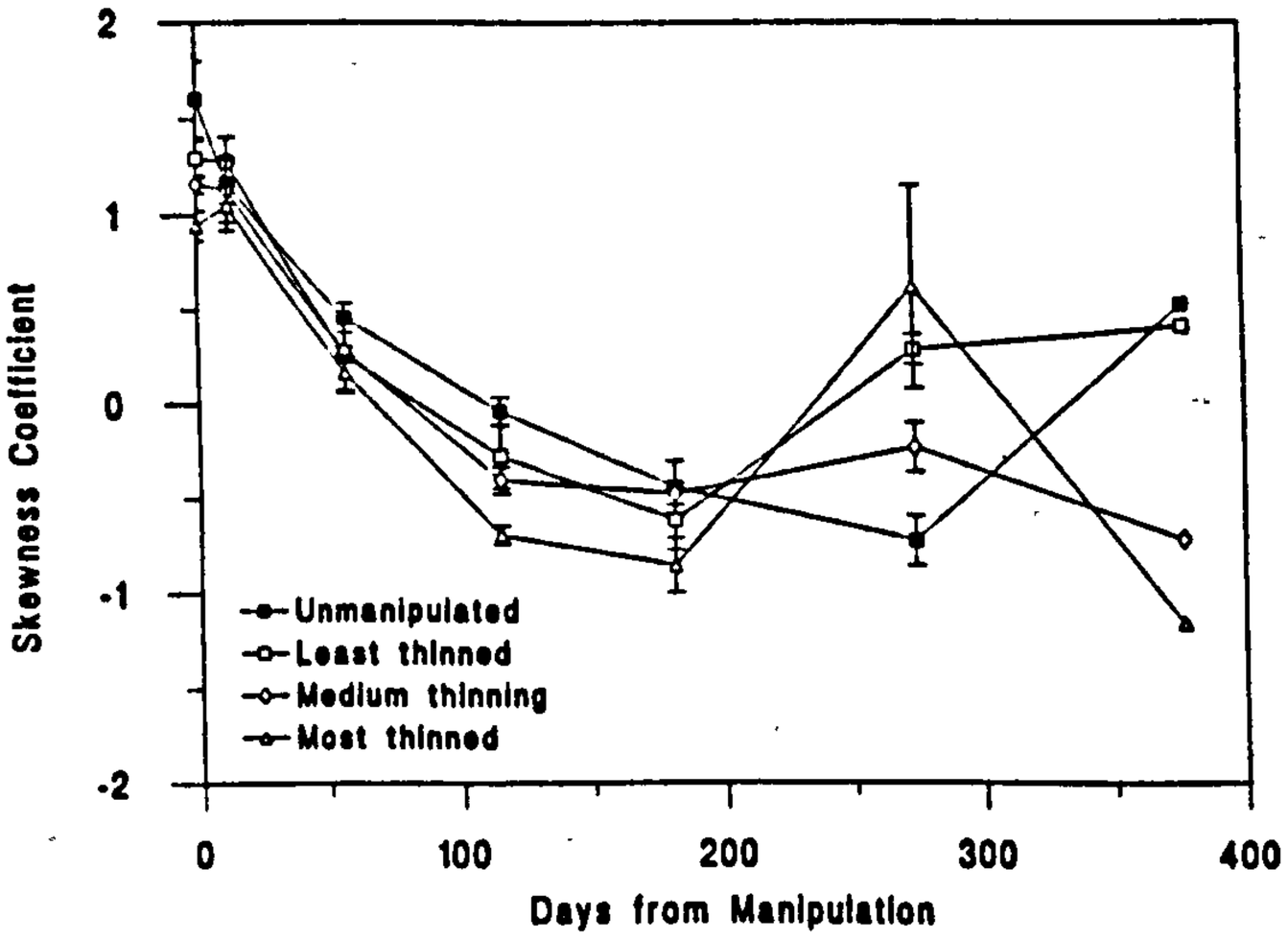


Figure 4.18 Skewness coefficient of button size in artificially thinned stands of *Himanthalia elongata* as they develop through time (bars = ± 1S.E.)



density decreases occured at different rates (Table 4.7). Oneway ANOVA verified a significant difference between densities at the start of the experiment, but not by day 57 (Table 4.8).

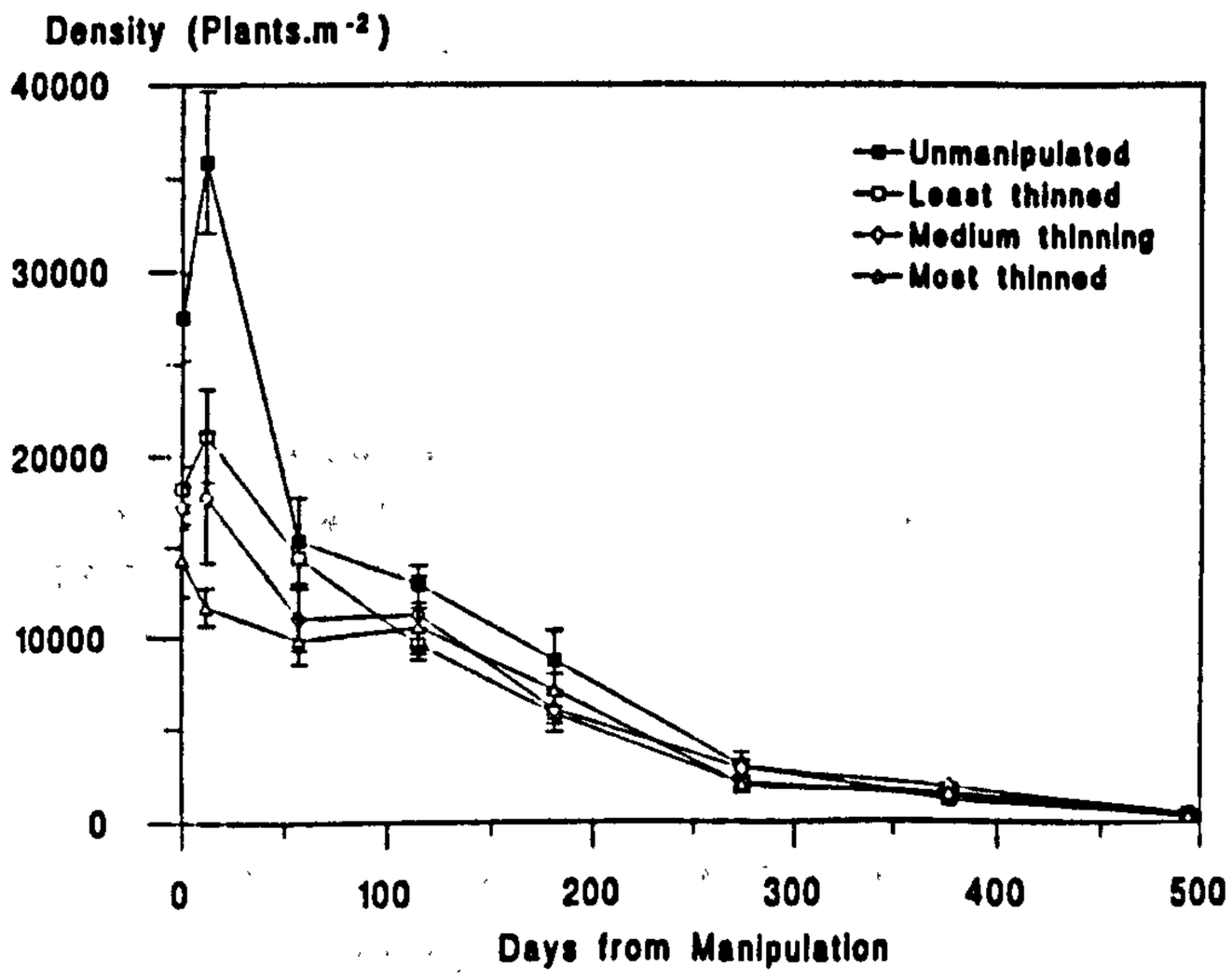
Table 4.7 Analysis of variance of time and artificial thinning manipulations on subsequent density in populations of *Himanthalia elongata*

Source of Variation	D.F.	M.S.	F.	*p* value
Time (A)	7	869437248	59.11	<0.001
Density (B)	3	167924880	11.42	<0.001
A x B	21	50932924	3.46	<0.001
Residuals	81	14709478		

Table 4.8 Analysis of variance of artificial thinning effects on density in *Himanthalia elongata* at the start of the study, and after 57 days

Time	Source of Variation	D.F.	M.S.	F.	*p* value
Start	Thinning manipulation	3	131096192	7.93	0.004
	Residual	12	16536982		
Day 57	Thinning manipulation	3	28211548	1.61	0.240
	Residual	12	17557960		

Figure 4.19 Density variation over time in four artificially thinned stands of *Himanthalia elongata*. Bars = ±1S.E.



4.3.2.3 Button diameter

Mean button diameter increased in all manipulations throughout the study (Figure 4.20). There was a significant (ANOVA) difference over time, between manipulations but no interaction between time and thinning levels (Table 4.9, Figure 4.20). Initially, mean button diameter was very similar for all manipulations. However, some differentiation was exhibited later, as the most thinned stand had a larger average plant size. This differentiation continued and by day 115 it was clear that the most thinned populations had larger plants (13.13 mm diameter) than the unmanipulated populations (11.82 mm diameter).

Maximum button diameter, calculated as the mean of the largest plant from each replicate increased from the start of the study (Figure 4.21, Table 4.9). There was no significant difference between thinning treatments, though there was an interaction between time and density (Table 4.9). Maximum button diameter correlated well with mean button diameter (Pearson product moment correlation coefficient 0.78, $n = 112$, $p = 0.05$), though this relationship was not linear (Figure 4.22).

Figure 4.20 Changes in mean button diameter over time in artificially thinned stands of *Himanthalia elongata*. Bars = ±1S.E.

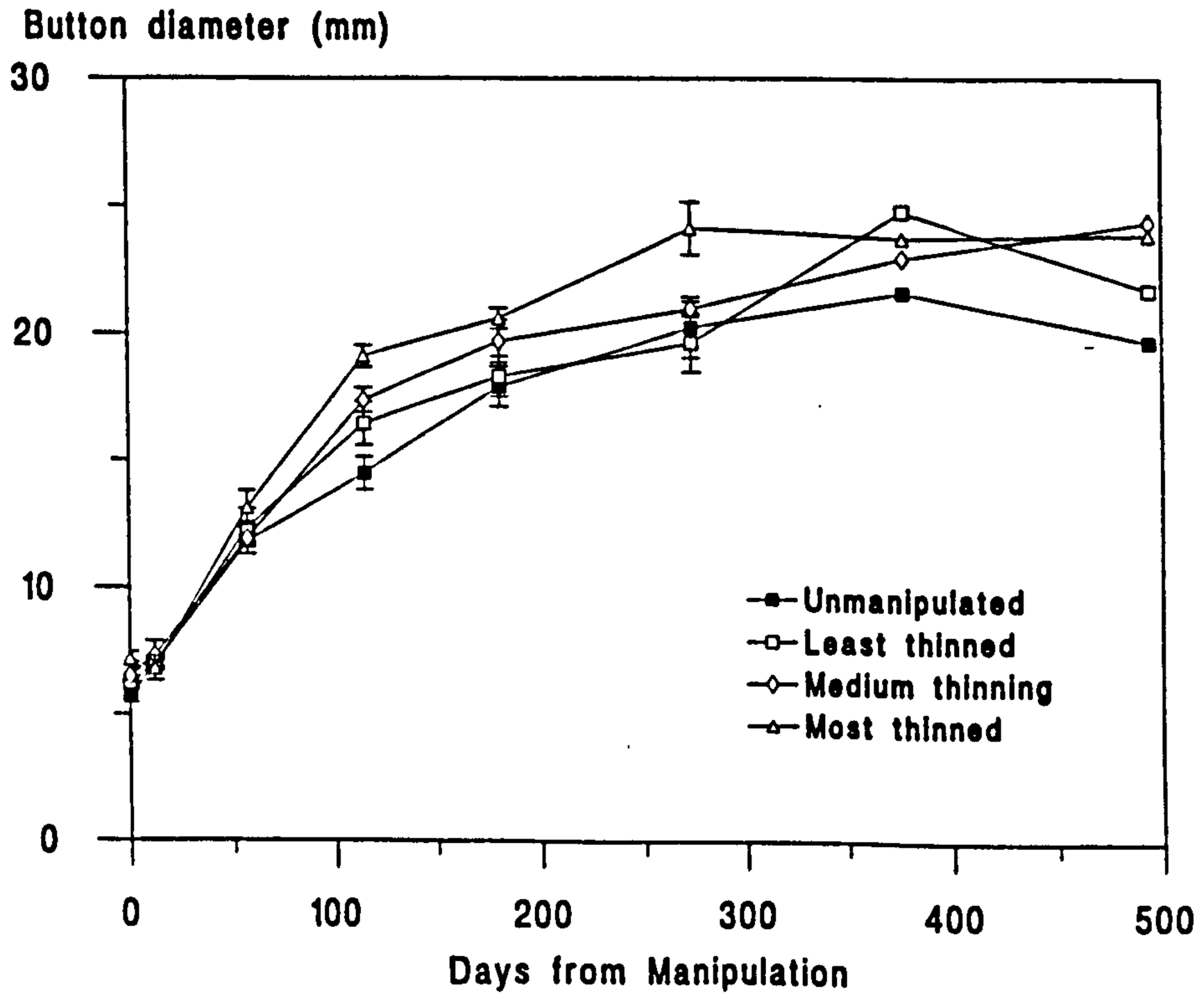


Table 4.9 Analysis of variance of time and artificial thinning effects on mean and maximum button diameter in *Himanthalia elongata* stands

Source of Variation	D.F.	M.S.	F.	p value
Mean button diameter				
Time (A)	7	562.39	175.78	<0.001
Density (B)	3	31.76	9.93	<0.001
A x B	21	5.27	1.65	0.059
Residuals	80	3.20		
Maximum button diameter				
Time (A)	7	336.65	64.51	<0.001
Density (B)	3	13.388	2.57	0.06
A x B	21	9.859	1.89	0.023
Residuals	80	5.218		

Figure 4.21 Change in maximum button diameter over time in artificially thinned stands of *Himanthalia elongata*. Bars = ±1S.E.

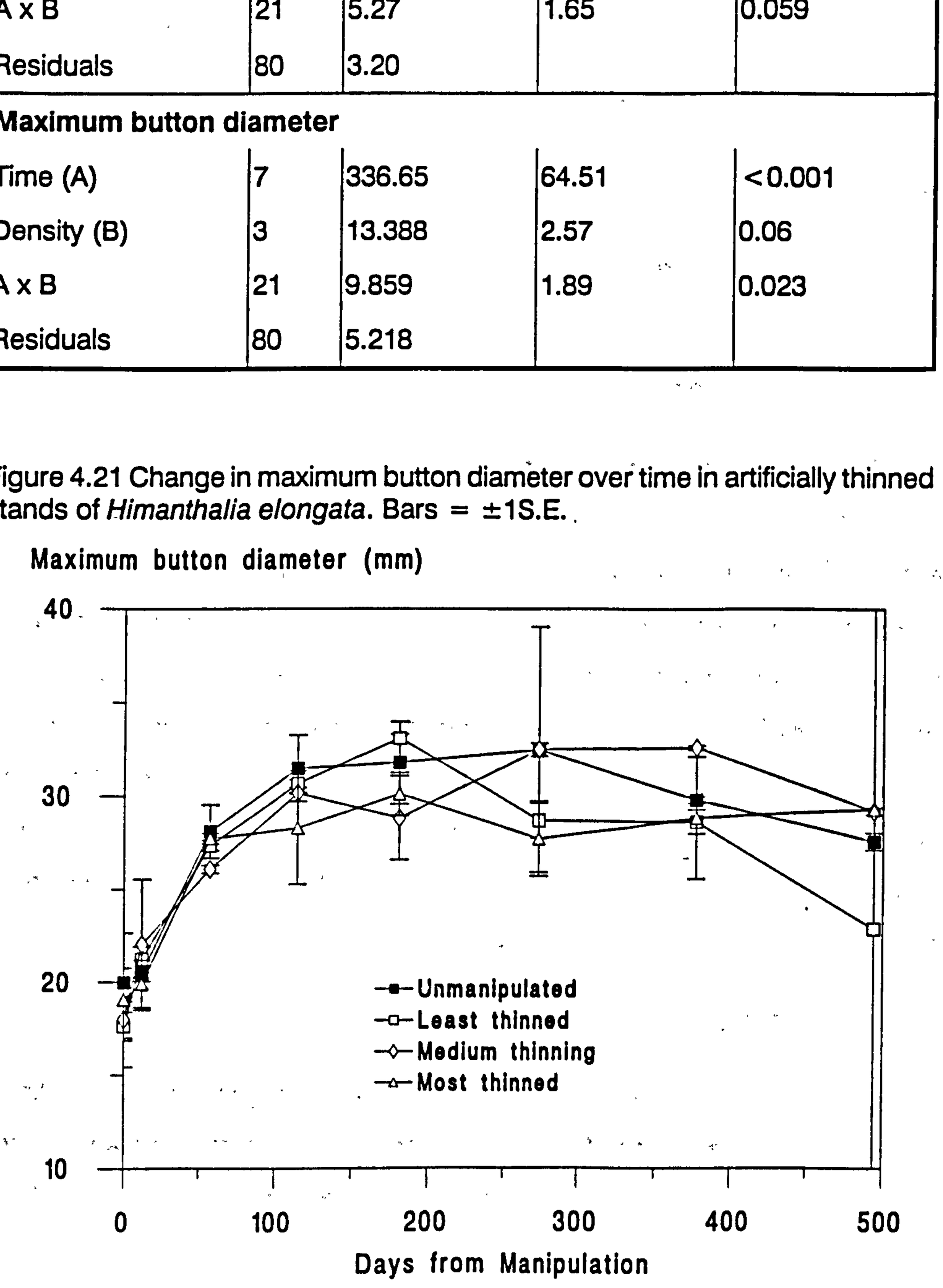
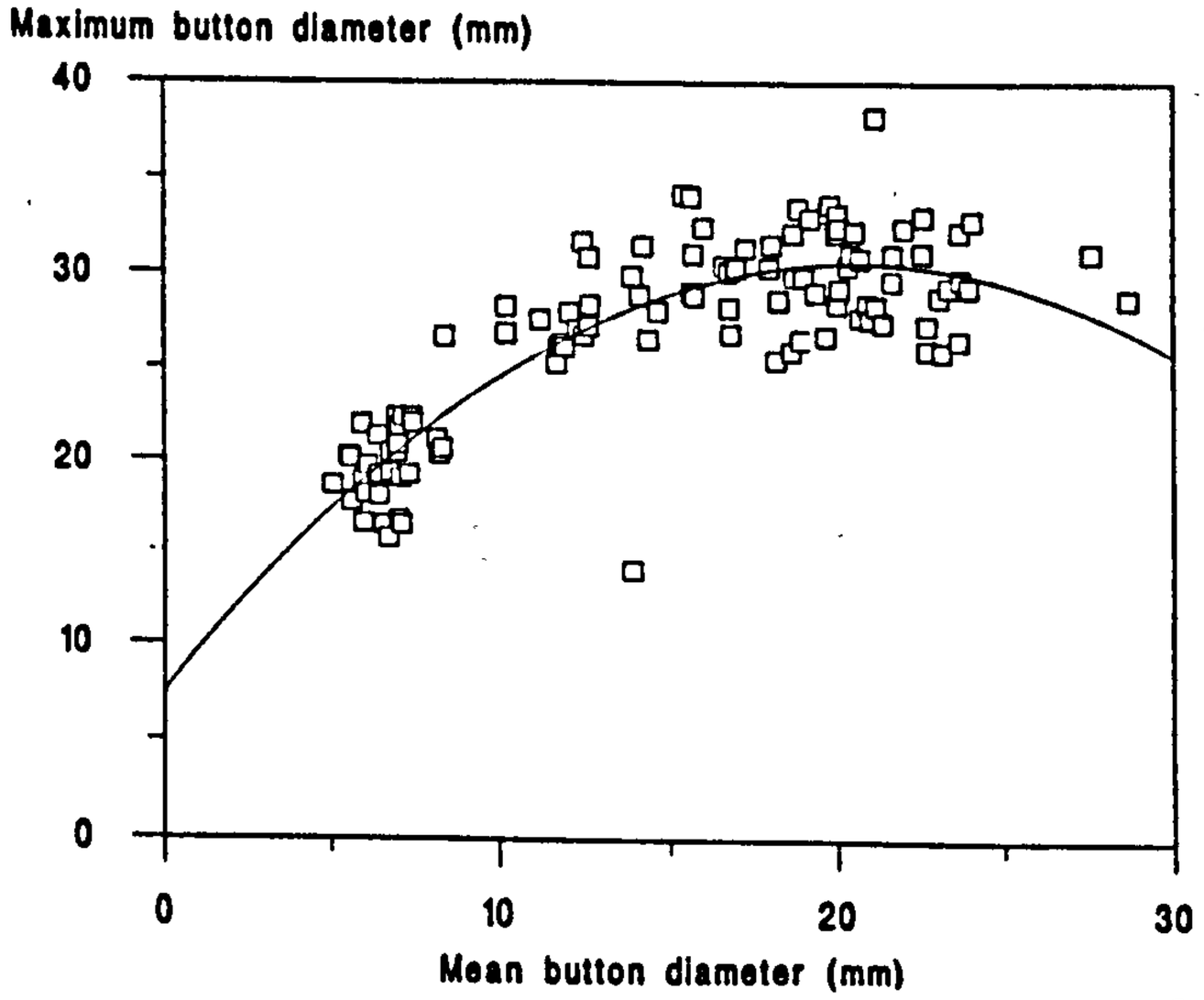


Figure 4.22 The relationship between mean and maximum button diameter in all the thinned populations of *Himanthalia elongata*.



Curve fit by second order polynomial regression $y = 7.44 + 2.24x - 0.06x^2$, $R^2 = 0.73$

4.3.2.4 Standing crop

Standing crop seemed highest in the unmanipulated populations and lowest in the most thinned ones at the start of the experiment (Figure 4.23), and this feature was preserved as standing crop increased until day 181, when the three thinned treatments all had similar standing crop (1098-1186 g dry weight.m^{-2}), though the unmanipulated populations had far higher standing crops (1991 g dry weight.m^{-2}). By day 274 there was no significant difference between treatments (600-1000 g dry weight.m^{-2}). After this time there were substantial increases in standing crop as thongs developed. Twoway ANOVA revealed a significant difference over time, but failed to detect a difference between treatments, and there was no interaction (Table 4.10).

4.3.2.5 Reproduction

Thongs initially became evident in October 1991, 181 days from manipulation. At this time the percentage of plants with thongs was highest in unmanipulated populations (1.22 %) and lowest in most thinned treatments (0 %, Figure 4.24),

Table 4.10 Analysis of variance of time and artificial thinning effects on standing crop development in *Himanthalia elongata*.

Source of Variation	D.F.	M.S.	F.	p value
Time (A)	7	2475.3	19.83	<0.001
Thinning (B)	3	259.4	2.08	<0.110
A x B	21	89.4	0.72	<0.805
Residuals	81	124.8		

Figure 4.23 Change in standing crop over time in artificially thinned stands of *Himanthalia elongata*. Bars = ±1S.E.

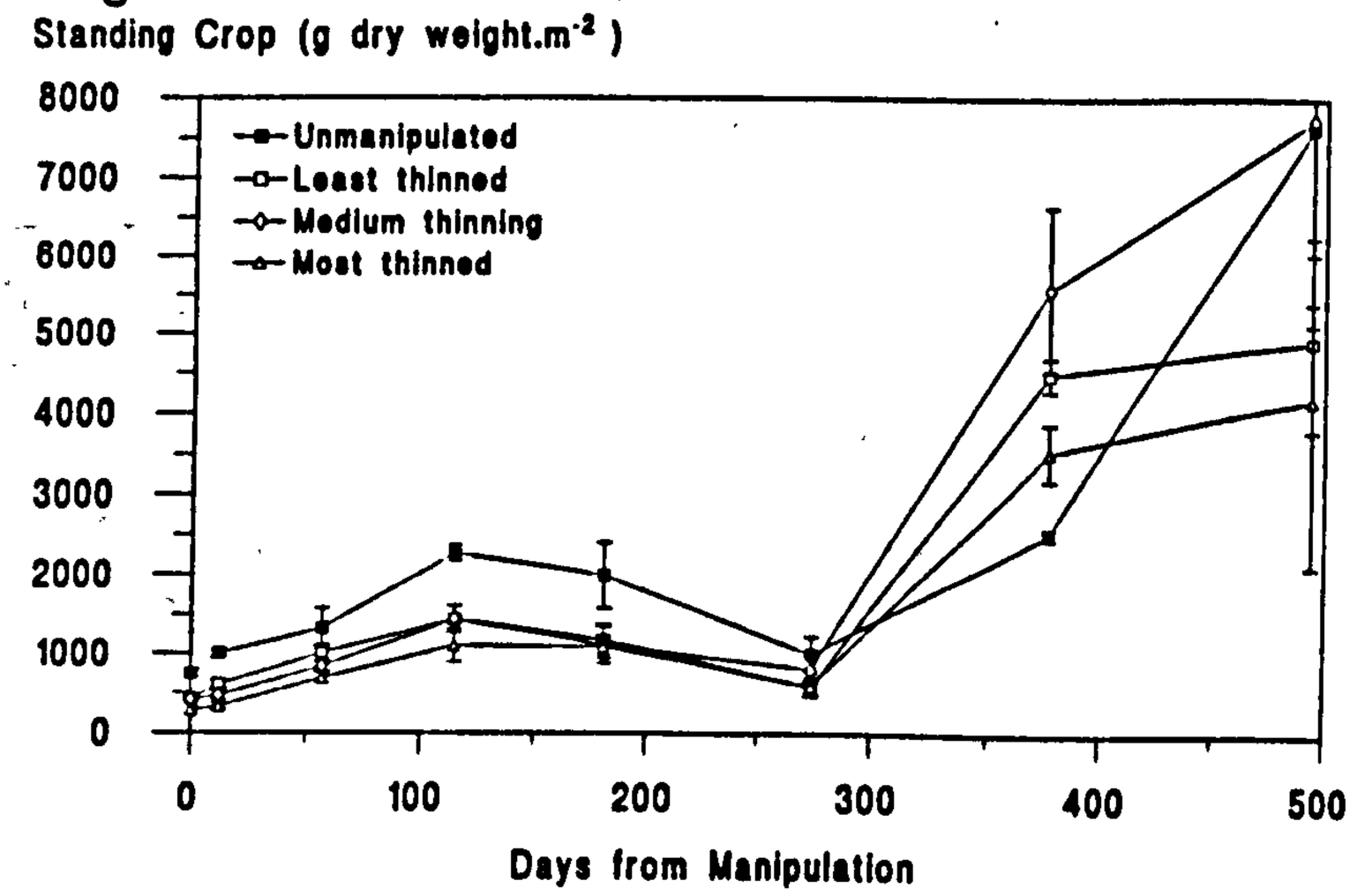
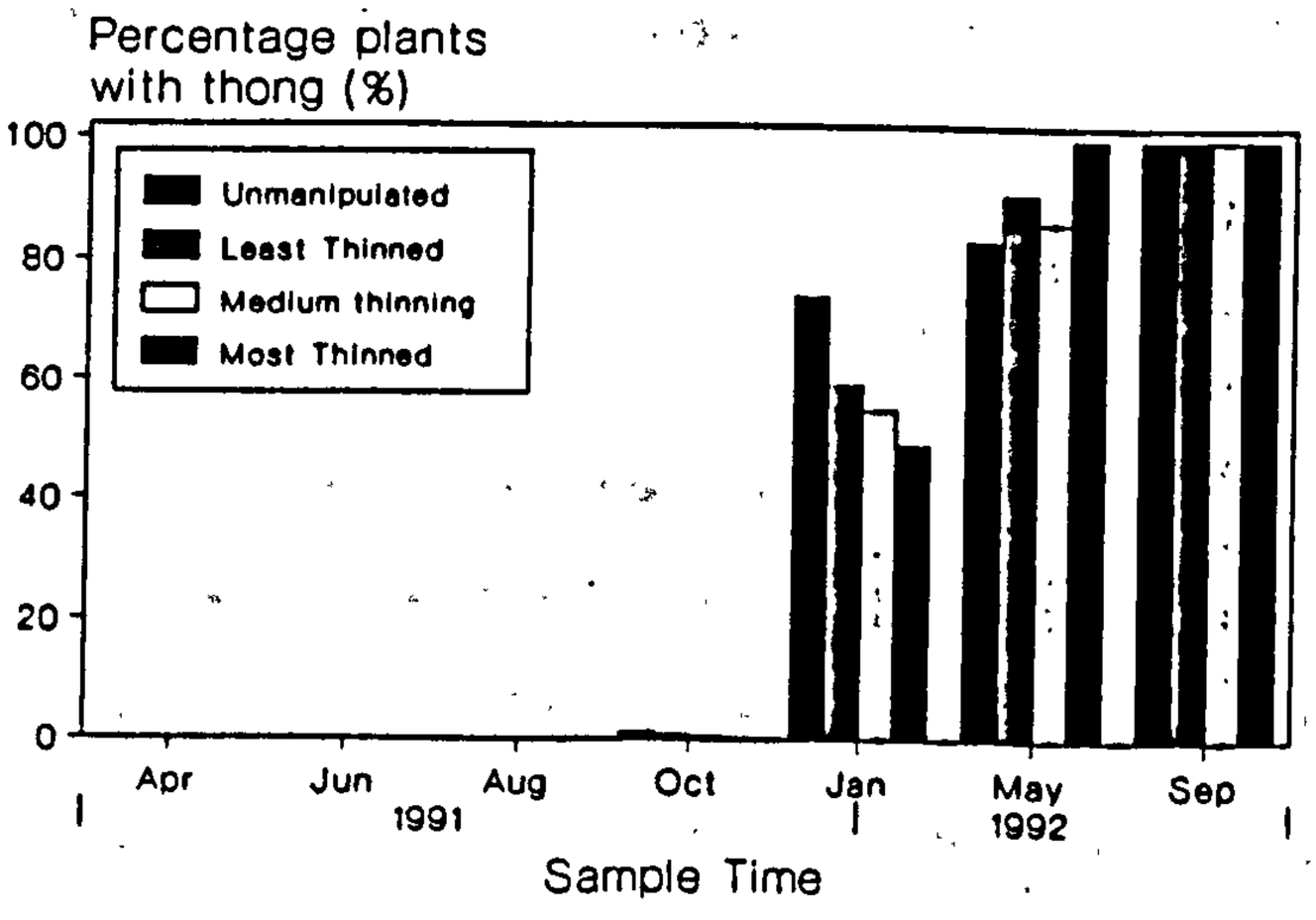
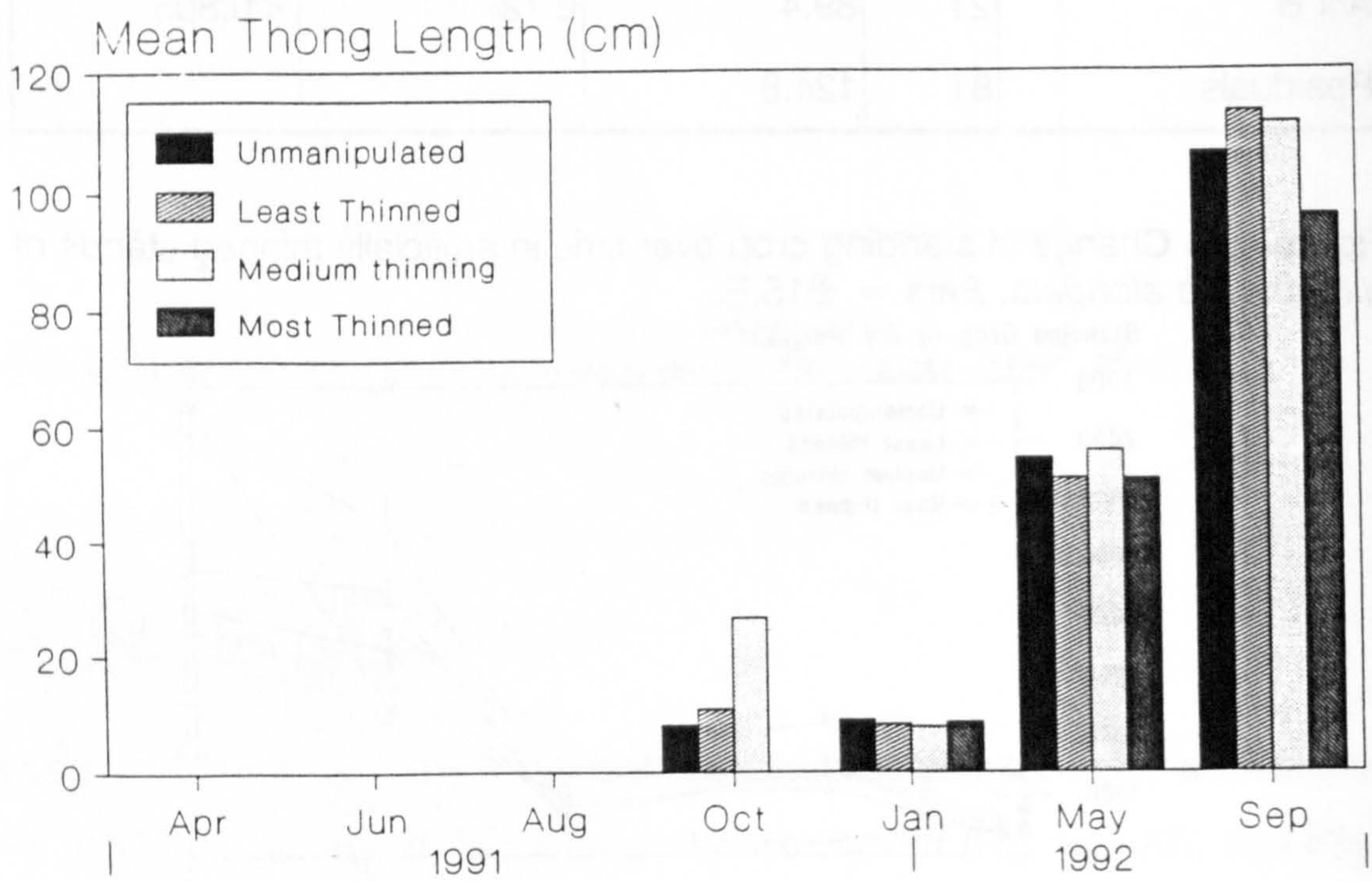


Figure 4.24 Percentage of *Himanthalia elongata* plants with thongs at different times.



but differences were lost by the end of the study. Mean thong length increased substantially from day 274 until day 494 (Figure 4.25). There was no difference in mean thong length between stands given different manipulations

Figure 4.25 Mean thong length of *Himanthalia elongata* over time



4.3.2.6 Density biomass relationships considering individual destructive samples

a) Log_{10} mean plant weight-log_{10} density

The log_{10} mean plant weight to log_{10} density relationship was considered for all data, and separately for button stages and thong stages and compared with the expected slope of -1.5 (Figure 4.26). Using both stages a slope of -1.50 was calculated, which was not significantly different from the expected (Table 4.11). Using button stage data only, the value of -1.88 was also found not to be significantly different from the expected. However, when only thong stage

populations were used, the slope of -2.06 was found to be significantly different from -1.5 (Table 4.11).

b) Log_{10} biomass-log_{10} density

For all data the log_{10} biomass to log_{10} density relationship gave a slope of -0.46, which was not significantly different from the expected slope of -0.5 (Figure 4.27, Table 4.11). However when just button stage or just thong stage points were used, they both gave slopes significantly different from -0.5, of -6.37 and -1.5 respectively (Table 4.11).

4.3.2.7 Density biomass relationships considering means of the data for different manipulations

a) Log_{10} mean plant weight-log_{10} density

When slopes were fitted to means for each of the four manipulations irrespective of stage of plant, none of the calculated slopes were significantly different from the expected -1.5 (Figure 4.28, Table 4.12). However, with increased thinning

Table 4.11 Self-thinning relationship between density, biomass and mean plant weight. Slopes fitted by PCA derived from considering individual stands

	β	Constant	Confidence limits	r (p = 0.05)	Significance
Density mean plant weight (Expected β = -1.5)					
Both stages	-1.503	4.921	-1.647, -1.376	-0.904	♥
Button stage	-1.882	6.522	-2.461, -1.490	-0.676	♥
Thong stage	-2.063	6.524	-2.824, -1.587	-0.799	
Density biomass (Expected β = -0.5)					
Both stages	-0.464	4.774	-0.658, -0.295	-0.445	♥
Button stage	-6.375	29.001	incalculable	-0.044NS	
Thong stage	-1.524	7.948	-11.111, -0.545	-0.380	

♥ indicates that the slope is not different from the expected.

Figure 4.26 Relationship between density (Log_{10} *N*) and mean plant weight (Log_{10} *m*)in *Himanthalia elongata*, using individual data points.

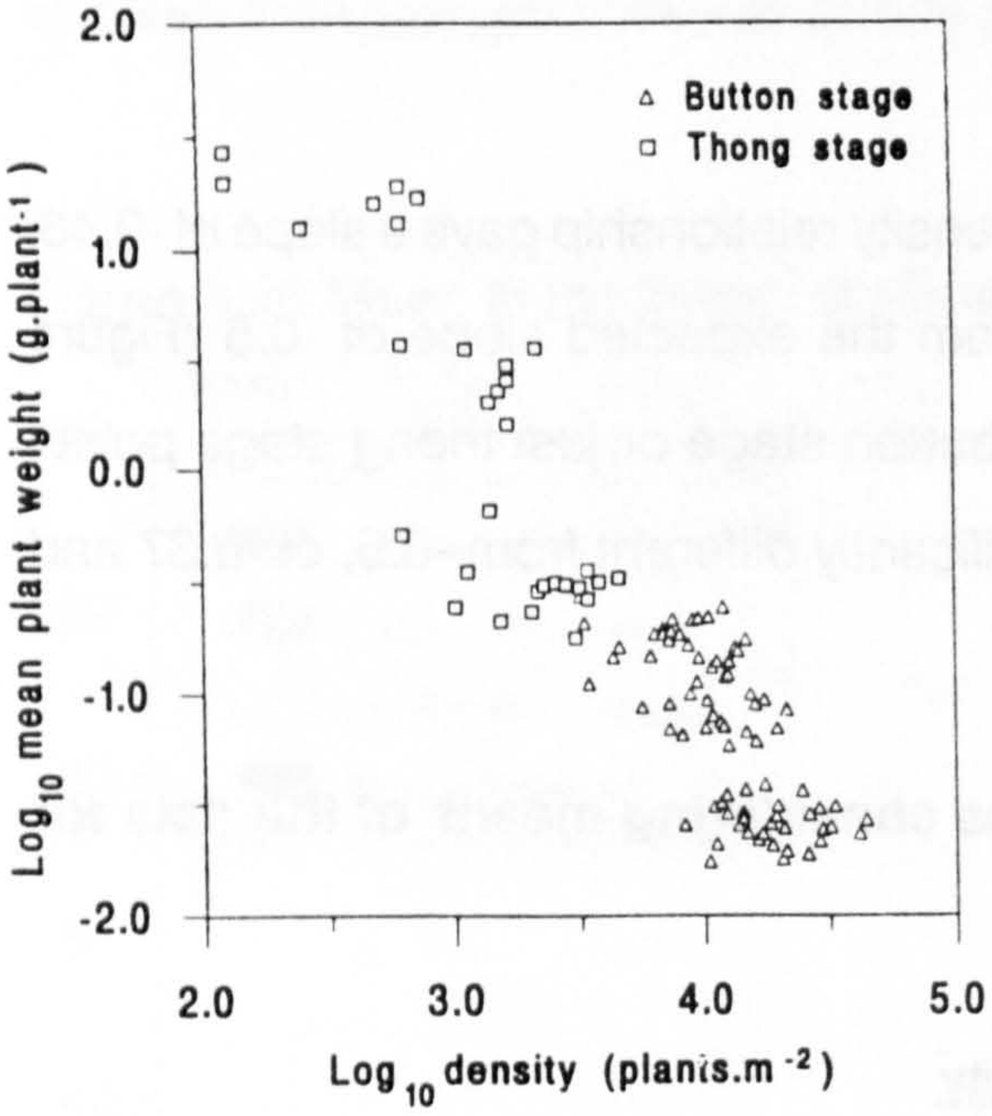
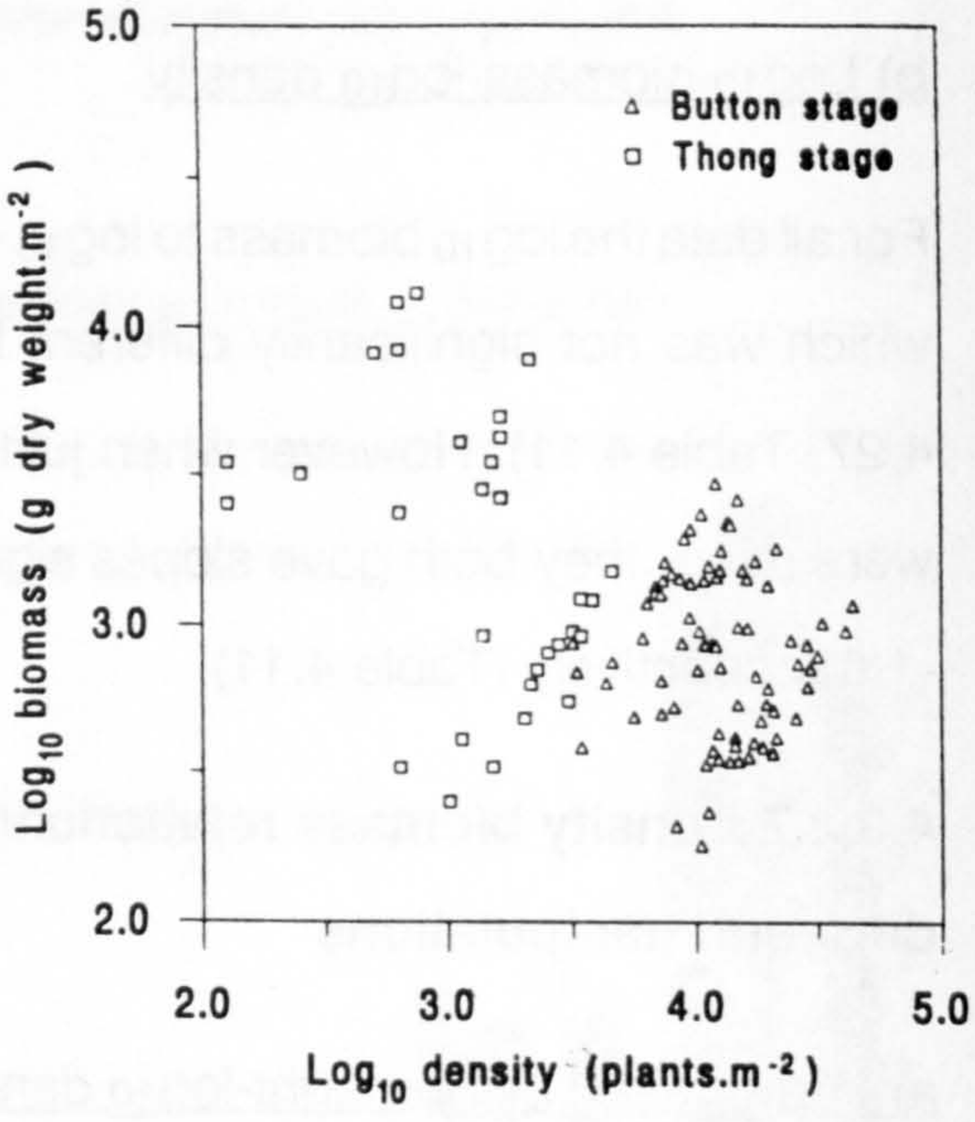


Figure 4.27 Relationship between density (Log_{10} *N*) and biomass (Log_{10} *B*)in *Himanthalia elongata*, using individual data points.



slopes got more steep. When considering the means of the button stage only, the unmanipulated populations were not significantly different from the expected (Table 4.12). However the three thinned populations were all significantly different from the expected, and there was also a steepening of slope with increased thinning. When thong stages were considered alone, the unmanipulated populations were found to be not significantly different from the expected (slope -2.105). The 95% confidence intervals could not be calculated for the other three thinning treatments due to the low numbers of points (Table 4.12).

b) Log_{10} biomass-log_{10} density

None of the manipulations were significantly different from the expected -0.5 when means of both plant stages were considered (Figure 4.29, Table 4.12). Again there was a trend of steepening in the slope with increased thinning (Table 4.12). This trend of steepening slope was also evident when the slopes of the button stage only were considered. However, an inability to calculate confidence intervals for these slopes, and those for the thong stages meant that slopes could not be tested for significance (Table 4.12).

Figure 4.28 Relationship between density ($Log_{10}N$) and mean plant weight ($Log_{10}m$) in *Himanthalia elongata*, means for each manipulation

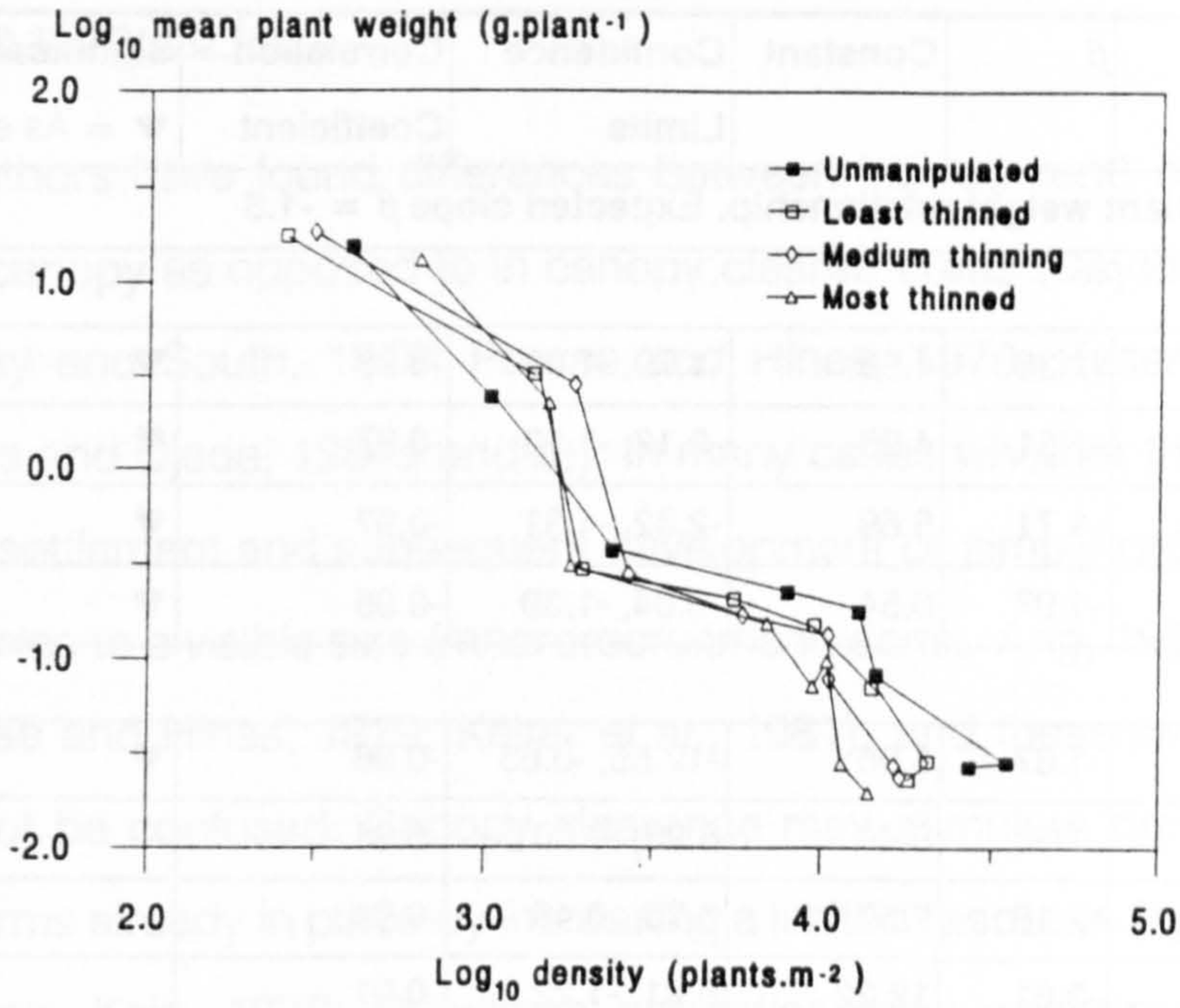


Figure 4.29 Relationship between density ($Log_{10}N$) and biomass ($Log_{10}B$) in *Himanthalia elongata*, means for each manipulation

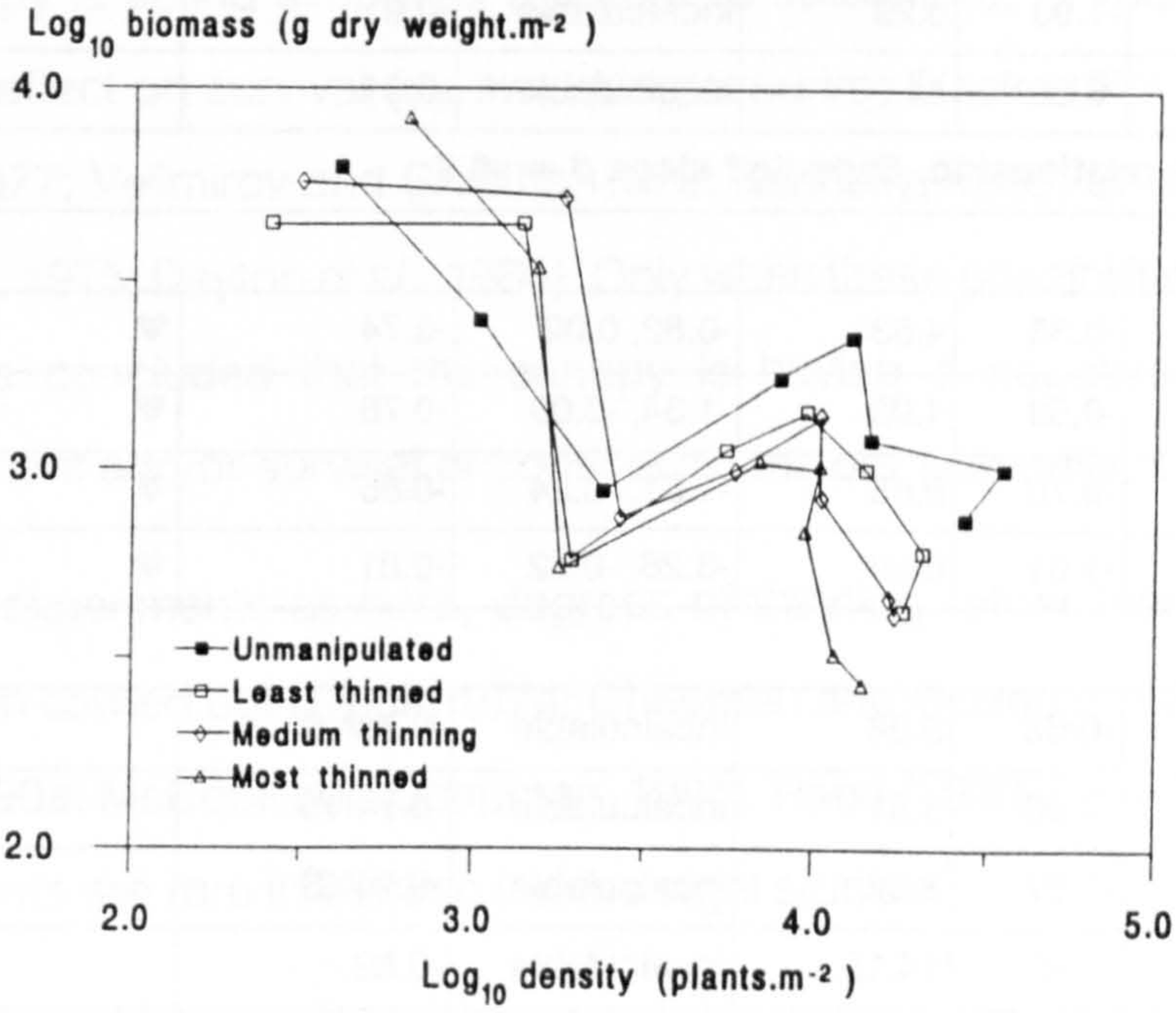


Table 4.12. Relationship between density, biomass and mean plant weight. PCA on slopes of means for different manipulations.

	β	Constant	Confidence Limits	Correlation Coefficient	Significance ♥ = As expected
Density-mean plant weight relationship. Expected slope β = -1.5					
Both stages					
Unthinned	-1.36	4.58	-1.79, -1.06	-0.98	♥
Least thinned	-1.51	4.96	-2.12, -1.13	-0.97	♥
Medium thinning	-1.71	5.69	-2.32, -1.31	-0.97	♥
Most thinned	-1.97	6.54	-3.04, -1.39	-0.95	♥
Button stage					
Unthinned	-1.67	5.96	-12.55, -0.65	-0.96	♥
Least thinned	-1.86	6.44	8.23, -0.50	-0.94	
Medium thinning	-2.16	7.57	3.75, -0.48	-0.92	
Most thinned	-3.61	13.22	6.91, -1.22	-0.91	
Thong stage					
Unthinned	-2.11	6.69	-3.93, -1.35	-1.00	♥
Least thinned	-2.02	6.35	incalculable	-0.89	
Medium thinning	-1.93	6.29	incalculable	-0.91	
Most thinned	-3.66	11.60	incalculable	-0.91	
Density-biomass relationship. Expected slope β = -0.5					
Both stages					
Unthinned	-0.35	4.53	-0.82, 0.02	-0.74	♥
Least thinned	-0.50	4.93	-1.34, -0.00	-0.76	♥
Medium thinning	-0.70	5.65	-1.51, -0.24	-0.85	♥
Most thinned	-1.01	6.69	-3.26, -0.32	-0.81	♥
Button stage					
Unthinned	-0.68	5.98	incalculable	-0.78NS	
Least thinned	-0.90	6.61	incalculable	-0.74NS	
Medium thinning	-1.27	8.02	incalculable	-0.74NS	
Most thinned	-2.85	14.18	incalculable	-0.82	
Thong stage					
Unthinned	-1.11	6.69	-7.85, -0.23	-1.00	♥
Least thinned	-1.15	6.75	incalculable	-0.63NS	
Medium thinning	-1.01	6.54	incalculable	-0.67NS	
Most thinned	-2.88	12.27	incalculable	-0.84NS	

4.4 Discussion

4.4.1 The story so far...

Some authors have found differences between 'recruitment' of conspecifics under a canopy as opposed to in canopy cleared areas (Dayton, 1975; Kain, 1976; Hay and South, 1979; Pearse and Hines, 1979; Keser *et al.*, 1981; Santelices and Ojeda, 1984*a* and *b*;). In many cases whether this recruitment is in fact settlement and subsequent development or simply growth of microscopic forms to a visible size (macrorecruitment, *sensu* Ang, 1991) is not clear (*eg* Pearse and Hines, 1979; Keser *et al.*, 1981), and these two possibilities should not be confused. Canopy clearance may stimulate growth of microscopic forms already in place by increasing a limited resource (*eg* in *Laminaria hyperborea*, Kain, 1976; *Durvillaea antarctica*, Hay and South, 1979 and *Ecklonia radiata*, Kirkman, 1981). However, if settlement has taken place after clearance, experiments must also take into consideration the possibility that the canopy is acting simply as a barrier to settlement, or has a subsequent physical effect on survival (*eg* sweeping/scouring Black, 1974; Menge, 1976; Grant, 1977; Velimirov and Griffiths, 1979; Kennelly, 1989) or chemical effects (Fletcher, 1975; Dayton *et al.*, 1984). Only when these possibilities are excluded can it be concluded that the canopy is having a negative effect on the development and/or survival of conspecific minors (Kennelly, 1989).

In some experiments as here, degrees of thinning rather than total removal have been carried out (Black, 1974; Chapman and Goudey, 1983; Reed 1987; Reed, 1990*a*; McCook and Chapman, 1991). Reed (1990*a*) points out that such experiments are rare in benthic marine algal studies.

Black (1974) found that growth rates of sporophytes in thinned stands of *Egregia leavigata* were significantly greater than in unthinned controls. Again it is not clear whether a sporophyte or gametophyte bank was present before thinning, though it was noted that most new plants (macrorecruits) grew up in cracks where they were protected from scouring. Unfortunately there is no

mention of whether numbers of macrorecruits increased in thinned areas as this was a tagging experiment, but significantly more small plants were found when old kelp plants were removed. Survivorship was higher in lower density plots for the first three months. Chapman and Goudey (1983), studying the annual brown alga *Leathesia difformis*, found that death rates were between two and eight times higher in control plots than thinned areas, and crowding was the most important determinant of mortality rates. Reed (1987) found that artificial thinning significantly increased sporophyll biomass at one site in *Macrocystis pyrifera*. In the most complete treatment of artificial thinning of natural populations Reed (1990a) thinned a population of the subtidal kelp *Pterygophora californica* to four different densities using tagged individuals to follow various population parameters.

4.4.2 The reactions of populations to density

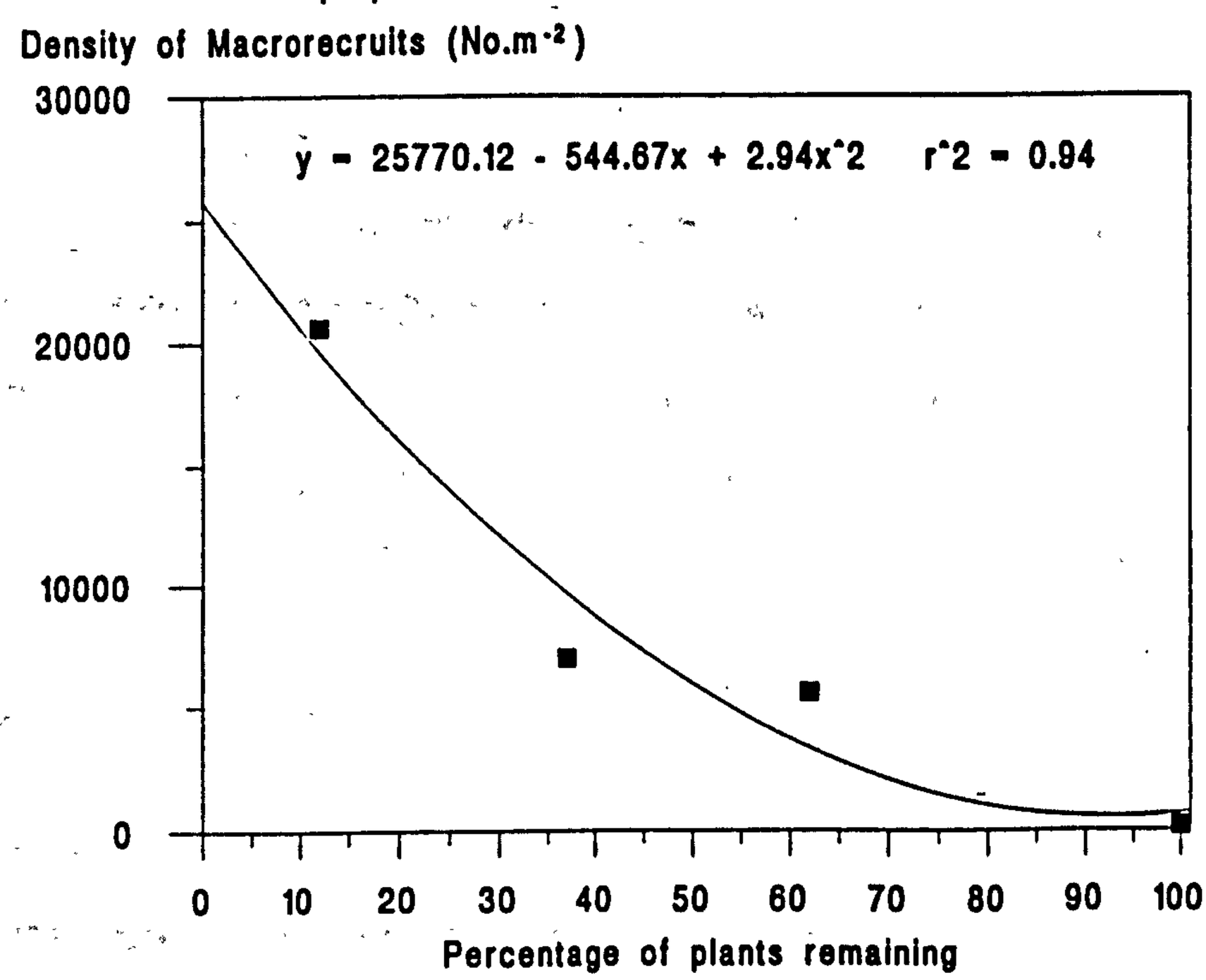
From an examination of the population structure, it was immediately obvious that the two species in this study reacted very differently to artificial thinning. The population structure of *Fucus vesiculosus* was soon dominated by thousands of macrorecruits (plants greater than 1 mm in length) when plants were thinned from the population. The number of macrorecruits was predominantly dependent on the degree of the initial thinning. *Himanthalia elongata*, on the other hand, showed no significant increases in the numbers of macrorecruits following thinning.

That increased thinning should ultimately increase the density is a somewhat paradoxical result, but it demonstrates an important mechanism in *F. vesiculosus*. There can be little doubt that a sporeling bank of microscopic plants exists in this species (see Hoffman and Santelices, 1991 for a review of algal seed banks). Thinnings were carried out at least two months before gamete release could have taken place in that season, and at least four months since the previous gamete release (Knight and Parke, 1950 and personal observation). A marked increase in macrorecruits took place in September 1991 which

must have originated from an April release, suggesting a lag period of five months between settlement and the appearance of plants. This contradicts Knight and Parke (1950) who cleared and burned areas and estimated that settled spores would be visible to the naked eye as germlings in a fortnight. Their areas were completely clear of canopy and a comparison of their data and this study suggests that even a severely thinned canopy can retard development of conspecific germlings quite considerably.

With a plot of the relationship between maximum post-thinning density against percentage of all plants remaining after thinning, we can extrapolate to estimate the potential bank of small plants (Figure 4.30) as about 26000 small plants .m^{-2} which were available in the microscopic spore/germling bank.

Figure 4.30 The relationship between thinning and the subsequent appearance of macrorecruits in the population



There is a variety of evidence from this study that suggests that a spore/germling bank exists for *F. vesiculosus* :

1. The first size class (1-10 mm) in unmanipulated populations remained larger than expected (Chapter 3), probably because a number of macrorecruits are

constantly emerging from the microscopic bank, or because the plants in this size class constitute a 'small-plant bank' with suspended development in their own right.

2. Thinning manipulations encouraged a substantial increase in density of macrorecruits at a time when no conspecific plants had been reproductive for at least four months.

3. A greater degree of thinning encouraged more macrorecruits to develop and to develop faster.

4. The growth and development of spores under a canopy, even a thinned one, was retarded substantially in the 1991 settlement season.

Recruitment stimulated by thinning or clearance has previously been found in fucoids. Knight and Parke (1950) cleared areas throughout the year and found that season made no difference to large numbers of macrorecruits in *F. vesiculosus* or *F. serratus*. They also cut mature populations of both species down to 30 and 15 cm in length and found that large numbers of small plants developed in severely pruned areas. McCook and Chapman (1991) completely cleared or reduced by 85 % a *F. vesiculosus* canopy. Recruitment was inhibited by a full canopy, while partial or total canopy clearance enhanced recruitment. Robertson (1987) hinted that recruitment is proportional to canopy biomass in *Fucus spiralis*. Cousens (1985) found that canopy removal resulted in an increase in growth rate, lateral initiation and colour change in *Ascophyllum nodosum*.

Lubchenco (1986) found that in the absence of herbivores recruitment was inhibited under the canopy of *F. vesiculosus*. Lubchenco (1983) showed that *F. vesiculosus* plants less than 3 cm long were susceptible to littorinid herbivory. I regularly removed herbivores in this study (though there were very few littorinids), so they could not have played a significant part. Chapman (1989) found that herbivores had no significant effect on juvenile density, but removal

of the *Fucus spiralis* canopy increased juvenile density greatly. Chapman (1990*b*) found that juvenile density of *Fucus distichus* increased only in the absence of herbivores when the canopy was removed. There was also an interaction of canopy and grazers, though it is not clear whether a test of the effect of canopy clearance on grazers was carried out. Ang (1991) and Ang and De Wreede (1992) found a germling bank in *Fucus distichus*.

The *H. elongata* population studied bore little relation to its fucoid relative *F. vesiculosus* in its response to thinning. That no perceptible increase in density resulted from thinning suggests that *H. elongata* populations do not suppress microscopic individuals, or that if they are suppressed, mortality is high in this fraction. Moss *et al*. (1973) concluded that *H. elongata* germlings are susceptible to silting which cuts down light and ultimately kills them. It was noted at the time of thinning that the closely packed button stage populations harboured a large amount of detritus and silt. These, together with the obvious light intercepting ability of the button 'canopy' probably precluded a germling bank in this species.

4.4.3 The sizes of plants and the hierarchy of exploitation

In *F. vesiculosus*, thinning resulted in a large macrorecruitment, and these small plants were responsible for considerably lowering the mean frond length of the population. Mean plant size can increase as a result of mortality of small plants rather than growth of all, whilst the thinning manipulations of *F. vesiculosus* demonstrated the converse, that an increase in the number of small plants decreases mean plant size. *H. elongata* developed an increase in mean plant size through time. The growth of the largest plants in both *F. vesiculosus* and *H. elongata* was unaffected by thinning. The decrease in maximum plant size found at the end of the study of *H. elongata* may be due to the selective removal of larger plants by wave action, or the abrasion of buttons as thong bearing *H. elongata* plants pivot between holdfast and button top when swept up and down the shore (personal observation). One might expect the largest plants to

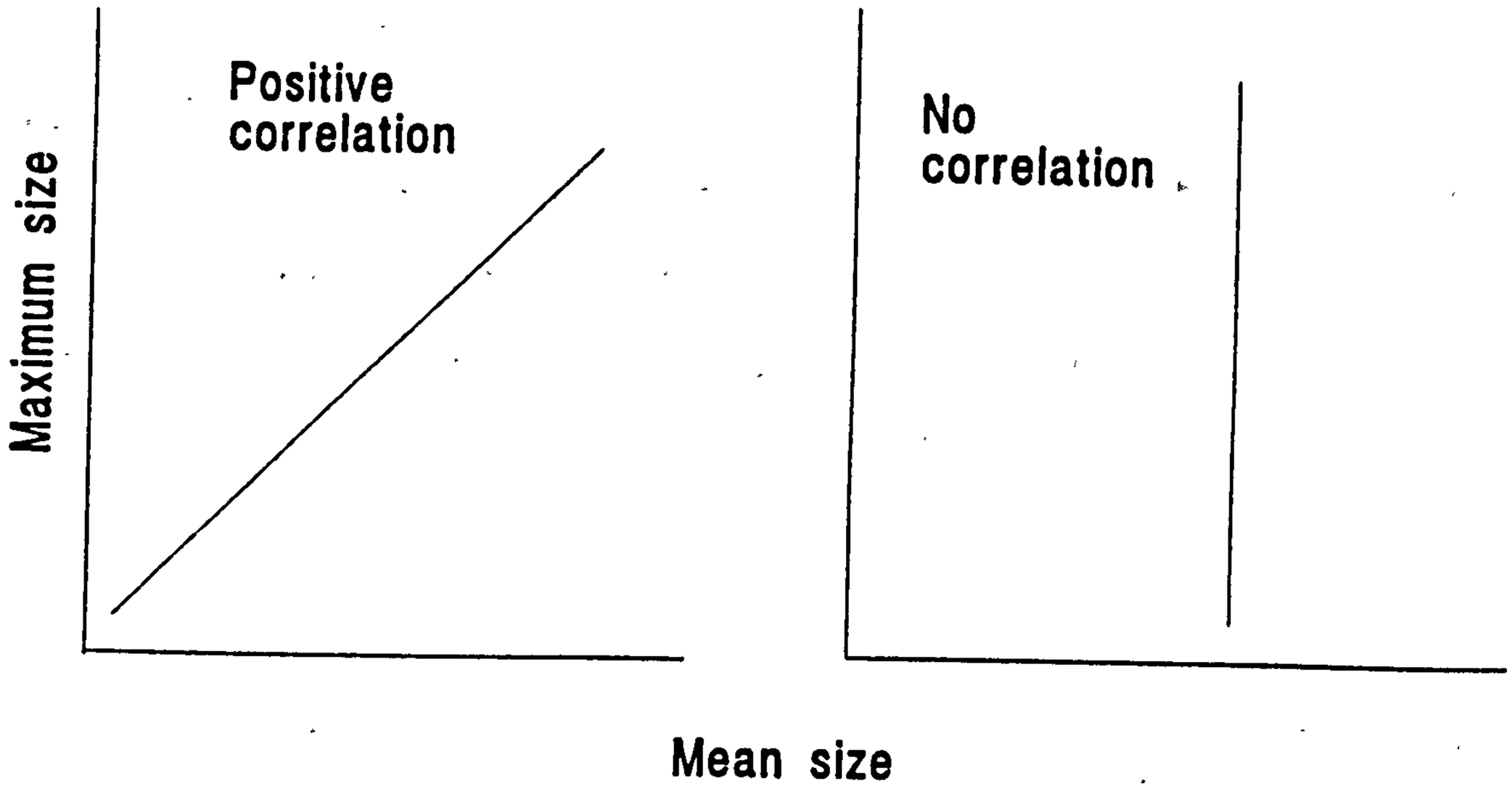
be unaffected by the density of their neighbours as they are the competitive dominants, and should not be influenced by asymmetrical competition (*ie* for light, Thomas and Weiner, 1989). This attribute may make a comparison of mean versus maximum length a useful descriptor of a populations reaction to density manipulation. Certainly in *H. elongata*, a positive correlation was found between these two variables, while in *F. vesiculosus* no correlation was found. No correlation may be expected in a population consisting of many small plants because growth of the largest plants will have little effect on mean plant size as there are so many small plants that the denominator will be large. Figure 4.31 diagrammatically describes this relationship.

Maximum frond length did increase in *F. vesiculosus* over time, and the rate of increase in maximum frond length was greater in the unthinned populations. This would suggest that some positive density dependent effect (not considering the recruits) was operating, at least in the large plants. Possibilities include selective removal of large plants by waves coupled with greater susceptibility to wave action in thinned populations. Alternatively, a phenotypic plastic response may have been brought about by a change in an environmental parameter in proportion to the degree of thinning. Certainly fucoids are highly variable (Norton *et al.*, 1981; Russell and Fielding, 1981; Norton *et al.*, 1982).

While the expected increase in mean frond length did not take place in manipulated *F. vesiculosus*, in *H. elongata* it was obvious. Mean button diameter was significantly higher in thinned populations of *H. elongata* than in unthinned ones. Negative density dependent growth was thus a feature of this species.

That thinning in *F. vesiculosus* stimulated growth from a young zygote/germling bank indicated a hierarchy of exploitation in this species. Skewness increased with time in the unmanipulated population, and this is indicative of intraspecific competition (Harper, 1977).

Figure 4.31 Two possible responses to thinning in seaweeds in the relationship between mean and maximum plant size of a population.



The developing population structure of *H. elongata* was extremely similar in all the manipulations, and seemed to be dictated by intraspecific competition. The initial positive skew was typical of a population under strong competition, the so called log-normal distribution of sizes (Harper, 1977) and it is assumed that at the start of the study competition was already intense. The positive skewness of the population gradually disappeared, mainly as a result of small plant competitive mortality, and a negative skew developed, followed by normality. This again is typical of population development when strong density dependent mortality removes small plants and stabilises the population hierarchy (Harper, 1977). In *H. elongata* mortality of small plants usually occurred by overgrowth of conspecific neighbours and subsequent burial. The development of temporary bimodality within the population was interpreted as a distinct boundary between winners and losers (Westoby and Howell, 1986). Concurrent with this was a general decrease in the variability and equality of the population, indicated by the coefficient of variation and Gini coefficient.

Positive skewness, a feature common to both species and the manipulation responses, is also a feature widely found in other seaweed populations (see General Introduction). It is possible that the two species studied here exemplify

the reasons for the predominance of positively skewed populations. Seaweed populations are subjected to stochastic events such as wave action or storm damage (Rosenthal *et al.*, 1974; Cowen *et al.*, 1982; Dayton and Tegner, 1984; Dayton *et al.*, 1984), and the resultant natural thinning may stimulate macrorecruitment which will result in large numbers of small plants entering a normally distributed population, making it skewed. Alternatively, as in the case of *H. elongata*, intraspecific competition may preserve a hierarchy in its own right.

A few larger buttons were lost from close packed populations. Instances have been noted of plants being physically squeezed out and detatched from the rock and washed away (personal observation), but this density dependent factor presumably acting on all plant sizes probably constitutes only a minor portion of the overall mortality.

Unfortunately, while many population studies have presented size-frequency histograms, few have statistically analysed the populations. Keser and Larson (1984) found coefficients of variation of 0-72 % in *F. vesiculosus* populations in Maine as compared to 66-340 % in this study in *F. vesiculosus* and 10-60 % in *H. elongata*. The effect of thinning obviously had a profound effect on variability in *F. vesiculosus*. Martínez and Santelices (1992) presented Gini coefficients of between 0.499 and 0.816 for their own studies on the red alga *Iridaea laminarioides*, and cited Lazo's (1987) values of 0.67 to 0.77 for *Chondrus crispus* . In *F. vesiculosus* in this study Gini values of between 0.377 and 0.822 were obtained, both higher and lower than in any other studies on seaweeds. *H. elongata* values were 0.08-0.35, lower still.

Cousens (1985) presented skewness values for frond length distribution in *Ascophyllum nodosum* of 0.9-2.3, while Schiel (1985*b*) found values of 0.1-6.6 in *Sargassum sinclairii* populations. In *F. vesiculosus* skewness coefficients were between 0.06 and 6.65, while in *H. elongata* they were between -1.1 and 1.6.

Survivorship cannot be considered in *F. vesiculosus* because of the effect of thinning on macrorecruitment. However, in *H. elongata* higher density populations were subject to greater mortality than lower density thinnings, and therefore mortality was positively density dependent.

Standing crop or biomass increased through time in both the species. In *H. elongata* standing crop increased during button growth at a slower rate than during thong growth. In *F. vesiculosus* there was an increase up to the period of reproduction, after which the standing crop decreased. This was not surprising as up to 30 % of the standing crop can be reproductive tissue, and necrosis of receptacles occurs after gametogenesis.

4.4.4 Reproduction

In *F. vesiculosus* the percentage of dry weight as reproductive material was higher in the unmanipulated populations early in receptacle development. In *H. elongata* the unmanipulated populations may have had a larger number of plants with thongs at first. Thinning obviously takes some potentially reproductive plants away from the population. There are few studies which have concentrated on the importance of density on reproductive potential in seaweeds and those which have are contradictory. Reed (1987) found no overall effect of density on sporophyll production in *Macrocystis pyrifera*. Cousens (1985) found that the percentage of reproductive laterals was highest in the most shaded shoot sections in *Ascophyllum nodosum*. He concluded that changes in reproductive effort were related to competition. Reed (1990a) found that only low density populations of *Pterygophora californica* produced sizeable sporophylls, while none of the few sporophylls found in high density populations bore sori. Terrestrial studies have shown that lower densities generally give a greater output per plant in reproductive terms (Clements *et al.*, 1929; Hogdson and Blackman, 1957). Verheij (1968) found that in apple trees the greater the density stress, the faster reproductive activity fell. This may be true in *F. vesiculosus* and *H. elongata*. High density stress might encourage

earlier development of reproductive tissue in *F. vesiculosus* and earlier necrosis.

4.4.5 Density Yield relationships

The response to thinning in *F. vesiculosus* and the loss of reproductive tissue made B-N and m-N plots very difficult to interpret. A central tenet of the self thinning rule is that populations must be even aged. These *F. vesiculosus* stands may have been even-aged, but with a zygote/sporeling bank it is impossible to know. Not many seaweeds can be aged unless followed from settlement (Ang, 1991). In nature, populations are often subject to natural stochastic thinning by storms and grazing, as well as large scale canopy loss through necrosis of reproductive parts. All these factors will open up canopies to macrorecruitment if a microscopic bank exists, and therefore a knowledge of the history of the population being studied is important to demographers interested in density-weight relationships.

Self thinning in *H. elongata* conformed to the expectations of self-thinning theory (*eg* Weller, 1987). Despite the two stage development of button and thong in *H. elongata*, when either all data or means of replicates were tested by principal component analysis it was found that slopes did not depart significantly from the -1.5 or -0.5 expectations, and correlations were significant. No data were removed from the analysis. However, when button and thong stage plants were analysed separately, slopes for either stage were significantly different (steeper) than expected. We can therefore conclude that the stage of development is an important factor in self-thinning.

The concept of the self-thinning rule has recently been divided into interspecific size-density relationship and single species thinning line (Weller, 1990). The first application of self-thinning theory to seaweed populations considered the former (Cousens and Hutchings, 1983), and this has historically dictated subsequent applications (Robertson, 1987; Cheshire and Hallam, 1988; Martínez and Santelices, 1992). In order to assess the single species thinning

line, experiments must follow populations over time, as in this study. This has been attempted in seaweed populations by Schiel and Choat (1980), but they used a number of populations naturally occuring at different densities at one time, rather than following the same populations through time. Though this technique is valid, it must only be employed with large numbers of observations to counteract environmental heterogeneity ("several hundred or more data points that represent various yield-density combinations" Osawa and Sugita, 1989), or at least there must be a sound knowledge of the specific history of the populations being studied.

Russell (1988) found that there was a negative relationship between mean plant weight and density in *H. elongata*, though the slope was much more shallow than -1.5 that the self-thinning rule dictates. Unfortunately he had no historical knowledge of the populations (*ie* whether they were even aged), used regression analysis rather than principal components analysis and did not discount points on the basis of their probable position below the line of constraint (see Weller, 1987*a*). None of the studies have utilised the statistical recommendations of Weller (1987*a*), most importantly the use of total biomass rather than mean plant weight as the *y* variable to get rid of spurious correlations, and the use of principal component analysis to fit slopes to the data.

Some authors have suggested a notional *y*-intercept constant to the boundary condition calculated from terrestrial studies as 4.3 (Cousens and Hutchings 1983; Robertson 1987; Cheshire and Hallam, 1988). Most of the intercepts in the *H. elongata* data breached this theoretical maximum, and the obvious conclusion is that in seaweeds the intercept should be higher.

We have seen that different species respond differently to density manipulation. This is an important conclusion, because these were natural populations. Much of the theoretical basis for population dynamics comes from the study of artificial populations of glasshouse plants or planted forest trees. Density dependent growth and mortality do take place in seaweed populations, and if

the prevalence of positively skewed populations is indicative of intraspecific competition, then most seaweed populations undergo this stress. There are however many variables which affect natural seaweed populations, and the next chapter will consider artificial stands of large plants under the more controlled conditions of tank culture.

Chapter 5

The effect of density on visible artificial seaweed populations

5.1 Introduction

The sea shore is a rough and tumble place for growing seaweeds. Manipulative experiments on natural populations can, at best, provide us with evidence that intraspecific competition is taking place in benthic marine macroalgal populations. At worst, numerous confounding factors may operate on the populations being studied, which in turn may also confound the biologist trying to study them.

In the last chapter two very different responses to similar thinning treatments were found. In this chapter the effects of density are studied in greater detail under semi-controlled conditions in *Fucus serratus* and *Laminaria digitata*. In order to achieve this, populations were artificially created and cultivated in tanks. There were a number of advantages in this approach:

1. In natural populations density can only be decreased, not increased. Artificial populations can be created at any density.

2. Exact densities of plants can be constructed.

3. Plants in tank culture are not subject to numerous factors which may confound the study of natural populations, particularly herbivores, storms and recruitment events.

4. Populations are accessible for sampling at any time.

5. The microscopic stages of development can be bypassed.

6. Environmental hetrogeneity is minimised in tanks.

Many authors (generally pursuing applied aspects of seaweed biology) have cultured plants on open sea culture systems (*eg* Druehl *et al.*, 1988; Hurtado-Ponce, 1990). Some studies have been carried out with open sea populations where the effects of density on various plant and population attributes have been considered with plants growing on rope (Hayakawa, 1987; Hurtado-Ponce, 1990; Kain *et al.*, 1990), nets (Yoshida, 1972; Yoshihara, 1977), cages (Guanzon and de Castro, 1992) or by bottom attachment (Luning, 1970; Neushul and Harger, 1985).

While transplantation of visible plants around the shore is a common technique for studying various ecological factors operating on plants (*eg* Schonbeck and Norton, 1980*a*) this technique has only been used to create artificial populations to study intraspecific competition in one species (Adams and Austin, 1979). Chapman (1990*a*) created mixed and single populations of two fucoids which were outplanted.

Russell (1963) used laboratory culture to overcome difficulties with transplanting. Many other authors have cultured visible plants in laboratory culture systems (*eg* Luning, 1970; Fletcher, 1975; Russell and Fielding 1974; Druehl *et al.*, 1988; Back *et al.*, 1992) in order to look at all sorts of plant developmental parameters, many of which may have a profound bearing on intraspecific competition (*eg* Cousens, 1985). No laboratory studies have been carried out to investigate intraspecific competition in populations of seaweeds consisting of visible plants.

In this study cultures of artificially created populations were subject to natural fluctuations in light, water temperature, salinity and nutrients, but the outdoor tank culture allowed other variables to be limited, and thus mechanisms which affected seaweed population dynamics to be considered in some detail.

5.2 Materials and Methods

5.2.1 Field collection

For each experiment fronds were collected from a small area of the shore in order to minimise variation in any frond attributes which may be expected to become more important with increased sampling area and thus environmental heterogeneity. For *Fucus serratus* it was possible to sample from within a cohort obviously derived from a single settlement event. For *Laminaria digitata* a patch left from a previous clearance experiment was used. Plants were removed using a knife to prize the holdfast away from the substrate.

5.2.2 Creation of populations

Artificial populations were created by inserting holdfasts through the twine of 5 mm three strand polypropylene laid rope. The rope was untwisted to insert the lower stipe and when released clamped it in place and the rope was wrapped round 15 x 10 cm pieces of asbestos-substitute roofing slate to make a two dimensional population. The rope was tied at either end of the slate through a hole previously drilled in the slate. In this way a range of densities could be constructed. In both species holdfast reattachment took place on the rope and/or plates quite quickly.

5.2.3 Aquaculture technique

For both experiments all densities and replicates were grown in a single tank, and conditions for both species were identical (Table 5.1). Both tanks were supplied with sea-water via a large header tank, and were kept outdoors and therefore subject to the seasonal variations in light, nutrient availability, salinity and temperature associated with the time when the experiments were carried out. The tanks were cleaned at fortnightly intervals, when all the populations were removed and exposed to air for one or two hours. This exposure process minimised the growth of epiphytes, predominantly Ectocarpales. The position in the tank of each plate was randomly changed weekly to negate any

across-tank heterogeneity. Repeated measures of all plates were made through time.

5.2.4 Measurement

At each sample time populations were laid on two-ply absorbent paper towels for 30 minutes, after which they were weighed wet. Length measurements for all plants in each treatment and each replicate were then taken. Each plant could be uniquely identified so that individual plants could be followed through time.

For *F. serratus* maximum frond length (rope to tip) was measured for each plant using a ruler. For *L. digitata* small holes were inserted into the frond using a No.1 cork borer (approximately 0.4 mm diameter) just above the meristematic region (Parke, 1948, Figure 5.1). Two frond measurements were taken (rope to hole and rope to tip) using a ruler so that growth and tip loss could both be measured. If growth resulted in the hole migrating close to the tip, a new hole was added lower down the plant. Subsequently populations were replaced in the tanks until the next sample time.

At the end of each experiment a final destructive harvest was performed subsequent to the half hour drying period. All plants were separated from the plates and ropes, and weighed. The wet plates and ropes were weighed separately. The plants from each plate were then oven dried collectively at 60°C in aluminium pie dishes until two consecutive dry weight measures agreed to within 0.001 g. A relationship between wet and dry weight for each species was obtained from these measures using simple linear regression analysis. It was assumed that the wet weight of the rope and plate was constant through time, and the plant population dry weight was calculated by the equation

$$\text{Dry Weight} = (\text{Total Wet Weight} - \text{Wet weight of Plate and Rope}) \times k_1 + k_2.$$

where k_1 was the slope of the relationship between wet and dry plant weight, and k_2 was the y intercept of this relationship.

Relative growth rates could be calculated based on individual plants, and population mean relative growth rate calculated. Relative growth rate (RGR) (*ie* the growth rate relative to the plant size) was calculated by the equation:

$$RGR = \frac{LnL_{t2} - LnL_{t1}}{t2 - t1}$$ Equation 5.1

Where *L* is the length of the plant (cm, at two successive times), and *t2* and *t1* are times (days).

In the case of *Fucus serratus*, RGR could be negative if plants lost tissue, and so two RGRs were calculated, RGR1 where negative RGRs were revalued as 0, and RGR2 which used negative values too. For *Laminaria digitata*, L_{t1} was the length of plant from holdfast to tip, and L_{t2} was calculated as L_{t1} plus the distance the hole had moved between the two times (Figure 5.1).

Figure 5.1 Diagramatic representation of measures taken in *Laminaria digitata*

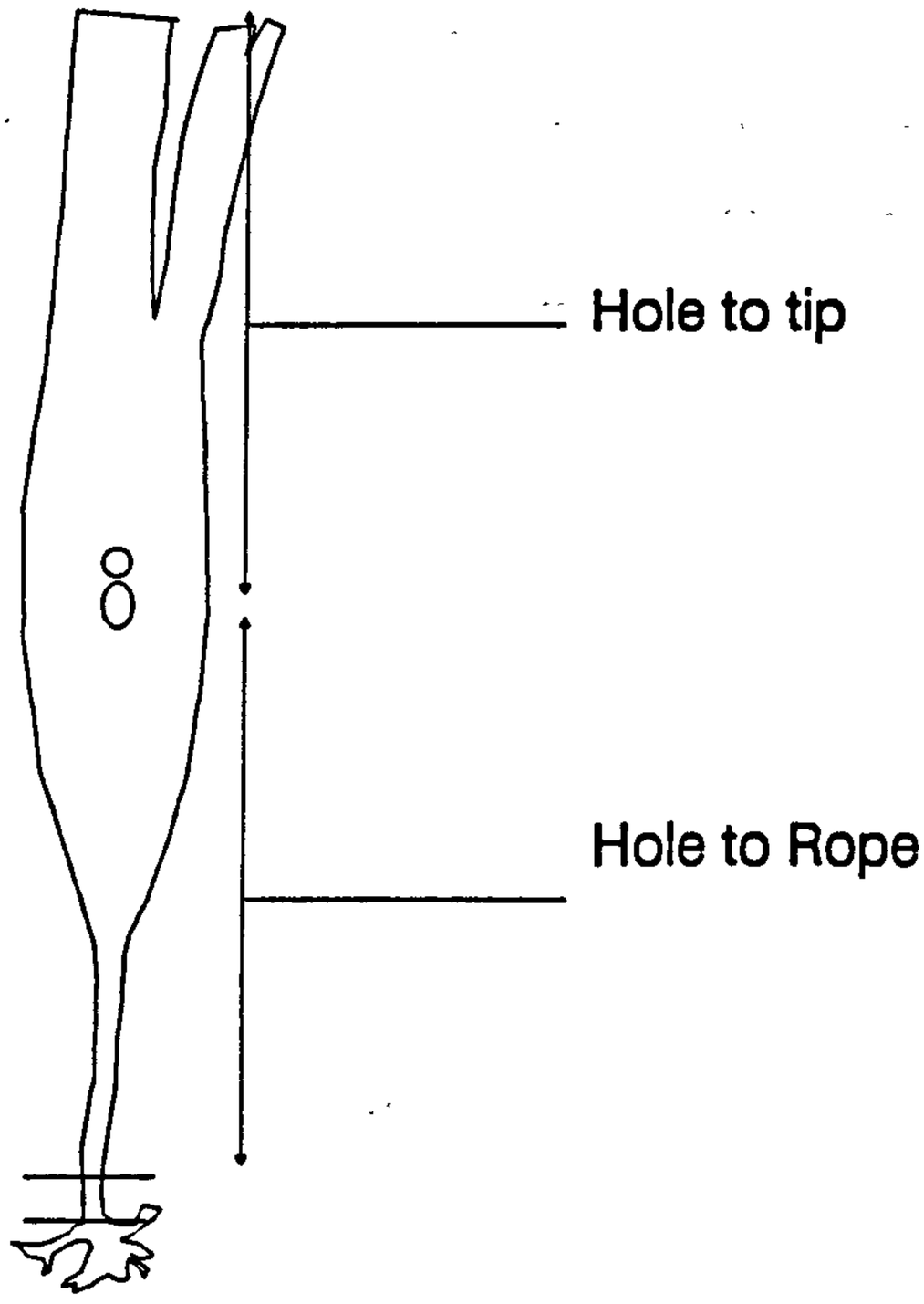


Table 5.1 Various experimental details for the tank culture experiments.

	Fucus serratus	*Laminaria digitata*
Tank Type	Round	Round
Length/Diameter (cm)	100	100
Width (cm)		
Depth (cm)	110	110
Flow rate ($l.min^{-1}$)	21	21
Density treatments	4	5
Starting densities	650, 1334, 2000, 2668	650, 1334, 2000, 2668, 5186
Replicates	4	4
Sample Time 1	25/4/92	28/1/92
Sample Time 2	14/5/92	13/2/92
Sample Time 3	4/6/92	26/2/92
Sample Time 4	5/7/92	10/3/92
Sample Time 5	12/8/92	24/3/92
Sample Time 6	11/9/92	15/4/92
Sample Time 7	13/10/92	28/4/92
Sample Time 8		16/5/92
Sample Time 9		5/6/92
Sample Time 10		6/7/92
Sample Time 11		13/8/92

5.3 Results

5.3.1 Fucus serratus

5.3.1.1 Wet weight-dry weight relationship

There was a strong relationship between wet and dry weight (Figure 5.2):

Dry Weight = -0.022 + 0.213Wet Weight. $n=16$, Std=0.004, $R^2=99.4\%$, $p<0.001$.

5.3.1.2 Population Structure

There were subtle changes in length frequency histograms between densities and through time (Figure 5.3). While all the densities started positively skewed, length distributions became more normal over time (Figure 5.4). There was a weak though significant inverse correlation between skewness coefficient and time when all data were considered collectively (Table 5.2). One-way ANOVA

Figure 5.2 The relationship between wet and dry weight in *Fucus serratus*.

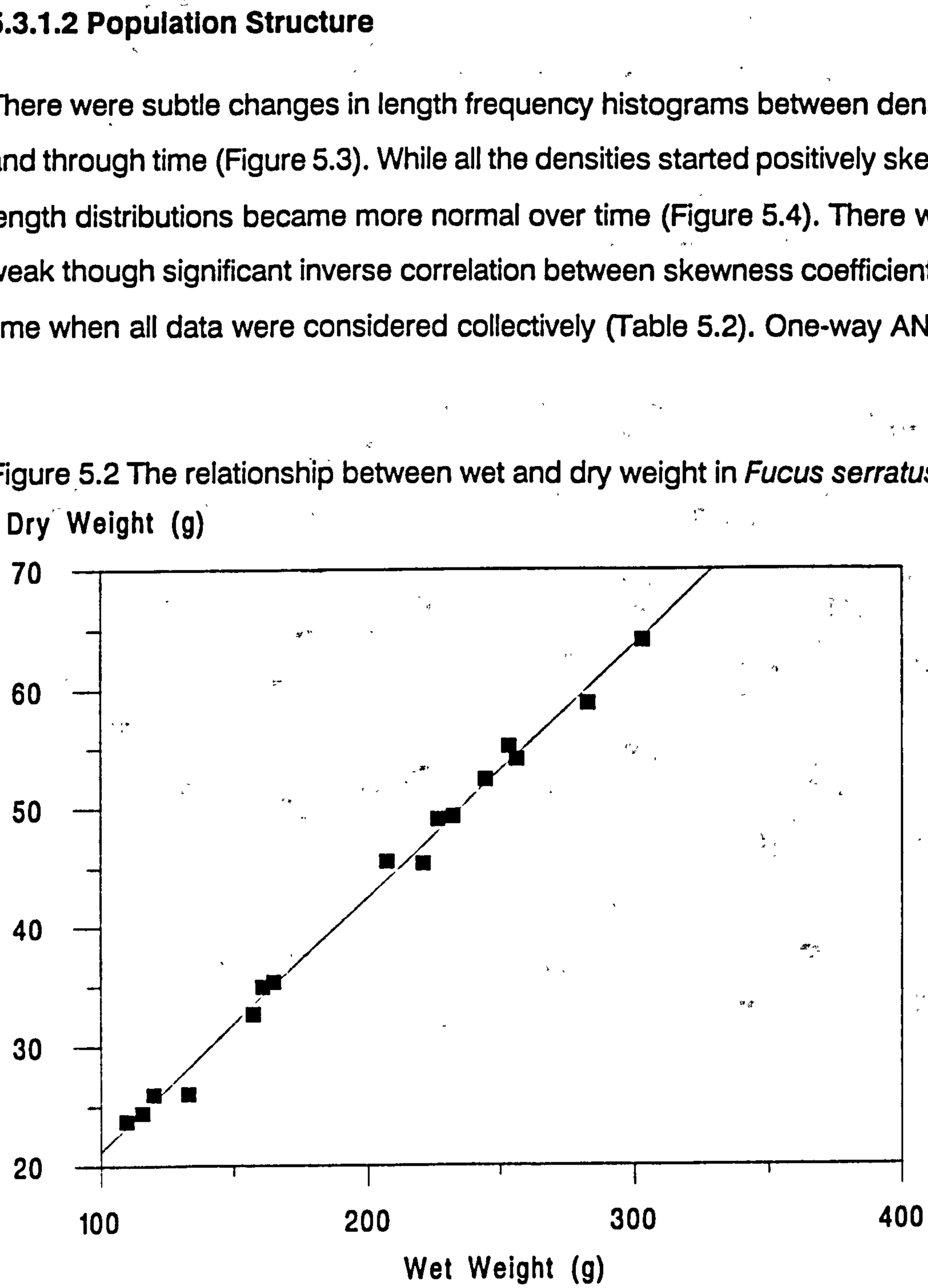
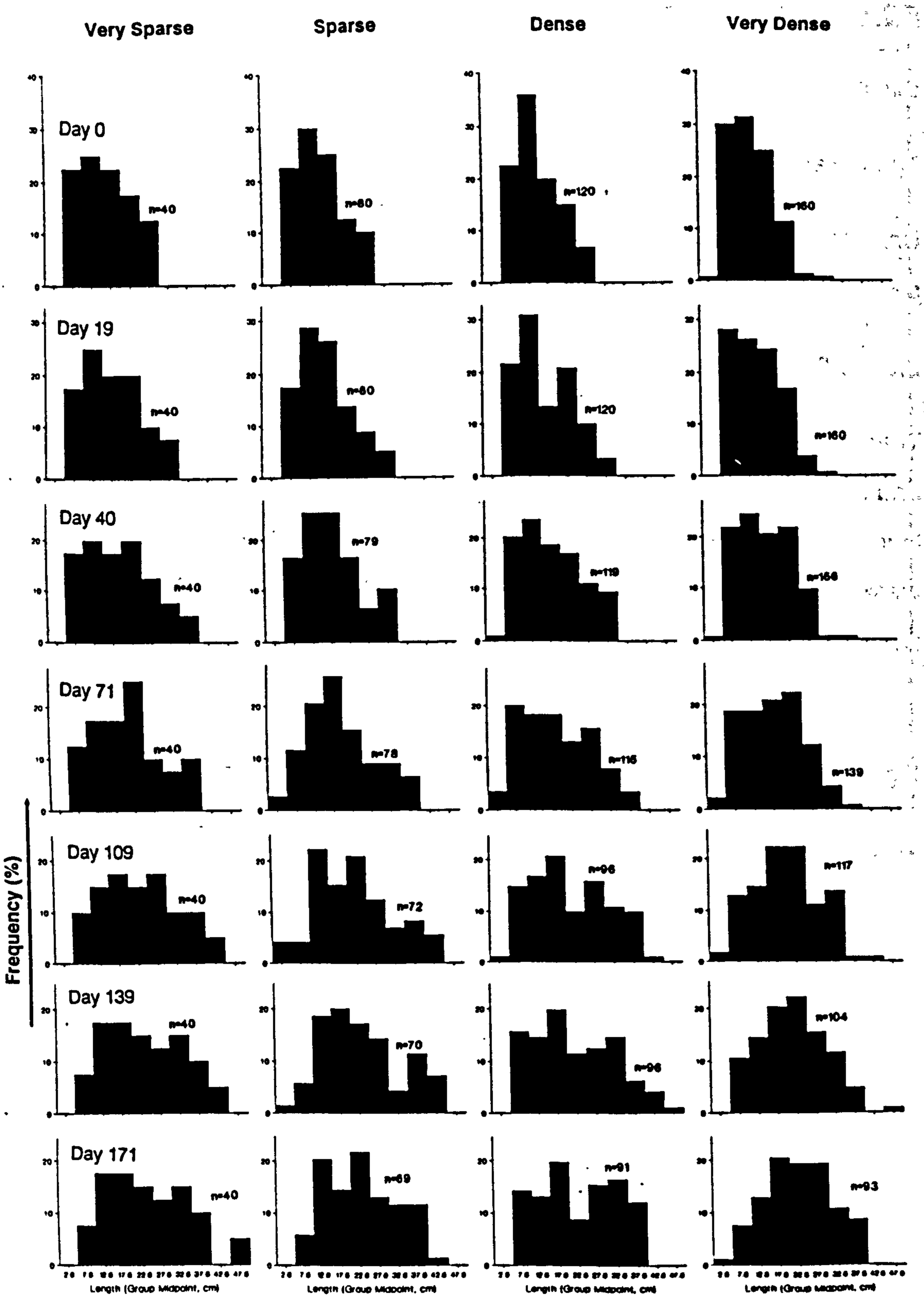


Figure 5.3 Frond length frequency histograms over time in artificial, tank cultured populations of *Fucus serratus* at different densities.



performed on skewness coefficients at each time revealed no significant differences between densities at any time (Table 5.3).

The size range increased as the populations developed, both by increase and decrease in plant size (Figure 5.3). Analysis of size inequality (Gini coefficient, *G*) and size variability (coefficient of variation, *CV*) exhibited similar trends (Figure 5.4), and there was a positive correlation between these two statistics when all data were pooled (Table 5.2). The very sparse populations exhibited an increase in variability and inequality over time (Figures 5.5 and 5.6). The three most dense populations increased in variability/inequality for the first 71 days of the study before decreasing to the end (Figures 5.5 and 5.6). One-way ANOVA performed at each time found no significant difference between *CV*s at different densities except on day 139 when the very dense populations were different from the dense ones, and day 171 when the very dense populations were significantly less variable in size than the dense and very sparse populations but not the sparse populations (Table 5.4). The results of ANOVA and Tukey test for Gini values were essentially similar (Table 5.5).

Table 5.2 Correlation coefficients between various measures in *Fucus serratus* for data of density and time pooled.

	1	2	3	4	5	6	7	8	9
1. Standing Crop									
2. Density	0.45*								
3. Mean Frond Length	0.44*	-0.52*							
4. Maximum Frond Length	0.47*	-0.34*	0.81*						
5. Coefficient of Variation	0.08	-0.10	0.07	0.47*					
6. Gini Coefficient	0.15	-0.01	0.06	0.43*	0.99*				
7. Skewness Coefficient	-0.27*	-0.04	-0.34*	0.08	0.43*	0.32*			
8. RGR1	-0.65*	0.07	-0.75*	-0.76*	-0.22*	-0.23*	0.22*		
9. RGR2	-0.60*	-0.06	-0.57	-0.61*	-0.16	-0.17	0.14	0.90*	
10. Time	0.62*	-0.27*	0.86*	0.78*	0.12	0.18	-0.31*	-0.87*	-0.70*

* = Significant @ p = 0.05, n=112. (Pearson)

Figure 5.4 Skewness coefficient of plant length in *Fucus serratus* at different densities over time. Bars = ±1S.E.

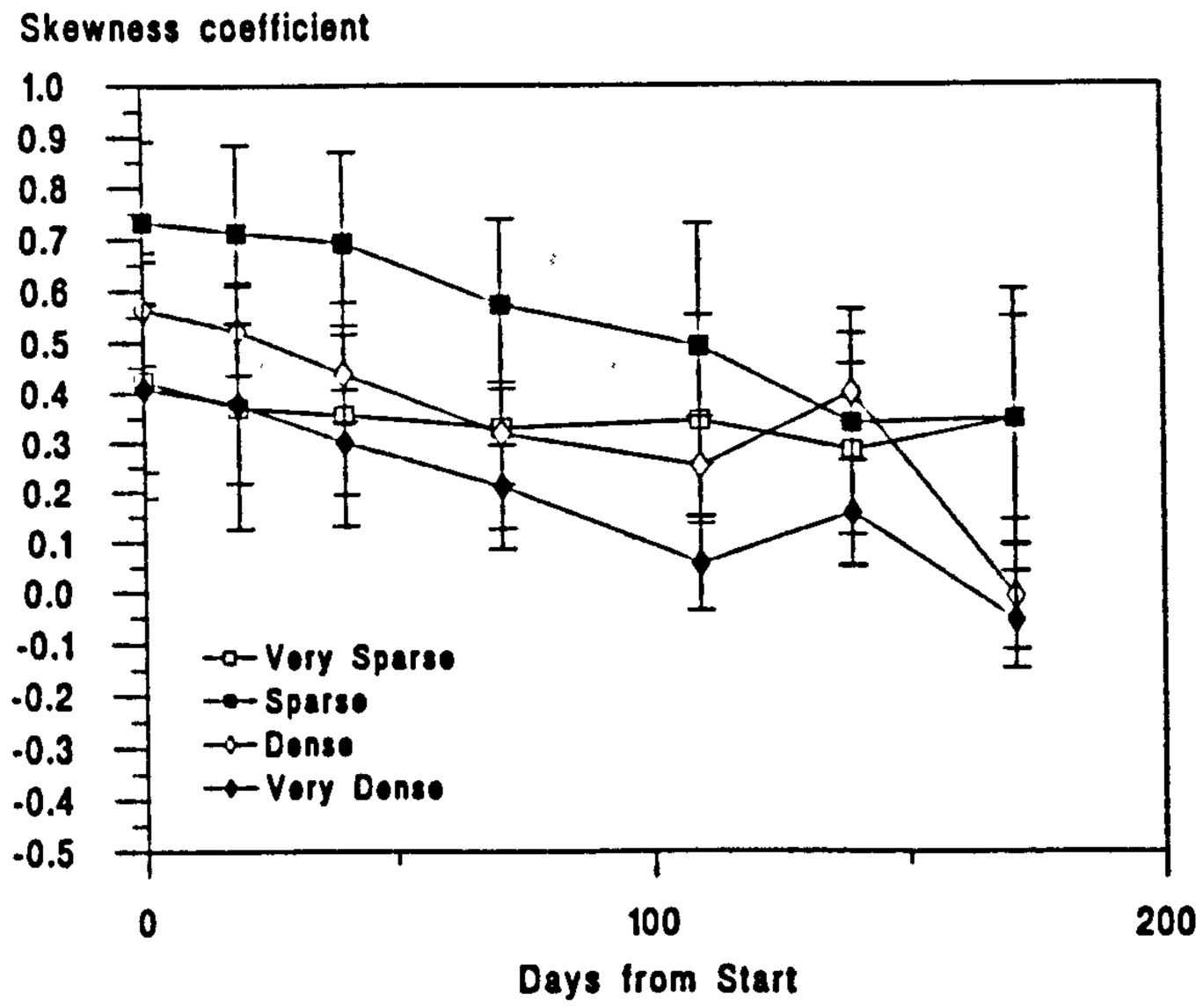


Table 5.3 Analysis of Variance (and Tukey Tests) of density effects on skewness coefficient of plant length in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	3	0.092	0.57	0.647	NA
	Residuals	12	0.161			
Day 19	Density	3	0.102	0.62	0.614	NA
	Residuals	12	0.164			
Day 40	Density	3	0.121	0.89	0.475	NA
	Residuals	12	0.136			
Day 71	Density	3	0.094	0.68	0.584	NA
	Residuals	12	0.140			
Day 109	Density	3	0.133	0.84	0.497	NA
	Residuals	12	0.158			
Day 139	Density	3	0.043	0.27	0.848	NA
	Residuals	12	0.160			
Day 171	Density	3	0.199	1.14	0.373	NA
	Residuals	12	0.167			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

Figure 5.5 Coefficient of variation of plant length in *Fucus serratus* at different densities over time. Bars = ±1S.E.

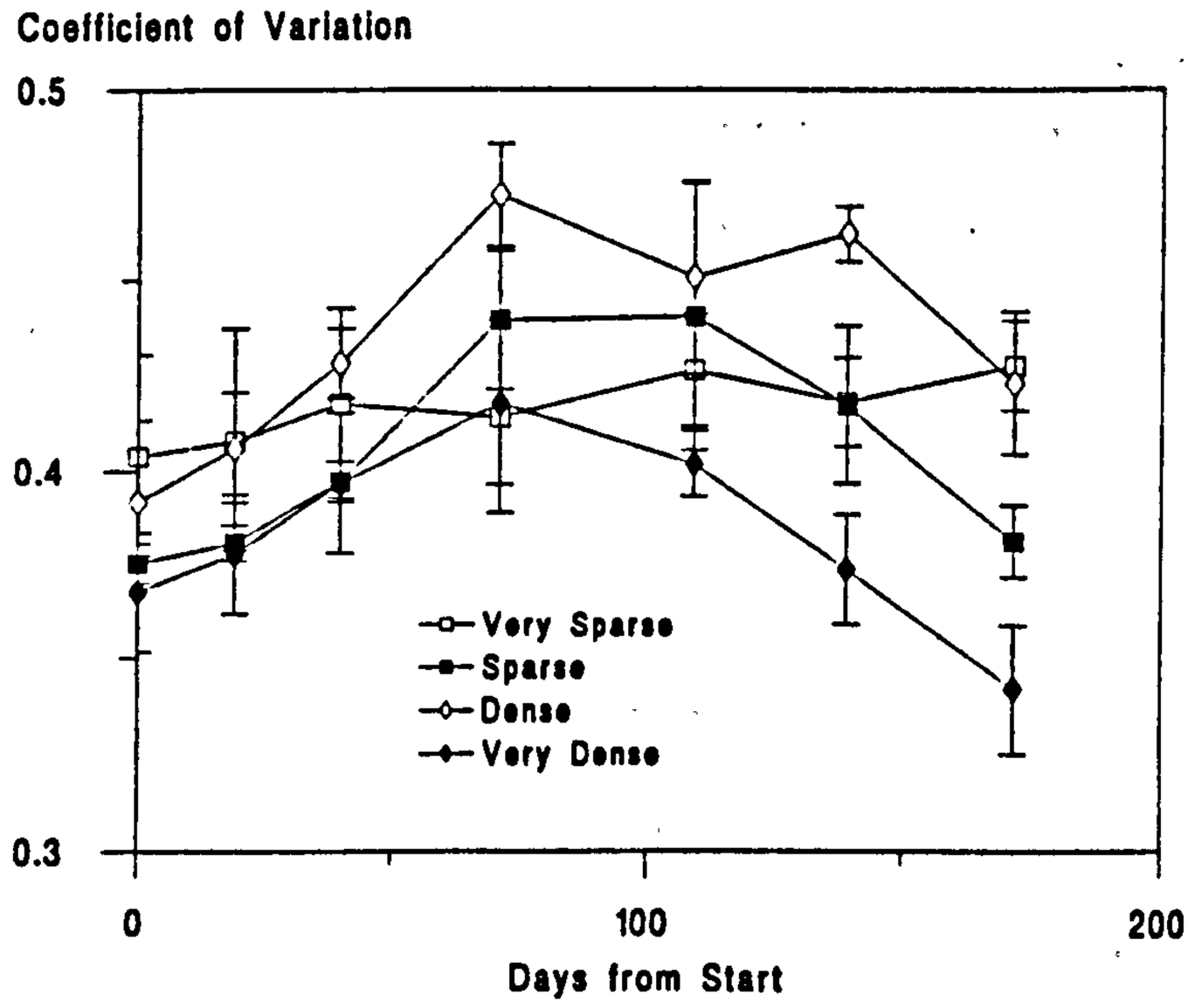


Table 5.4 Analysis of Variance (and Tukey Tests) of initial density on coefficient of variation of plant length in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	3	0.00109	0.55	0.656	NA
	Residuals	12	0.00196			
Day 19	Density	3	0.00106	0.58	0.641	NA
	Residuals	12	0.00183			
Day 40	Density	3	0.00099	0.68	0.582	NA
	Residuals	12	0.00146			
Day 71	Density	3	0.00285	1.32	0.313	NA
	Residuals	12	0.00216			
Day 109	Density	3	0.00178	0.62	0.613	NA
	Residuals	12	0.00286			
Day 139	Density	3	0.00524	4.71	0.021	VD≠D
	Residuals	12	0.00111			
Day 171	Density	3	0.00652	5.69	0.012	VS and D≠VD
	Residuals	12	0.00115			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

Figure 5.6 Gini coefficient of plant length in *Fucus serratus* at different densities over time. Bars = ±1S.E.

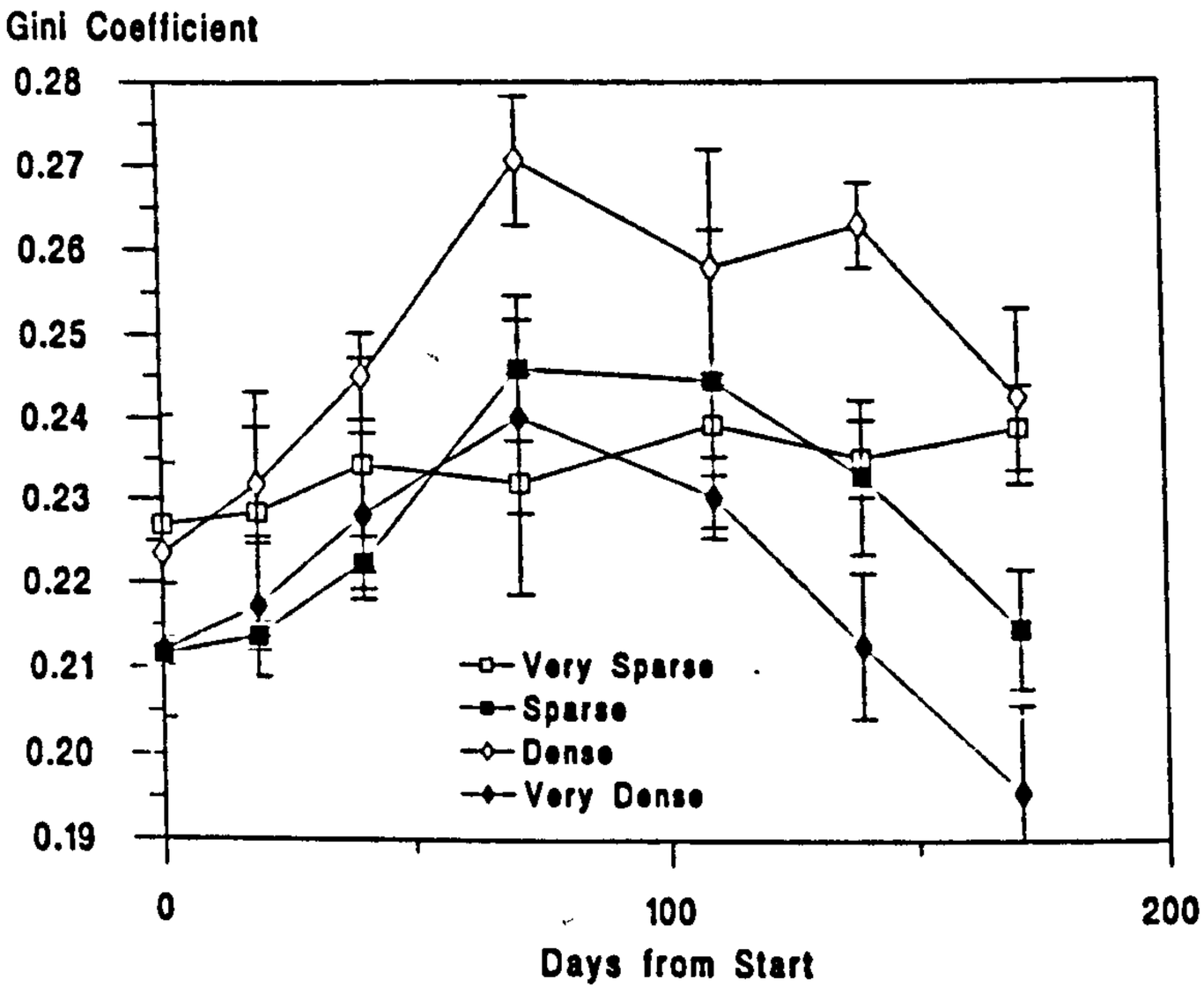


Table 5.5 Analysis of Variance (and Tukey Tests) of initial density on Gini coefficient of plant length in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	3	0.000246	0.51	0.683	NA
	Residuals	12	0.000482			
Day 19	Density	3	0.000301	0.67	0.589	NA
	Residuals	12	0.000453			
Day 40	Density	3	0.000373	0.91	0.464	NA
	Residuals	12	0.000409			
Day 71	Density	3	0.001108	1.84	0.193	NA
	Residuals	12	0.000601			
Day 109	Density	3	0.000538	0.70	0.571	NA
	Residuals	12	0.000771			
Day 139	Density	3	0.001705	6.19	0.009	D≠VD
	Residuals	12	0.000275			
Day 171	Density	3	0.001932	4.97	0.018	VS and D≠VD
	Residuals	12	0.000388			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

5.3.1.3 Frond Length

Mean frond length increased in all the populations through time (Figure 5.7) and there was a strong positive correlation between these two variables (Table 5.2). The effect of density on mean frond length was examined by one-way ANOVA at successive sample times (Table 5.6). The most dense populations had a significantly lower mean frond length than the most sparse populations at the first three sample times (Figure 5.7 and Table 5.6). The dense or sparse populations were not significantly different from any other densities (Table 5.6). After day 40 there was no significant difference between mean frond length in different densities.

There was a positive correlation between maximum frond length and time (Table 5.2 and Figure 5.8). At no time did ANOVA detect a significant difference in maximum frond length at different densities (Table 5.7).

There was a strong positive correlation between mean and maximum frond length (Table 5.2).

5.3.1.4 Density and survivorship

The density of the very sparse populations did not change throughout the experiment (*ie* there was no mortality, Figure 5.9). However, in the three more dense populations there was mortality (Figure 5.9) and from standardised survivorship it seemed that mortality was density dependent (Figure 5.10). In the course of the experiment, over 40 % of the plants in very dense populations died (Figure 5.10).

At the start of the experiment all the populations obviously had significantly different densities (Table 5.8). This continued for the first 71 days of the experiment. 109 days after the start of the experiment, the two most dense sets of populations were not significantly different (ANOVA), and this was also the case after 139 days. At the end of the experiment, the very sparse populations were significantly different from all the other populations, but the three most

Figure 5.7 Mean frond length in populations of *Fucus serratus* grown in tanks at different densities. Bars = ±1S.E.

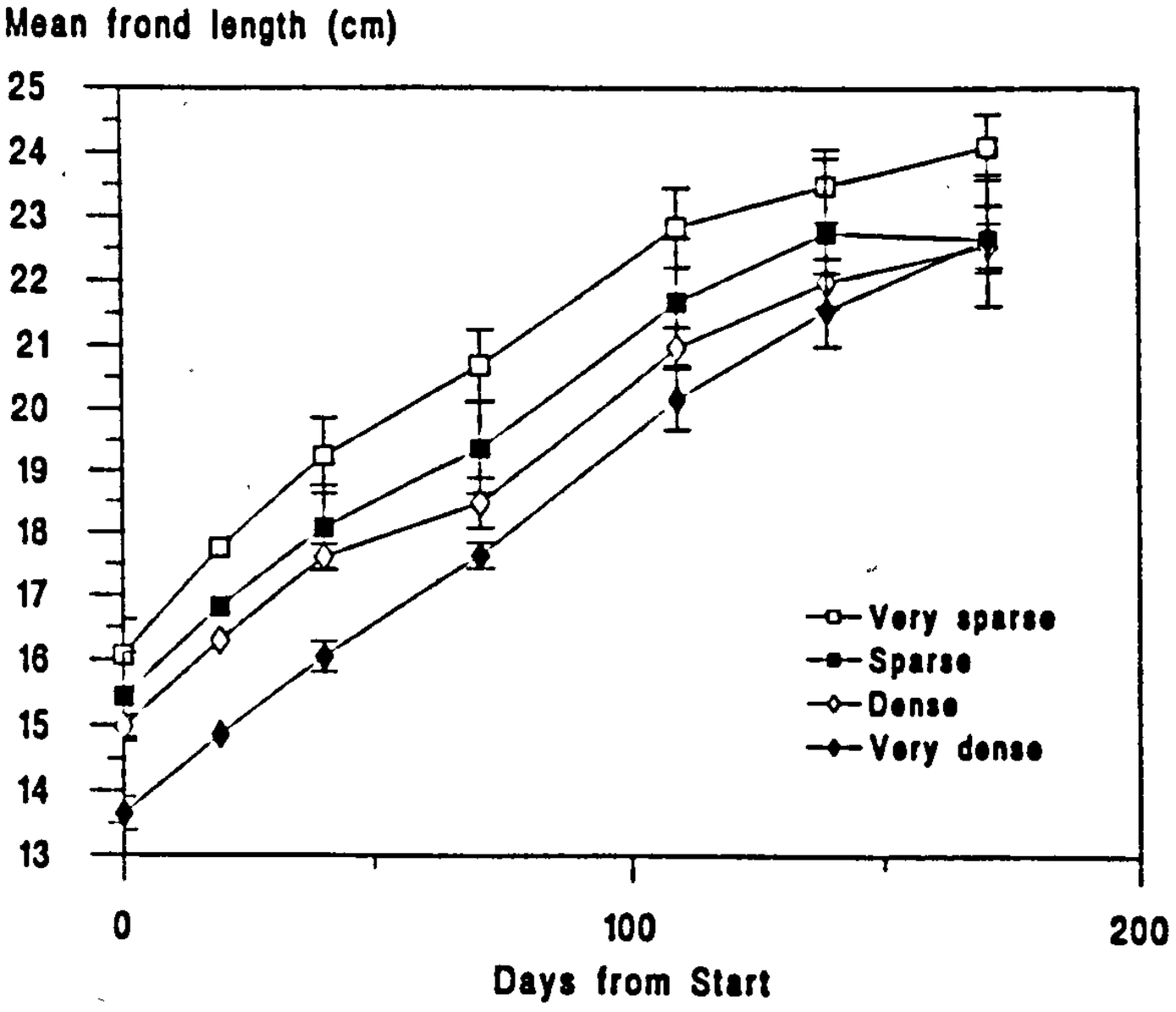


Table 5.6 Analysis of Variance (and Tukey Tests) of initial density on mean plant length in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	3	4.21	3.71	0.042	VS≠VD
	Residuals	12	1.13			
Day 19	Density	3	5.79	4.70	0.022	VS≠VD
	Residuals	12	1.23			
Day 40	Density	3	6.95	4.89	0.019	VS≠VD
	Residuals	12	1.42			
Day 71	Density	3	6.81	3.03	0.071	NA
	Residuals	12	2.25			
Day 109	Density	3	5.15	1.82	0.197	NA
	Residuals	12	2.83			
Day 139	Density	3	2.88	1.29	0.323	NA
	Residuals	12	2.23			
Day 171	Density	3	2.16	0.48	0.703	NA
	Residuals	12	4.51			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

Figure 5.8 Maximum frond length in populations of *Fucus serratus* grown in tanks at different densities. Bars = ±1S.E.

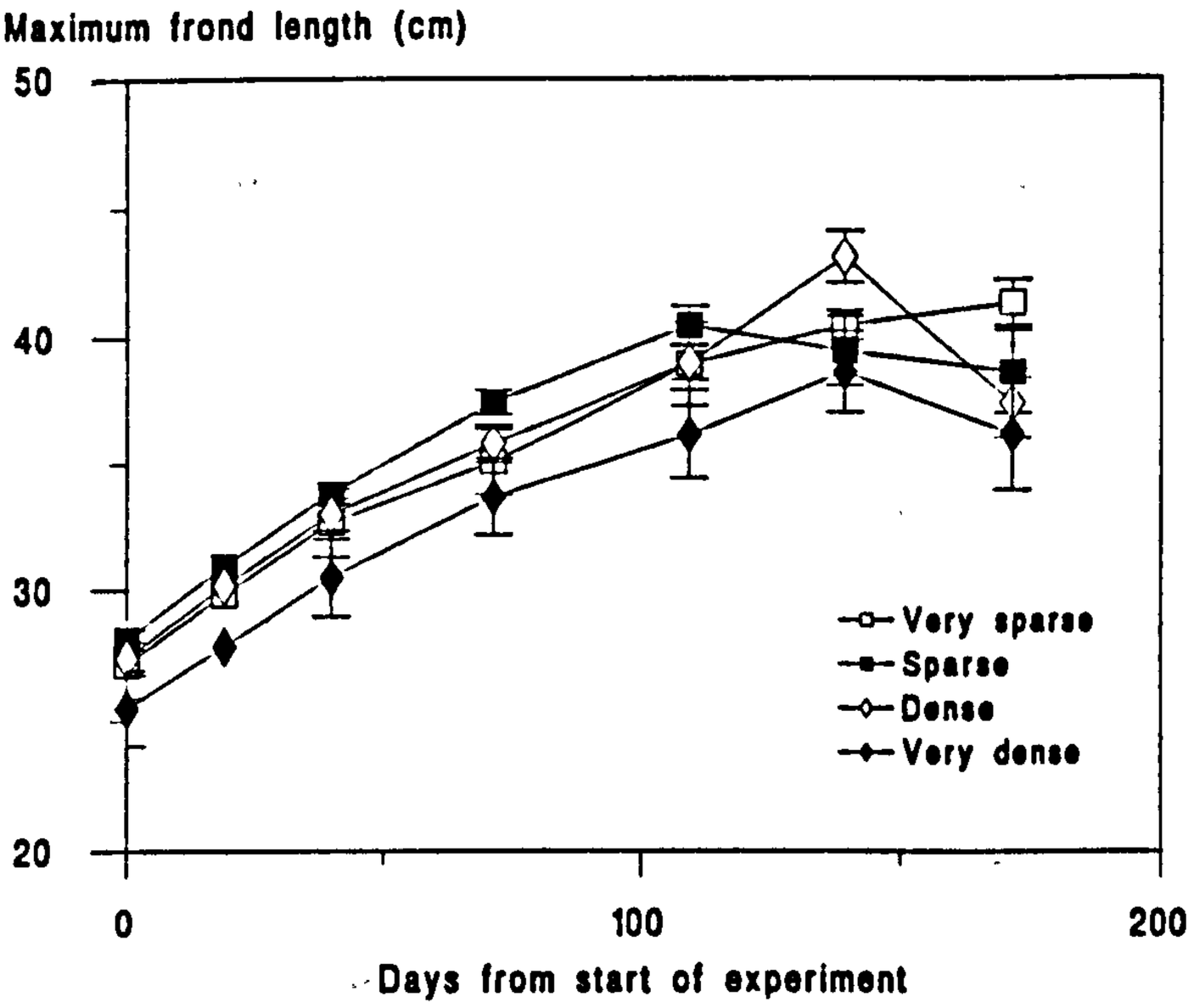


Table 5.7 Analysis of Variance (and Tukey Tests) of initial density effects on maximum plant length in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	3	4.86	0.85	0.493	NA
	Residuals	12	5.71			
Day 19	Density	3	6.90	1.09	0.392	NA
	Residuals	12	6.34			
Day 40	Density	3	8.00	1.20	0.350	NA
	Residuals	12	6.65			
Day 71	Density	3	9.99	1.10	0.386	NA
	Residuals	12	9.07			
Day 109	Density	3	12.89	1.69	0.221	NA
	Residuals	12	7.61			
Day 139	Density	3	15.1	1.09	0.389	NA
	Residuals	12	13.8			
Day 171	Density	3	19.6	1.40	0.290	NA
	Residuals	12	14.6			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

Figure 5.9 Density change in populations of *Fucus serratus* grown in tanks at different initial densities. Bars = ±1S.E.

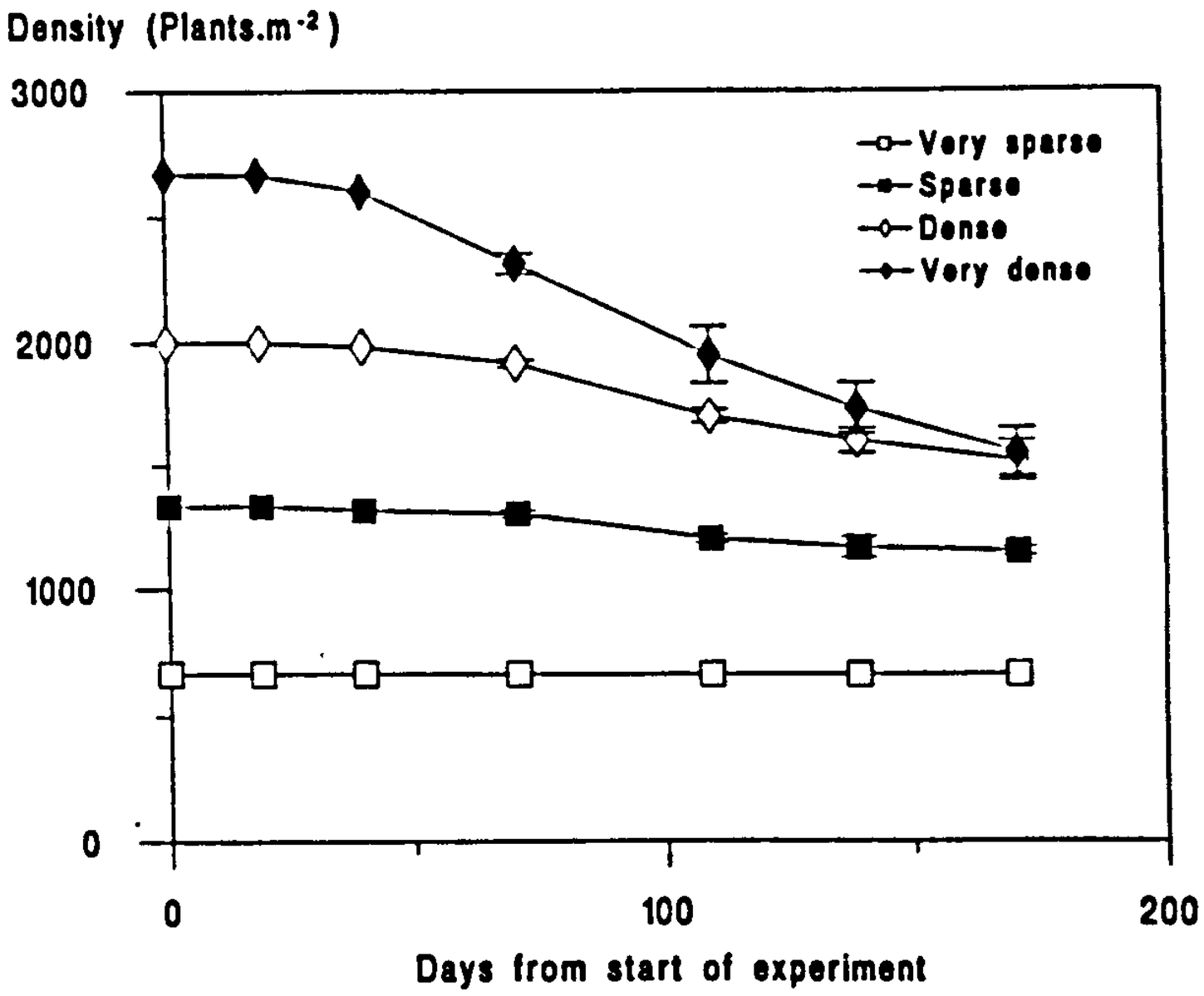
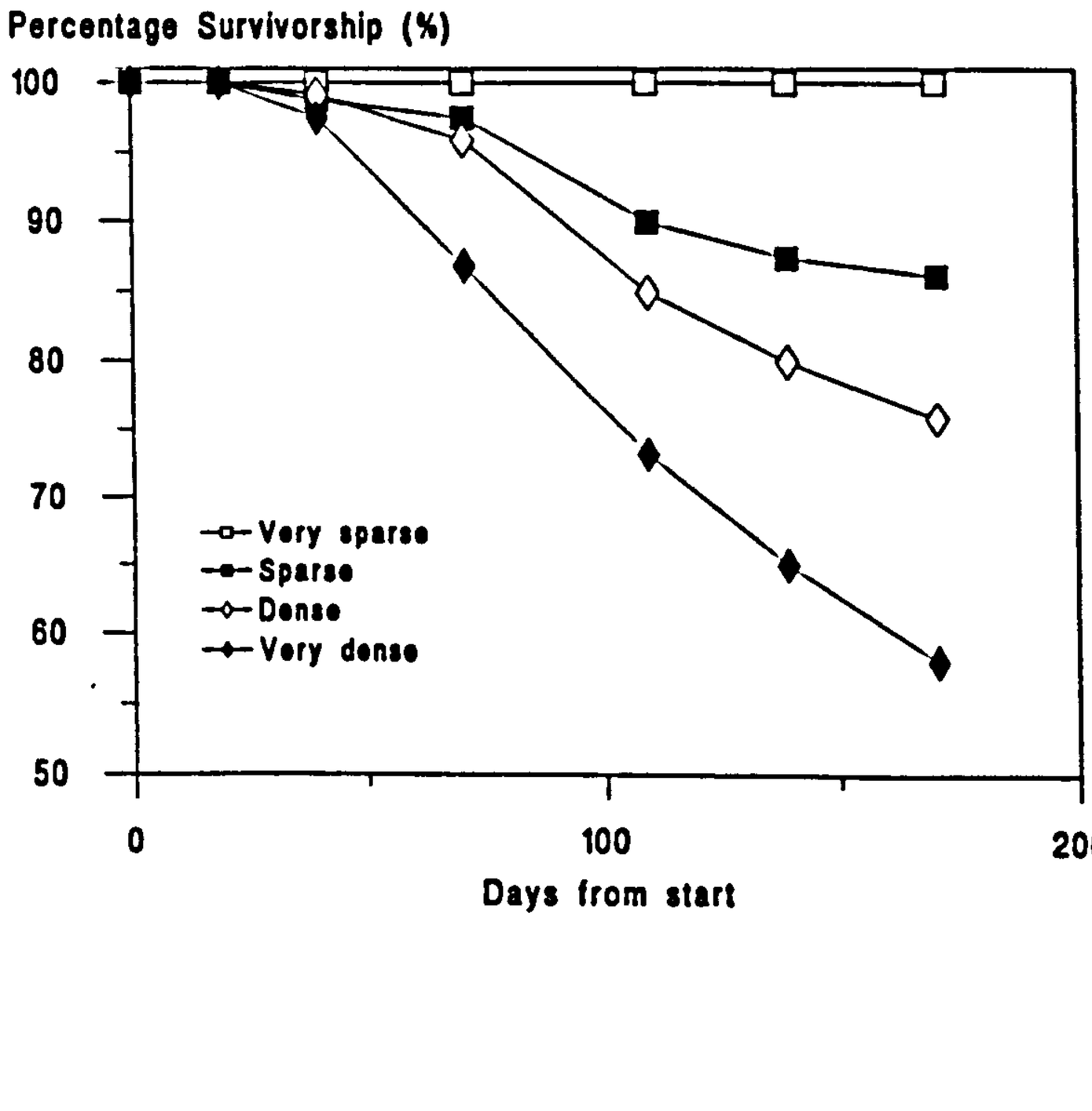


Figure 5.10 Standardised survivorship in populations of *Fucus serratus* grown in tanks at different initial densities



dense populations were not different from one another with respect to density (Table 5.8). There was a significant though weak negative correlation between density and time (Table 5.2)

Table 5.8 Analysis of Variance (and Tukey Tests) of initial density on subsequent density in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
(Day 0)	Density	3	2962963	-	-	(All different)
	Residuals	12	0			
Day 19	Density	3	2962963	-	-	(All different)
	Residuals	12	0			
Day 40	Density	3	2788519	1003.87	<0.001	All different
	Residuals	12	2778			
Day 71	Density	3	2086667	111.56	<0.001	All different
	Residuals	12	18704			
Day 109	Density	3	1291389	64.87	<0.001	
	Residuals	12	19907			D≠S≠VS, VD≠S≠VS
Day 139	Density	3	928519	41.10	<0.001	
	Residuals	12	22593			D≠S≠VS, VD≠S≠VS
Day 171	Density	3	677315	13.04	<0.001	VS≠S or D or VD
	Residuals	12	51944			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

5.3.1.5 Standing crop

Standing crop increased over time in all populations (Table 5.2 and Figure 5.11). At the start of the experiment there was a significant difference between densities for standing crop (Table 5.9, ANOVA). After 71 days there was no difference between standing crop in the three most dense populations, though the very sparse populations remained with a significantly lower standing crop throughout the experiment (Figure 5.11 and Table 5.9).

Figure 5.11 Standing Crop (dry weight) in populations of *Fucus serratus* grown in tanks at different initial densities. Bars = ±1S.E.

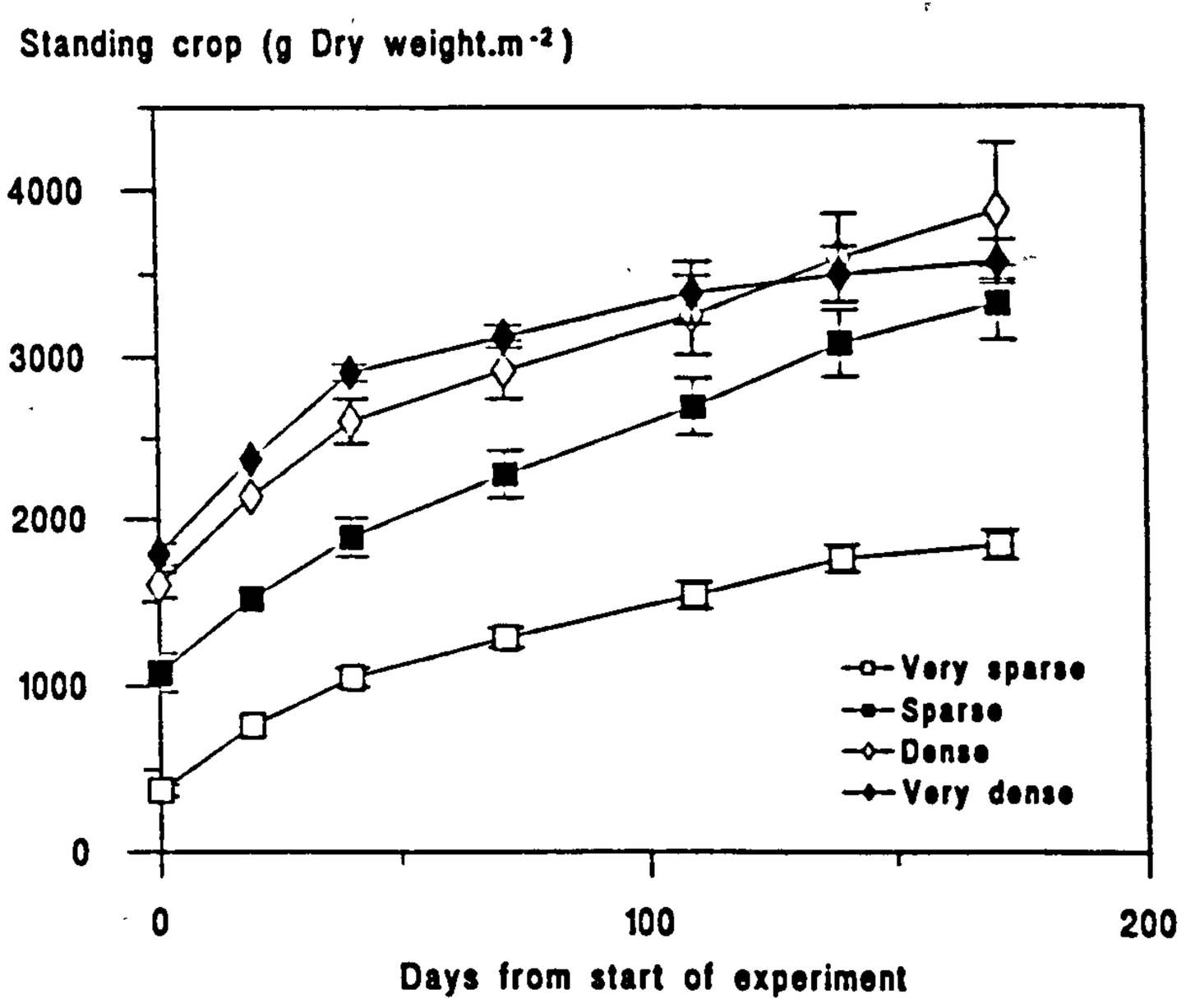


Table 5.9 Analysis of Variance (and Tukey Tests) of initial density on standing crop (dry weight) in *Fucus serratus* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	3	1595684	49.07	<0.001	
	Residuals	12	32520			D≠S≠VS, VD≠S≠VS
Day 19	Density	3	2066681	40.54	<0.001	
	Residuals	12	50968			D≠S≠VS, VD≠S≠VS
Day 40	Density	3	2731340	33.57	<0.001	
	Residuals	12	81372			D≠S≠VS, VD≠S≠VS
Day 71	Density	3	2732497	15.85	<0.001	
	Residuals	12	172451			VS≠S or D or VD
Day 109	Density	3	2826910	14.57	<0.001	
	Residuals	12	193965			VS≠S or D or VD
Day 139	Density	3	2855362	8.96	0.002	
	Residuals	12	318536			VS≠S or D or VD
Day 171	Density	3	3254011	8.10	0.003	
	Residuals	12	401637			VS≠S or D or VD

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

5.3.1.6 Relative growth rate

Relative growth rate was calculated for all plants in each set of populations for each of the six time periods between censuses as growth rate per day. At no time was mean relative growth rate (calculated either by including negative values, RGR2 or reassigning them as zero, RGR1) found to be significantly different for the different density populations (Tables 5.10 and 5.11, Figures 5.12 and 5.13). There seemed to be a trend of higher growth rates in lower density populations, but high variability made this impossible to detect. There was a significant negative correlation between both the relative growth rate measures and time and a very strong positive correlation between RGR1 and RGR2 (Table 5.2).

Table 5.10 Analysis of Variance (and Tukey Tests) of initial density on RGR1 in *Fucus serratus* over different periods.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0-19	Density	3	0.0000005	1.74	0.211	NA
	Residuals	12	0.0000003			
Day 19-40	Density	3	0.0000005	1.07	0.399	NA
	Residuals	12	0.0000005			
Day 40-71	Density	3	0.0000004	0.49	0.694	NA
	Residuals	12	0.0000009			
Day 71-109	Density	3	0.0000006	2.12	0.151	NA
	Residuals	12	0.0000003			
Day 109-139	Density	3	0.0000001	0.52	0.678	NA
	Residuals	12	0.0000002			
Day 139-171	Density	3	0.0000001	0.92	0.461	NA
	Residuals	12	0.0000001			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

Figure 5.12 RGR1 in populations of *Fucus serratus* grown in tanks at different initial densities. Bars = ±1S.E.

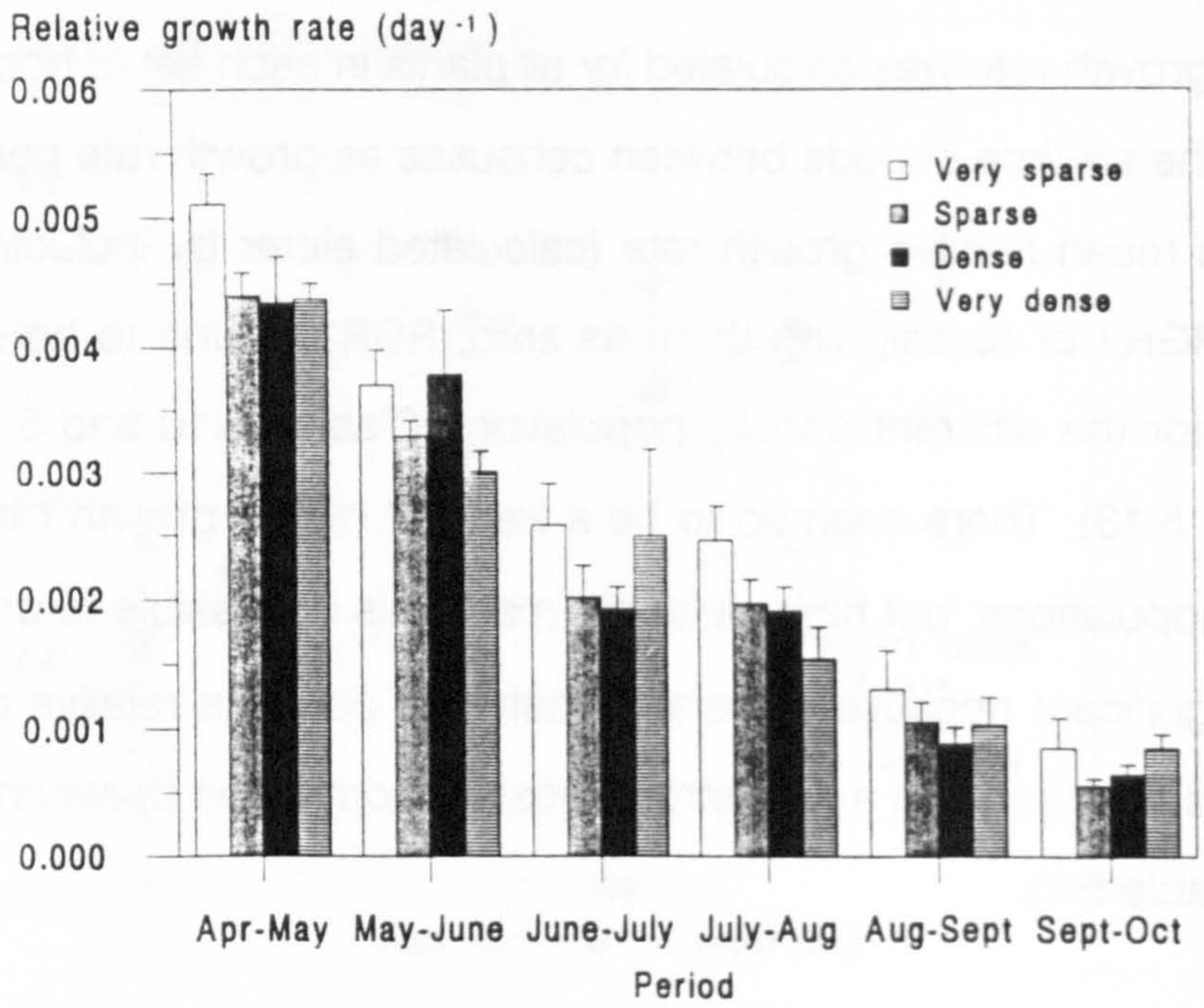


Figure 5.13 RGR2 in populations of *Fucus serratus* grown in tanks at different initial densities. Bars = ±1S.E.

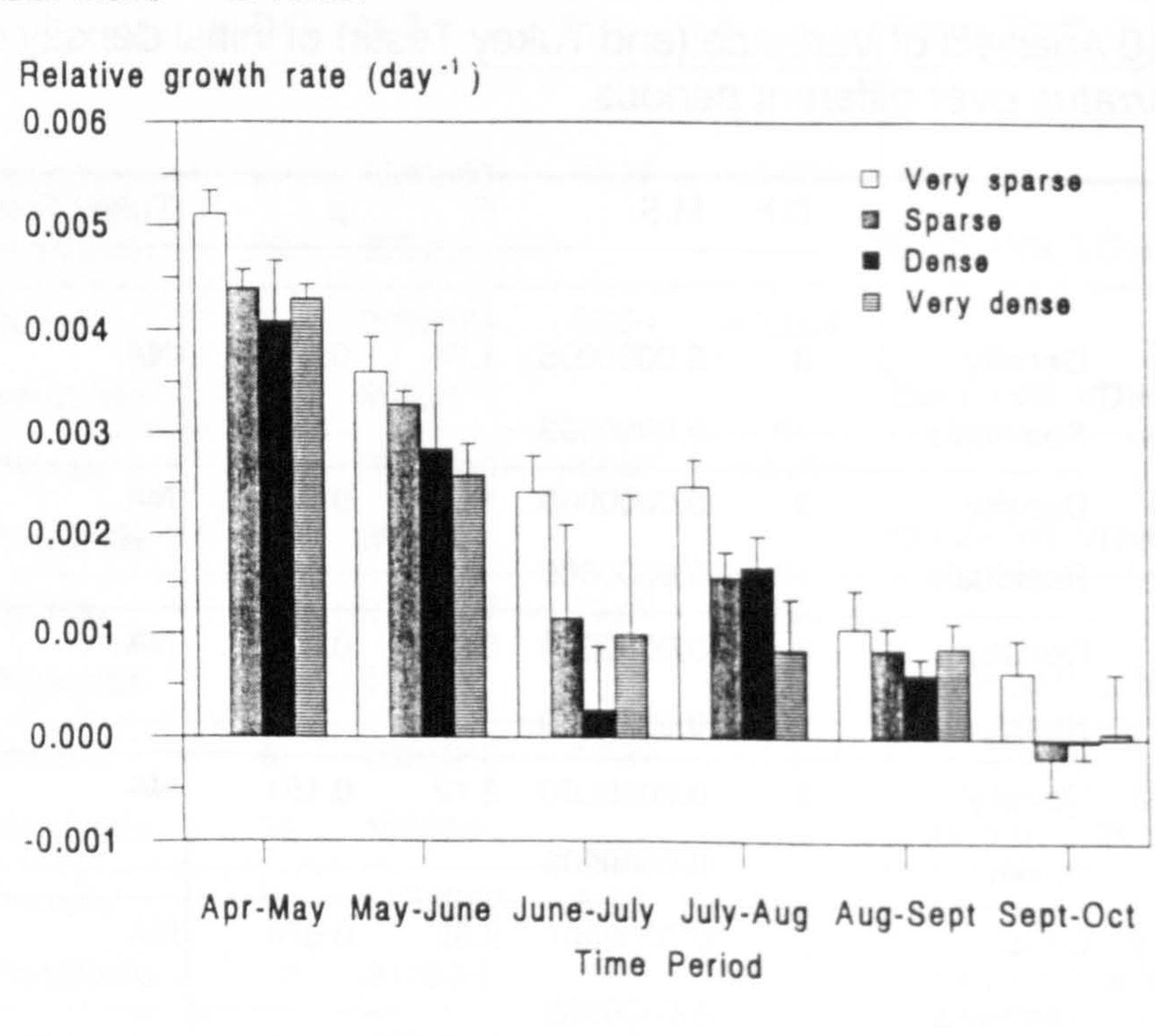


Table 5.11 Analysis of Variance (and Tukey Tests) of initial density on RGR2 in *Fucus serratus* over different periods.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0-19	Density	3	0.0000008	1.35	0.305	NA
	Residuals	12	0.0000006			
Day 19-40	Density	3	0.0000008	0.36	0.782	NA
	Residuals	12	0.0000023			
Day 40-71	Density	3	0.0000031	0.73	0.555	NA
	Residuals	12	0.0000043			
Day 71-109	Density	3	0.0000017	2.75	0.089	NA
	Residuals	12	0.0000006			
Day 109-139	Density	3	0.0000001	0.37	0.774	NA
	Residuals	12	0.0000004			
Day 139-171	Density	3	0.0000005	0.67	0.586	NA
	Residuals	12	0.0000008			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different

5.3.1.7 Density biomass relationships

From plots of $\log_{10}$ mean plant weight-$\log_{10}$ density (Figure 5.14) and $\log_{10}$ biomass-$\log_{10}$ density (Figure 5.15) it was obvious that many of the points fell below any potential thinning line. Rejection of points below the suspected thinning line was carried out prior to testing of slopes. The points used are represented in Figures 5.14 and 5.15, only points above the lines being used to fit PCA slopes. Of 112 points, 76 were rejected. The remaining points gave slopes not significantly different from the expected for both $\log_{10}$ biomass-$\log_{10}$ density and $\log_{10}$ mean plant weight-$\log_{10}$ density, and both relationships gave significant negative correlations (Table 5.12).

Table 5.12 The relationship between Density, Biomass and Mean Plant Weight in artificial *Fucus serratus* populations grown in tanks. Slopes fit by PCA.

β	Constant	Confidence Limits	r (p = 0.05)	Significance*
Density-Mean Plant Weight (Expected β = -1.5)				
-1.58	5.43	-1.808, -1.393	-0.938	
Density-Biomass (Expected β = -0.5)				
-0.574	5.411	-0.856, -0.347	-0.638	

*S indicates that the slope *is* different from the expected

Figure 5.14 Density-mean plant weight relationship in artificial *Fucus serratus* populations grown at different densities in tanks. Only points above the line used for PCA slope fitting.

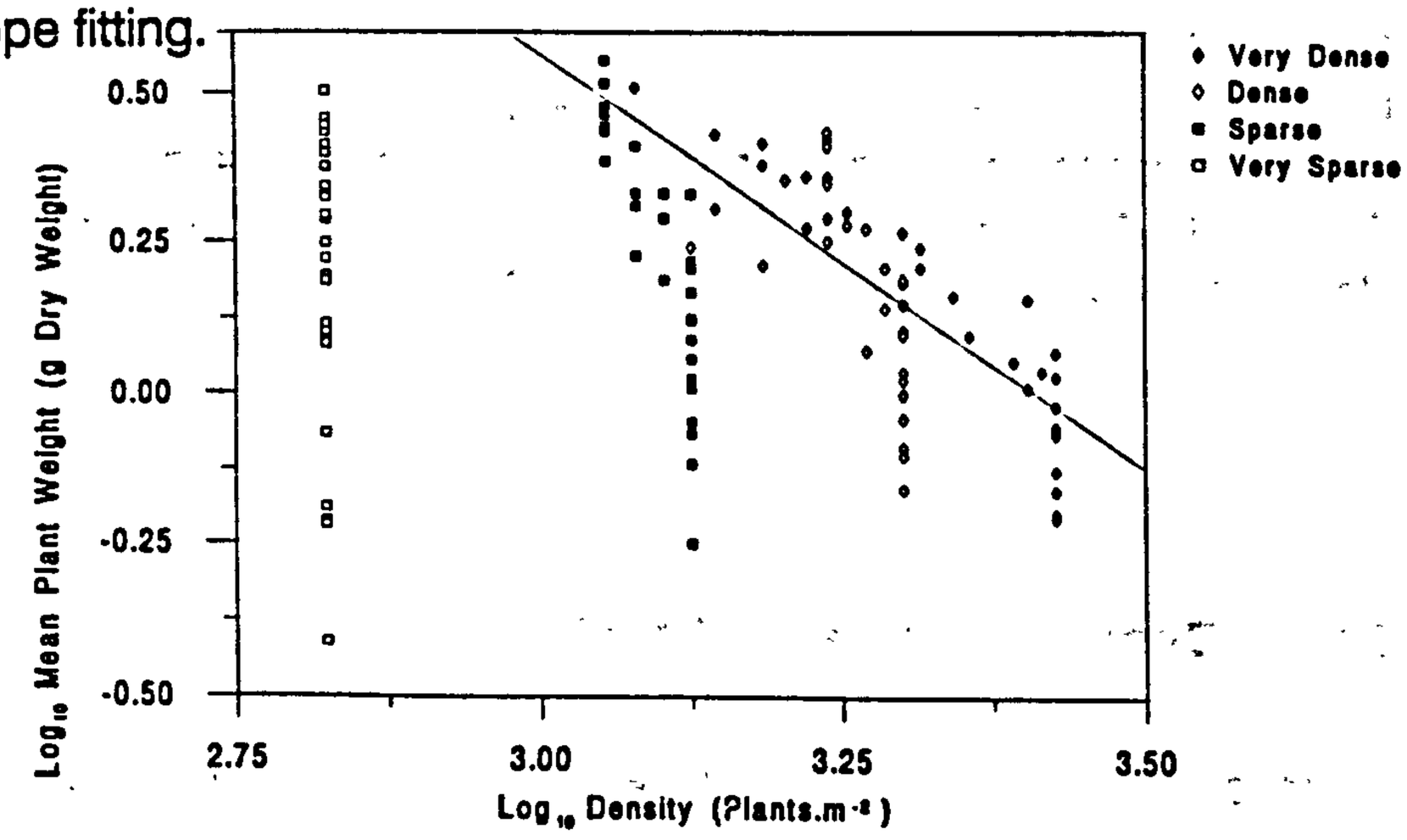
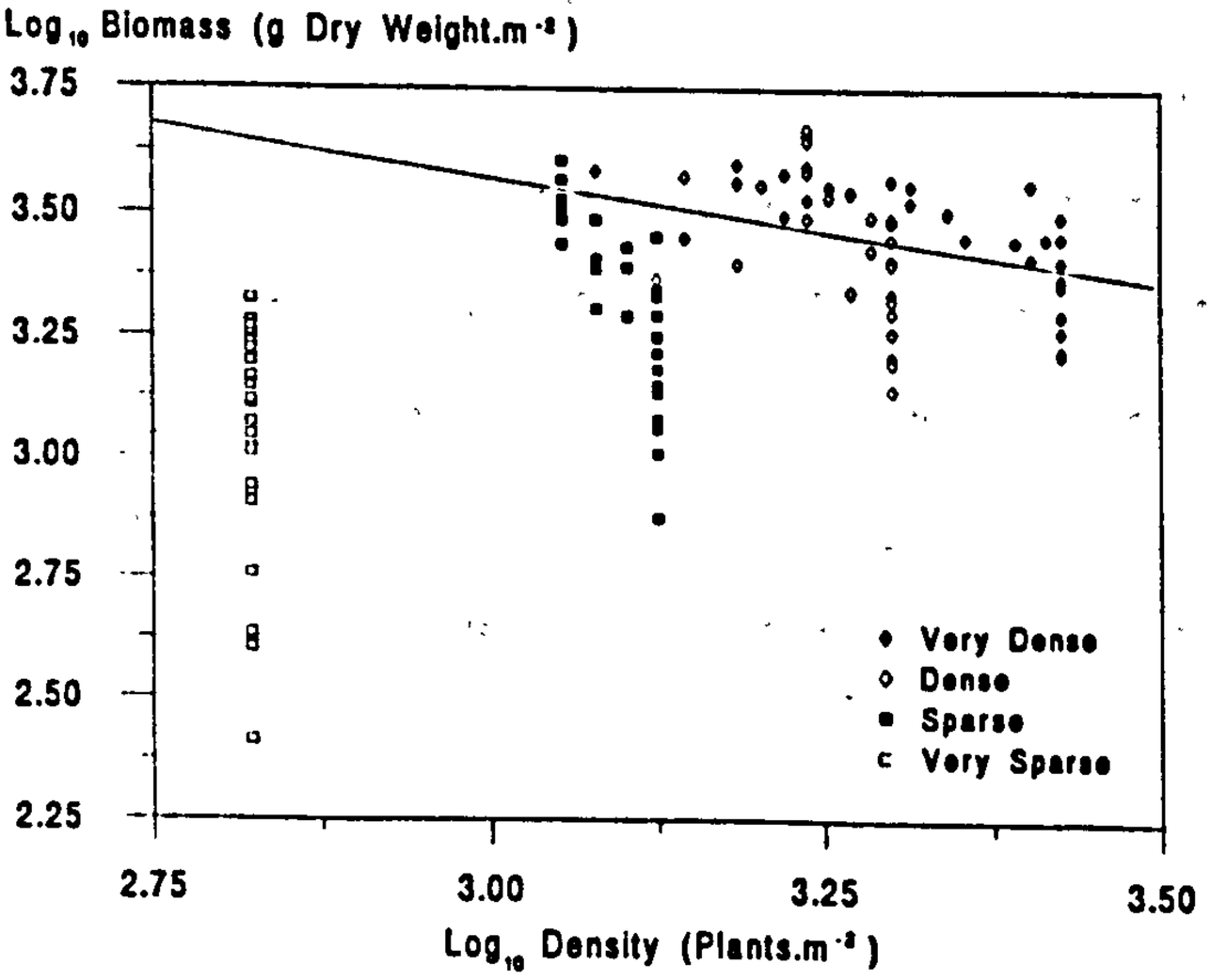


Figure 5.15 Density-biomass relationship in artificial *Fucus serratus* populations grown at different densities in tanks. Only points above the line used for PCA slope fitting.



5.3.2 Laminaria digitata

5.3.2.1 Wet weight-dry weight relationship

There was a strong relationship between wet and dry weight in *L. digitata* calculated by simple linear regression (Figure 5.16):

Dry Weight = 0.436 + 0.136 Wet Weight. $n=34$, STD=0.001, $R^2=99.6$, $p<0.001$

5.3.2.2 Population Structure

Graphical portrayal of size structure as frond length-frequency histograms showed rather similar features for all five density treatments (Figure 5.17). Size structure was initially tightly distributed about the mean and highly peaked. Subsequently, two major changes occurred in all the treatments. The histograms broadened as some plants remaining small and others grew. A second feature of the length-frequency histograms was a tendency towards increasing positive skew, particularly in the four most dense populations. The length distribution of fronds about the mean in the most sparse population was generally normal.

Figure 5.16 Wet weight-dry weight relationship in *Laminaria digitata*.

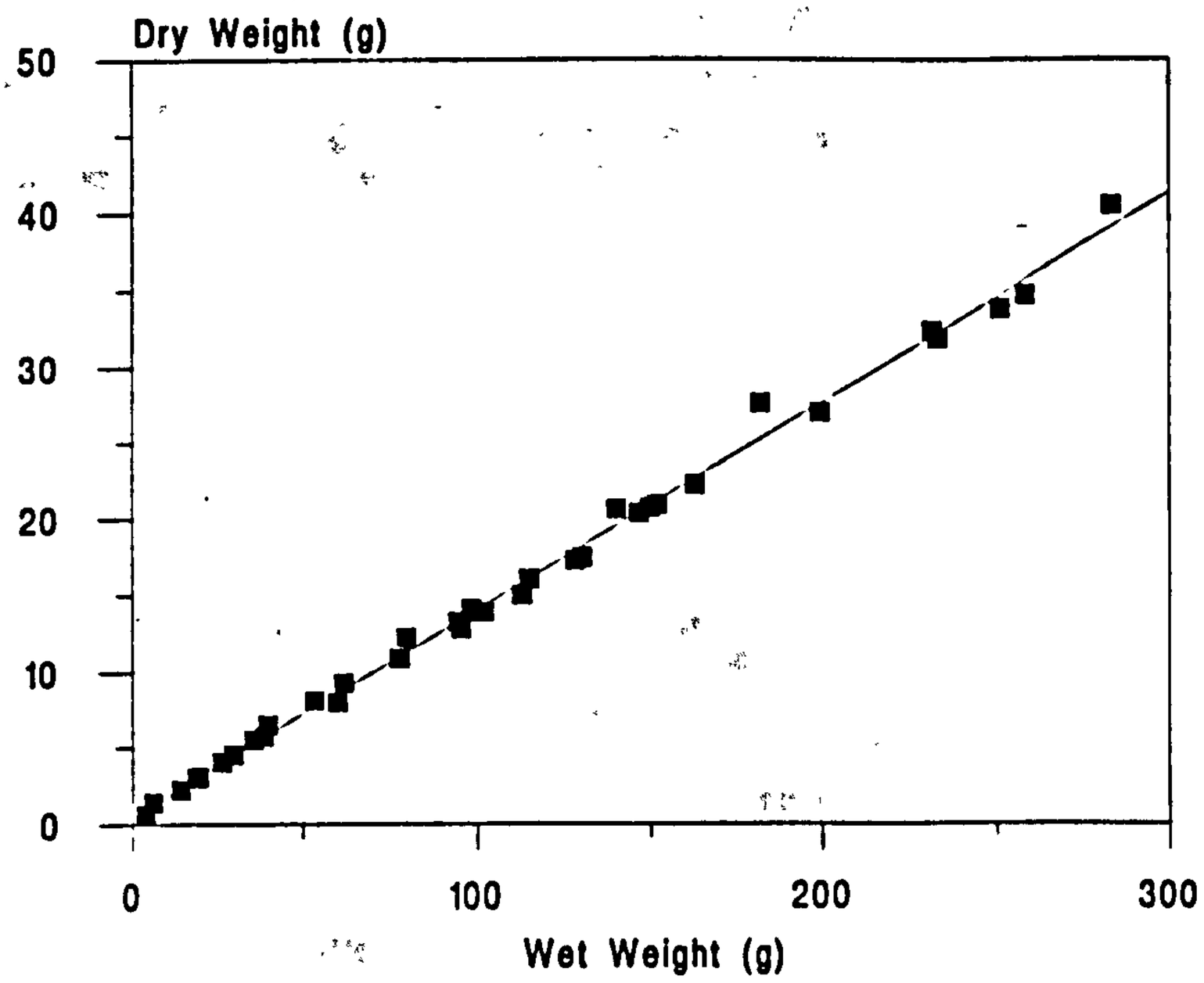


Figure 5.17 Length percentage frequency histograms for populations of *Laminaria digitata* at different initial densities over time. All scales identical.

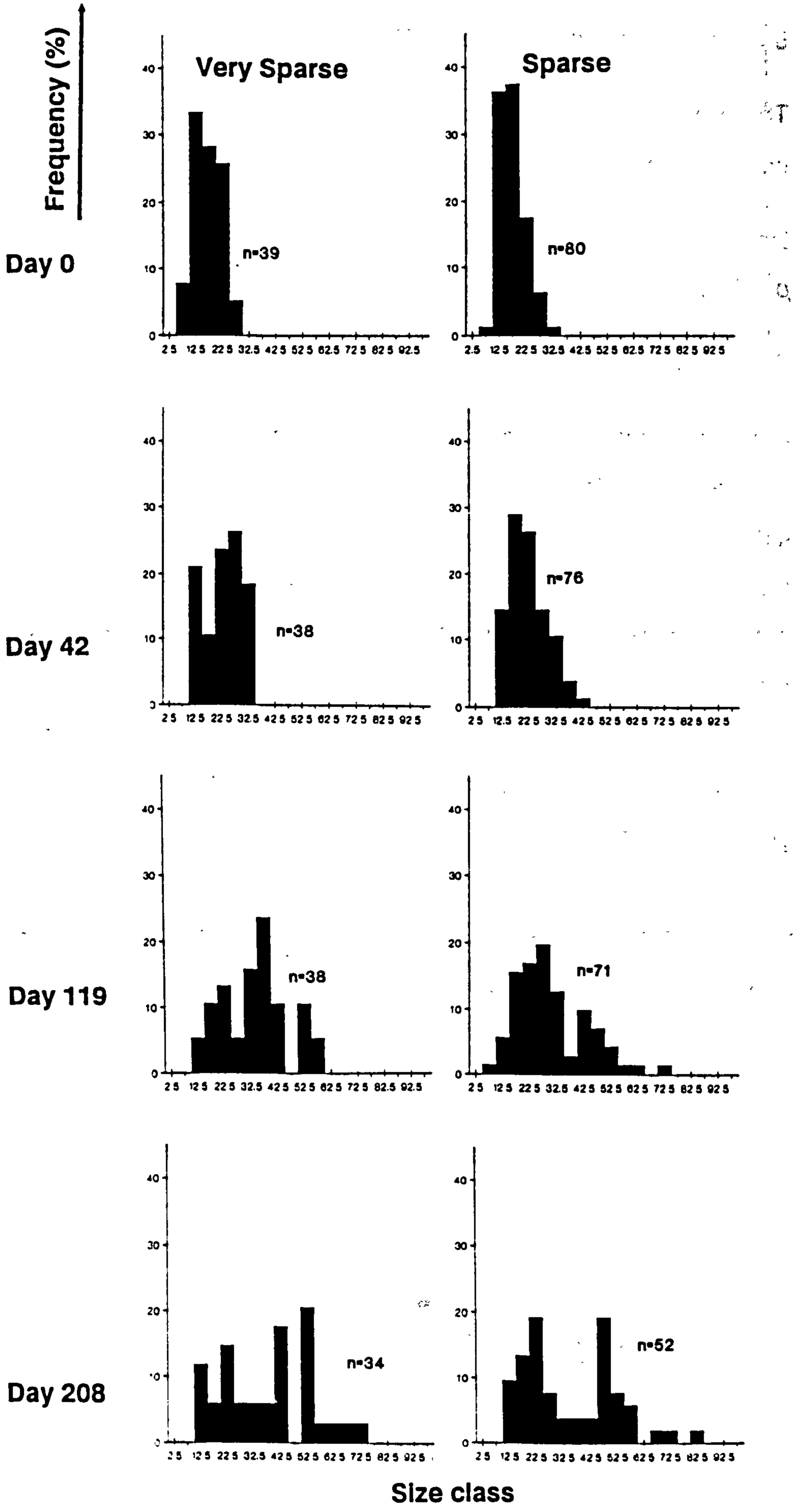
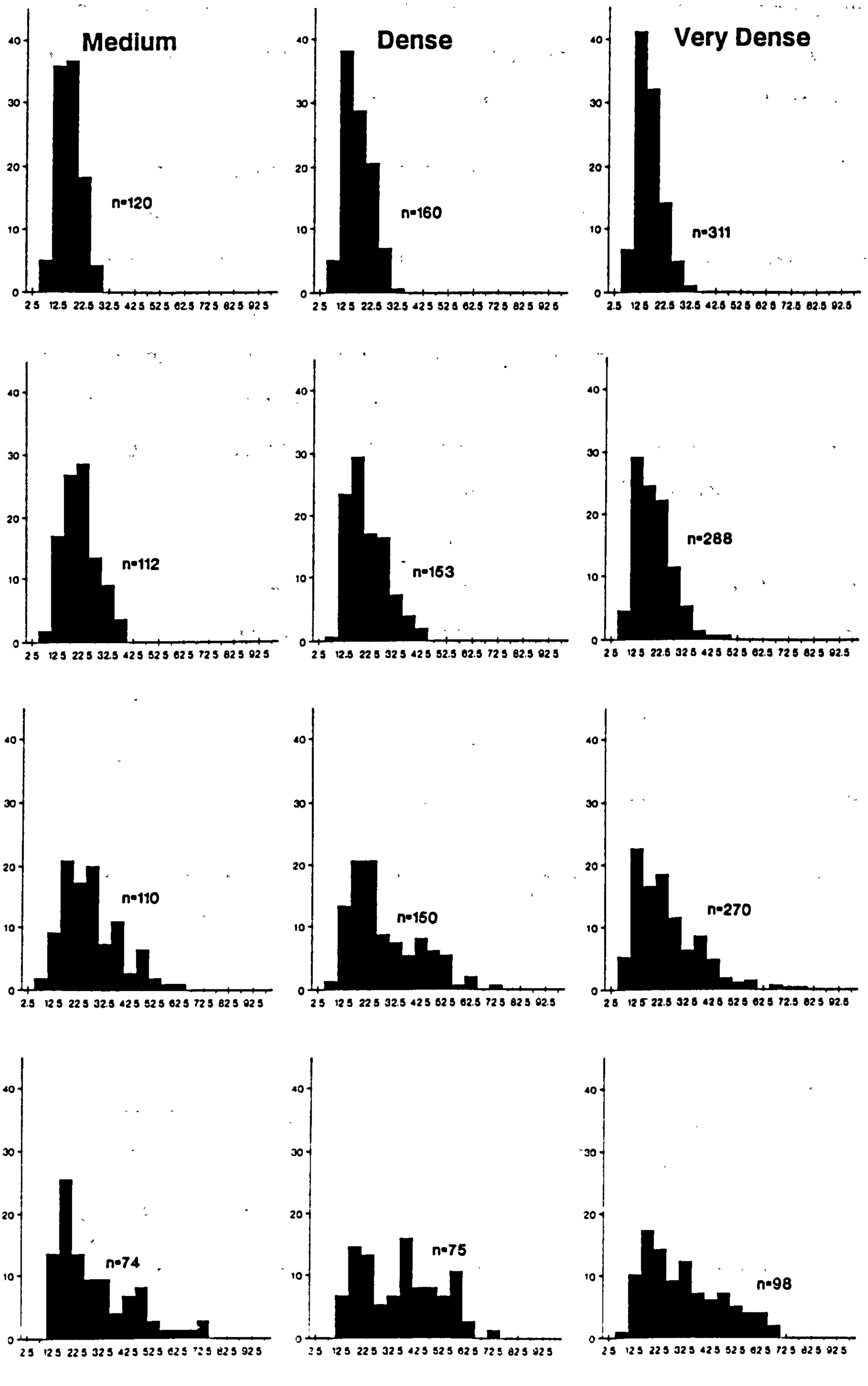


Figure 5.17 Cont. Length percentage frequency histograms for populations of *Laminaria digitata* at different initial densities over time. All scales identical.



a) Coefficient of Variation

The variability (as coefficient of variation) was similar to the measure of inequality, the Gini coefficient, and there was a strong positive correlation between these two measures (Table 5.13).

Generally, variability in frond length as coefficient of variation increased from the start of the study until day 139 after which variability of size decreased in the two most dense populations (Figure 5.18). There was a positive correlation between time and coefficient of variation (Table 5.13). However the three most sparse sets of populations continued to increase in size variability until the end of the experiment at day 208 (Figure 5.18). The higher density populations increased in size variability at a higher rate than the low density populations from the start of the experiment until day 139 (Figure 5.18). Though the different density populations were equally variable at the start and end of the experiment, from day 42 to day 170 higher density populations were more variable in size than lower density ones (Table 5.14), and this was a general feature of these populations (Figure 5.18).

Table 5.13 Correlation coefficients between various measures for data of density and time pooled.

	1	2	3	4	5	6	7	8
1. Standing Crop								
2. Density	0.32*							
3. Mean Frond Length	0.58*	-0.43*						
4. Maximum Frond Length	0.87*	-0.04	0.75*					
5. Coefficient of Variation	0.72*	0.34*	0.26*	0.77*				
6. Gini Coefficient	0.73*	0.33*	0.27*	0.76*	0.99*			
7. Skewness Coefficient	0.27*	0.50*	-0.27*	0.30*	0.59*	0.55*		
8. RGR	-0.71*	-0.25*	-0.48*	-0.72*	-0.65*	-0.65*	0.33*	
9. Time	0.69*	-0.25*	0.79*	0.80*	0.59*	0.58*	0.08	-0.71*

* = Significant @ p = 0.05, n = 220 except 8, n = 200. (Pearson)

b) Gini Coefficient

This measure of equality of frond sizes within a population performed very similarly to the coefficient of variation (Figure 5.19 cf Figure 5.18). ANOVA performed at each time for density differences gave essentially similar results

Table 5.14 Analysis of Variance (and Tukey Tests) of initial density on coefficient of variation of plant length in *Laminaria digitata* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	0.002681	0.66	0.631	NA
	Residuals	15	0.004078			
Day 16	Density	4	0.004377	0.99	0.442	NA
	Residuals	15	0.004410			
Day 29	Density	4	0.009056	2.08	0.134	NA
	Residuals	15	0.004352			
Day 42	Density	4	0.016294	4.14	0.019	S≠VD
	Residuals	15	0.003934			
Day 56	Density	4	0.022388	5.24	0.008	VD≠VS, S or M
	Residuals	15	0.00427			
Day 88	Density	4	0.037533	11.21	<0.001	VD≠VS, S or M
	Residuals	15	0.003348			D≠VS
Day 101	Density	4	0.043071	12.25	<0.001	VD≠VS, S or M
	Residuals	15	0.003515			D≠VS or S
Day 119	Density	4	0.041226	9.45	0.001	VD≠VS, S or M
	Residuals	15	0.004361			D≠VS
Day 139	Density	4	0.050932	10.12	<0.001	VD≠VS, S or M
	Residuals	15	0.005031			D≠VS or S
Day 170	Density	4	0.024321	3.92	0.023	VS≠VD
	Residuals	15	0.006203			
Day 208	Density	4	0.010497	2.66	0.074	NA
	Residuals	15	0.003950			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

Figure 5.18 Coefficient of variation of plant length in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.

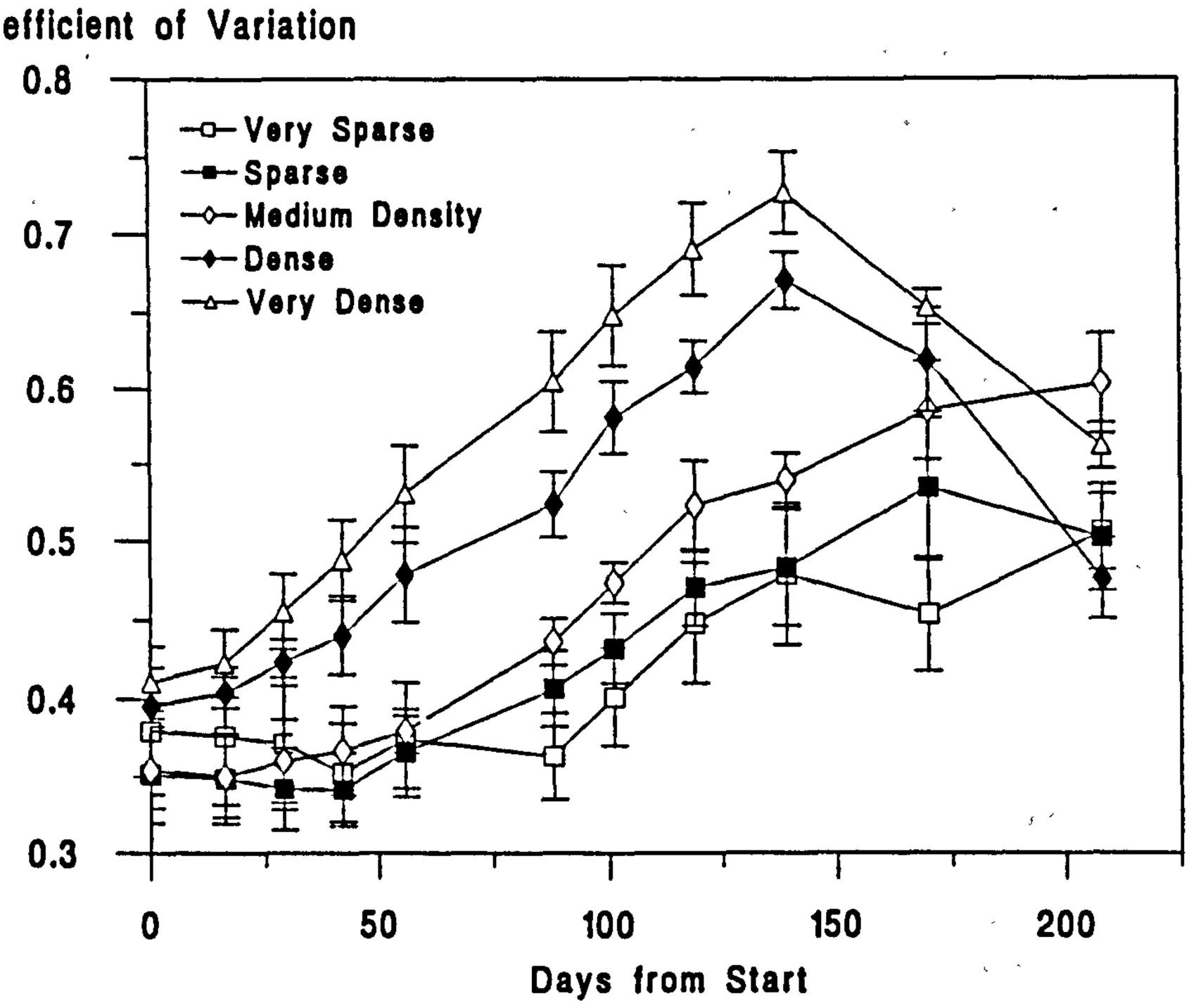
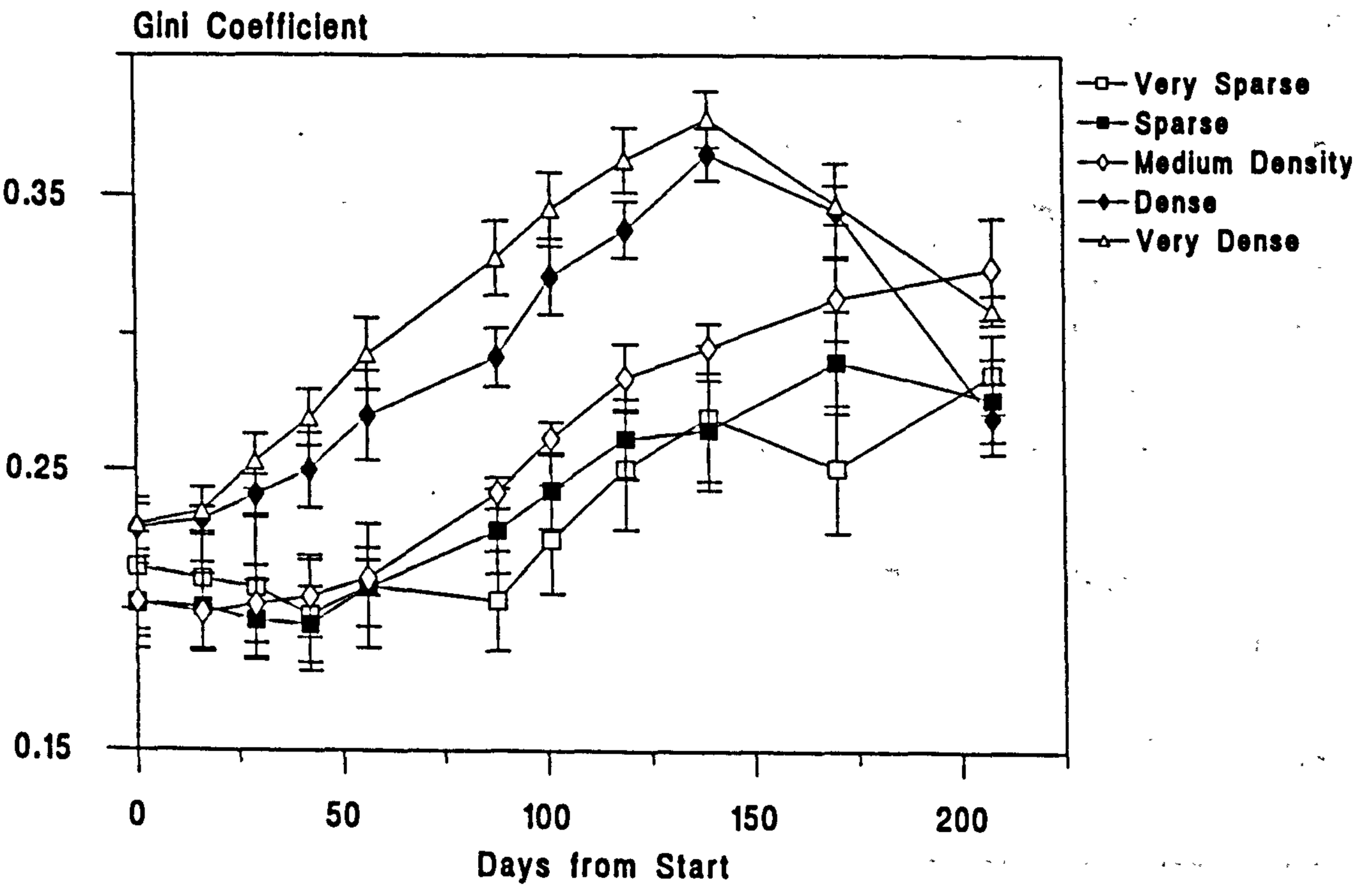


Figure 5.19 Gini coefficient of plant length in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.



to variability measured as coefficient of variation (Table 5.15 cf Table 5.14). There was generally an increase in frond size inequality for the first 139 days of the experiment (Figure 5.19). However, the three most sparse density sets of populations continued to increase in size inequality until the end of the experiment, as in size variability above (Figure 5.19). Though frond size

Table 5.15 Analysis of Variance (and Tukey Tests) of initial density on Gini Coefficient of plant length in *Laminaria digitata* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	0.000733	0.68	0.615	NA
	Residuals	15	0.001074			
Day 16	Density	4	0.001154	0.94	0.466	NA
	Residuals	15	0.001224			
Day 29	Density	4	0.002559	2.07	0.136	NA
	Residuals	15	0.001236			
Day 42	Density	4	0.004603	4.03	0.020	VD≠S
	Residuals	15	0.001142			
Day 56	Density	4	0.006484	5.19	0.008	VD≠VS, S or M
	Residuals	15	0.001250			D≠VS
Day 88	Density	4	0.0101038	10.91	<0.001	VD≠VS, S or M
	Residuals	15	0.0009264			D≠VS or S
Day 101	Density	4	0.01067	10.42	<0.001	VD≠VS, S or M
	Residuals	15	0.001025			D≠VS or S
Day 119	Density	4	0.009537	8.26	0.001	VD≠VS, S or M
	Residuals	15	0.001155			D≠VS or S
Day 139	Density	4	0.011338	8.07	0.001	VD≠VS, S or M
	Residuals	15	0.001405			D≠VS or S
Day 170	Density	4	0.006474	4.14	0.019	VD≠VS, S or M
	Residuals	15	0.001565			D≠VS or S
Day 208	Density	4	0.002141	2.05	0.139	NA
	Residuals	15	0.001046			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

inequality was the same in all densities at the beginning and end of the experiment, the higher density populations increased in frond size inequality faster than the low density populations, and generally frond size inequality was higher in higher density populations (Figure 5.19 and Table 5.15).

The Gini coefficient was positively correlated with time, standing crop, mean and maximum length, density and population skewness (Table 5.13).

c) Population Skewness

All densities except the most sparse exhibited positive skewness in length for most of the study (Figure 5.20), and in general terms populations exhibited a positive skew (Figure 5.20). In the four highest density treatments there was an increase in the degree of positive skew until 139 days after the start. Subsequently, the most dense, dense and sparse treatments became less positively skewed. The lowest density treatment exhibited fluctuations in skewness which straddled zero, suggesting that this treatment was essentially normally distributed. There was no difference in skewness between densities at the start of the experiment and for the first 29 days (Table 5.16), but after this time the highest density populations were significantly more positively skewed than the lower density ones, and this was the case for most of the time (Table 5.16, Figure 5.20).

The skewness coefficient was weakly negatively correlated with mean frond length, and positively correlated with the coefficient of variation, Gini coefficient and density (Table 5.13).

5.3.2.3 Frond length

Mean frond length increased in all populations throughout the course of the study (Figure 5.21). There was a steady increase in mean frond length in all densities until day 119 (Figure 5.21). After this time the two highest density sets of populations continued to increase at the same rates, while the three least dense populations ceased to increase and maintained a constant level (Figure

Table 5.16 Analysis of Variance (and Tukey Tests) of initial density on skewness coefficient of plant length in *Laminaria digitata* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	0.2166	0.63	0.651	NA
	Residuals	15	0.3454			
Day 16	Density	4	0.4852	1.17	0.364	NA
	Residuals	15	0.4156			
Day 29	Density	4	0.6689	2.13	0.128	NA
	Residuals	15	0.3147			
Day 42	Density	4	1.1412	5.94	0.005	VS≠M, D or VD
	Residuals	15	0.1921			
Day 56	Density	4	0.7005	4.14	0.019	VS≠M or VD
	Residuals	15	0.1692			
Day 88	Density	4	1.0599	6.54	0.003	VS≠M, D or VD
	Residuals	15	0.1621			
Day 101	Density	4	0.7575	6.50	0.003	VS≠M or VD
	Residuals	15	0.1166			
Day 119	Density	4	0.8046	5.46	0.006	VS≠VD
	Residuals	15	0.1474			
Day 139	Density	4	1.0890	8.00	0.001	VS≠M, D or VD
	Residuals	15	0.1361			
Day 170	Density	4	2.3242	5.27	0.007	VS≠M or VD
	Residuals	15	0.4411			
Day 208	Density	4	0.8627	4.10	0.019	VS≠M
	Residuals	15	0.2102			M≠D

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

Figure 5.20 Skewness coefficient of plant length in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.

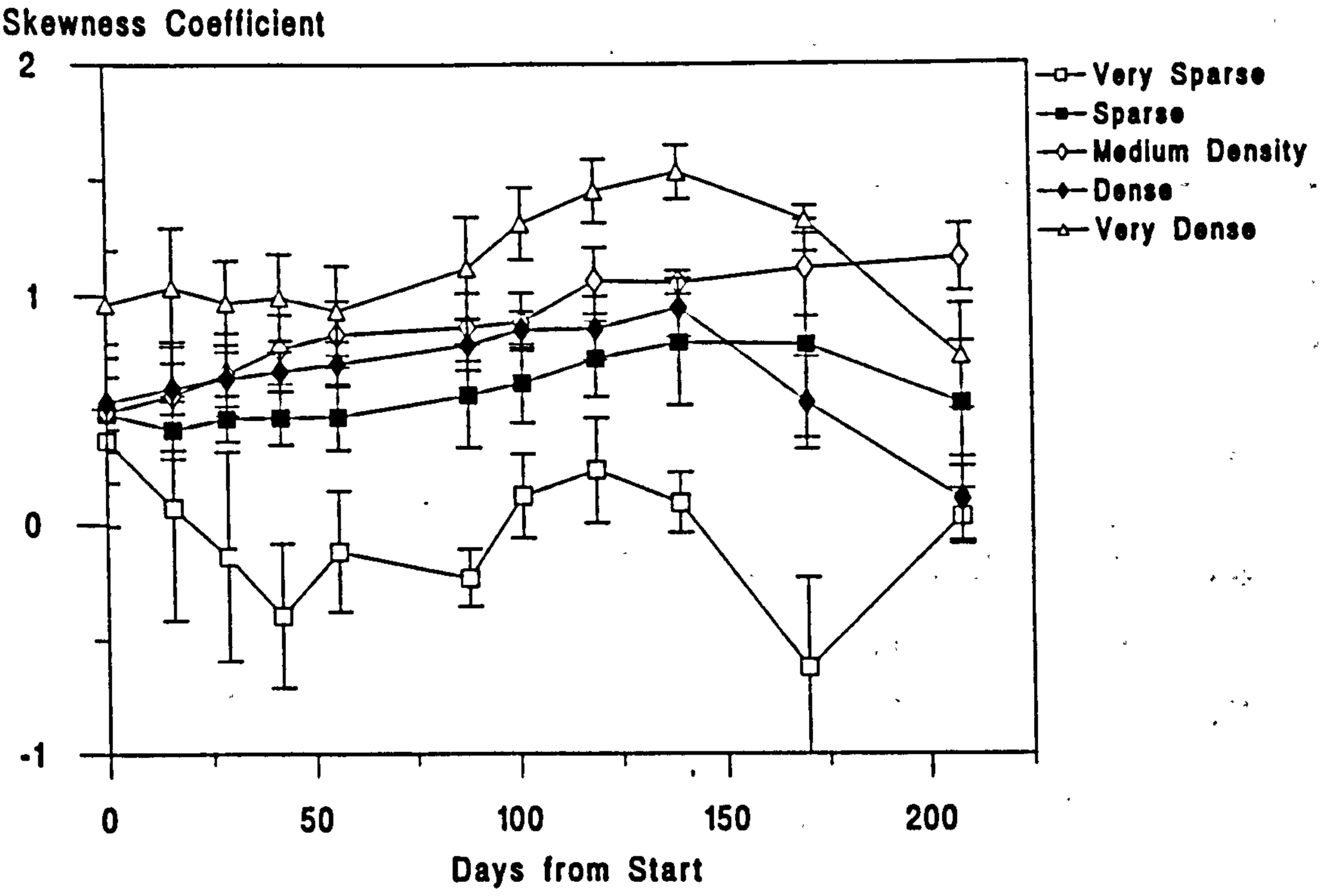


Figure 5.21 Mean frond length in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.

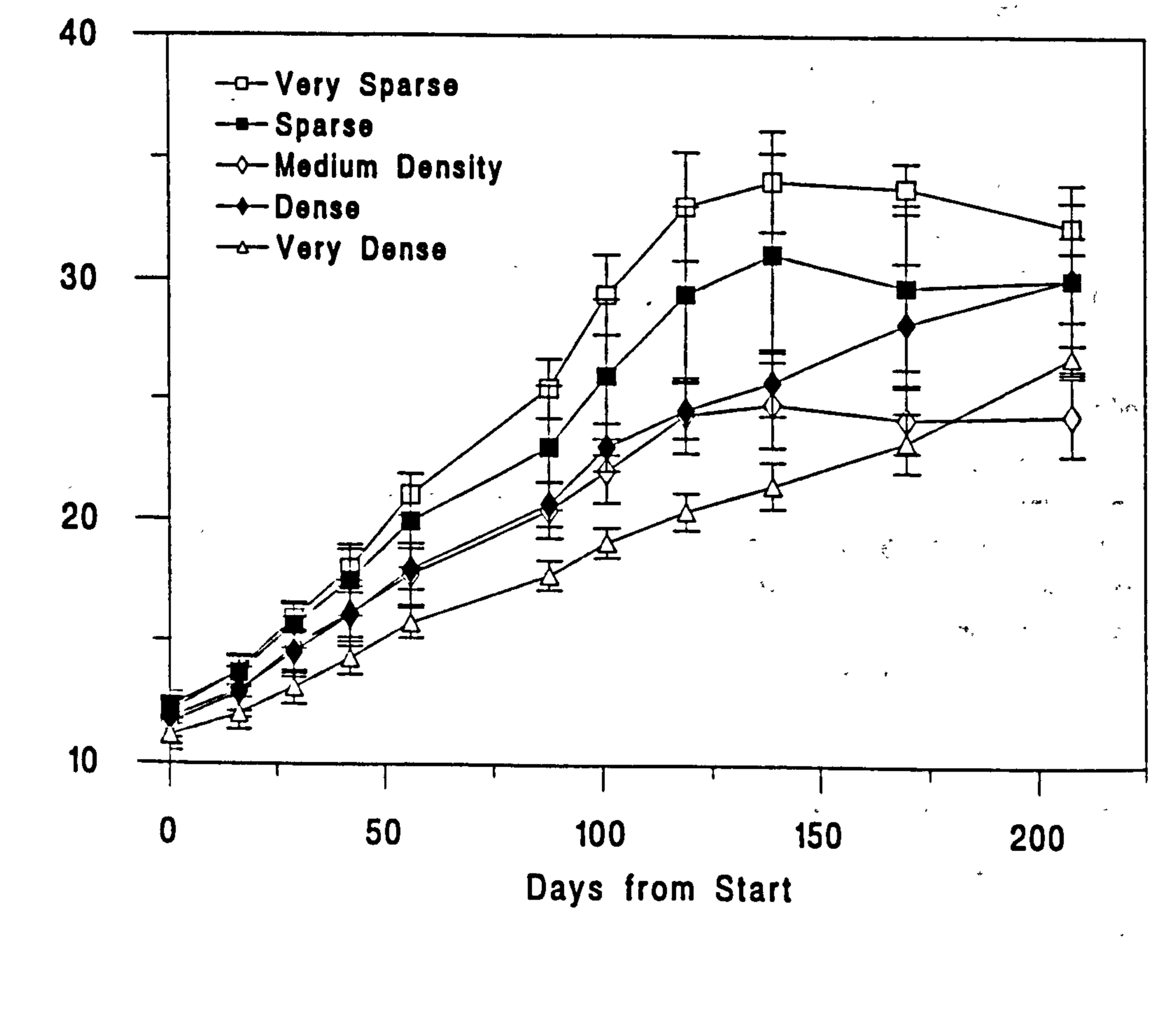


Table 5.17 Analysis of Variance (and Tukey Tests) of initial density on mean frond length in *Laminaria digitata* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	0.833	0.33	0.855	NA
	Residuals	15	2.538			
Day 16	Density	4	2.063	0.64	0.640	NA
	Residuals	15	3.209			
Day 29	Density	4	4.870	1.14	0.373	NA
	Residuals	15	4.254			
Day 42	Density	4	8.452	1.33	0.302	NA
	Residuals	15	6.331			
Day 56	Density	4	16.943	2.20	0.118	NA
	Residuals	15	7.690			
Day 88	Density	4	33.53	2.99	0.053	NA
	Residuals	15	11.23			
Day 101	Density	4	61.23	3.50	0.033	VD≠VS
	Residuals	15	17.51			
Day 119	Density	4	96.58	4.04	0.020	VD≠VS
	Residuals	15	23.88			
Day 139	Density	4	102.46	3.54	0.032	VD≠VS
	Residuals	15	28.95			
Day 170	Density	4	73.33	3.04	0.051	NA
	Residuals	15	24.12			
Day 208	Density	4	38.65	1.61	0.222	NA
	Residuals	15	23.96			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

5.21). ANOVA revealed no significant difference in mean frond length between densities at the start of the experiment and for the subsequent 88 days (Table 5.17). Between days 88 and 139 mean frond length in the lowest density populations was significantly higher than in the highest density populations. From day 170 to 208 (the end of the experiment) there was no significant

difference in mean frond length between densities (Table 5.17). Generally, lower density populations had higher mean plant lengths (Figure 5.21). Mean frond length was strongly correlated with time and maximum frond length (Table 5.13).

Maximum frond length increased throughout the experiment until day 139 (Figures 5.22). At no time was maximum frond length found to be significantly different between densities (Table 5.18, Figure 5.22). Maximum frond length was highly correlated with time, standing crop, Gini coefficient and coefficient of variation, but not density (Table 5.13).

Figure 5.22 Maximum frond length in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.

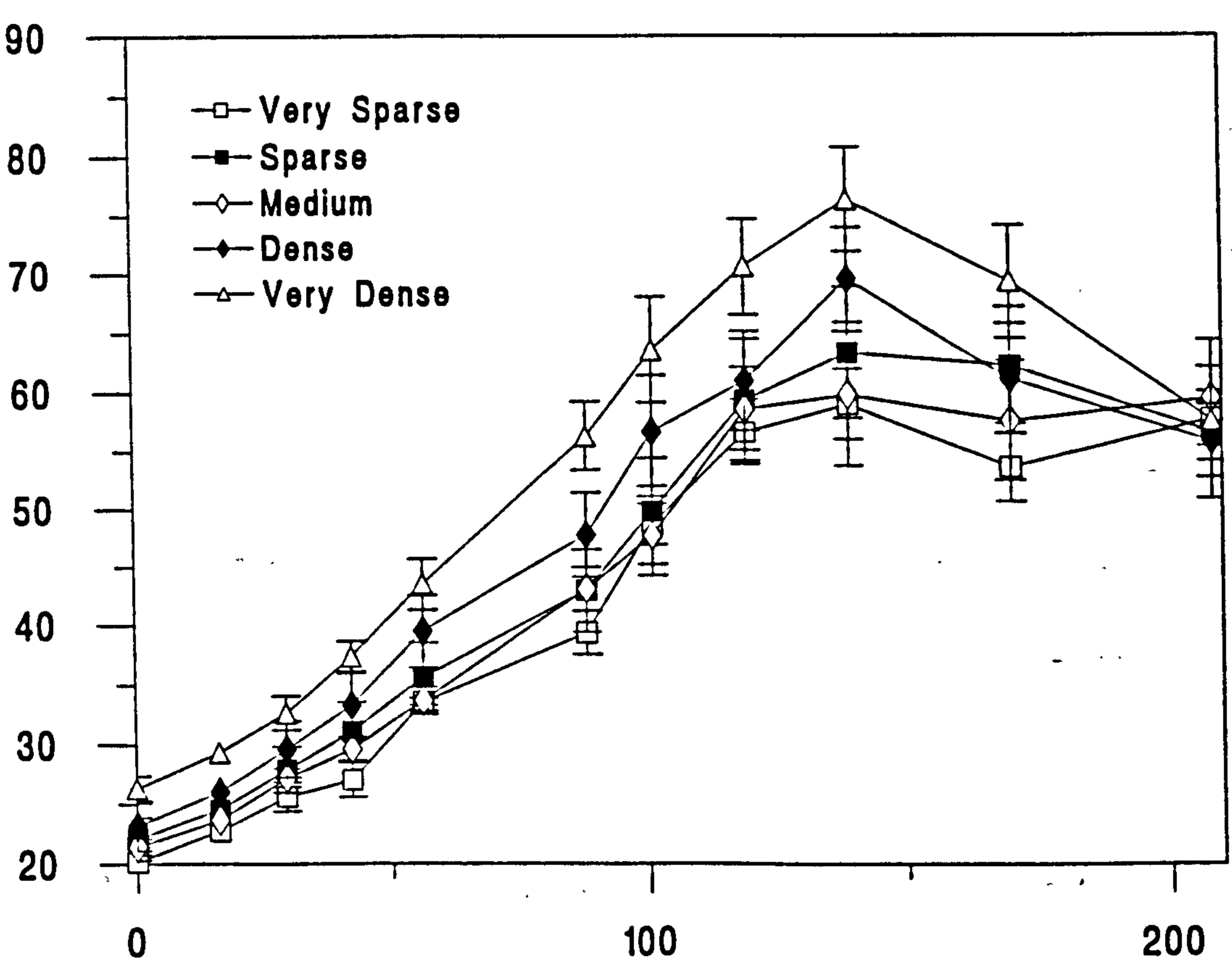


Table 5.18 Analysis of Variance (and Tukey Tests) of initial density on maximum frond length in *Laminaria digitata* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	21.75	1.99	0.148	NA
	Residuals	15	10.92			
Day 16	Density	4	26.63	1.84	0.174	NA
	Residuals	15	14.49			
Day 29	Density	4	28.85	1.49	0.256	NA
	Residuals	15	19.42			
Day 42	Density	4	61.31	2.43	0.093	NA
	Residuals	15	25.22			
Day 56	Density	4	72.20	1.65	0.214	NA
	Residuals	15	43.78			
Day 88	Density	4	170.05	2.03	0.142	NA
	Residuals	15	83.77			
Day 101	Density	4	183.34	2.10	0.131	NA
	Residuals	15	87.24			
Day 119	Density	4	119.7	0.97	0.453	NA
	Residuals	15	123.6			
Day 139	Density	4	212.6	1.92	0.160	NA
	Residuals	15	110.8			
Day 170	Density	4	137.93	1.73	0.195	NA
	Residuals	15	79.67			
Day 208	Density	4	7.78	0.08	0.987	NA
	Residuals	15	94.57			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

5.3.2.4 Density and survivorship

Density decreased in all treatments from the start to the end of the experiment, though decrease was most pronounced later on, between days 139-208 (Figures 5.23). Mortality was density dependent, and while 87 % of the plants remained in the lowest density populations at the end of the experiment, only 31 % remained in the highest density populations (Figure 5.24). For most of the experiment (day 0-139) ANOVA (Table 5.19) revealed that all populations remained significantly different as at the start of the experiment. However

Figure 5.23 Change in density in *Laminaria digitata* at different initial densities over time. Bars = ± 1.S.E.

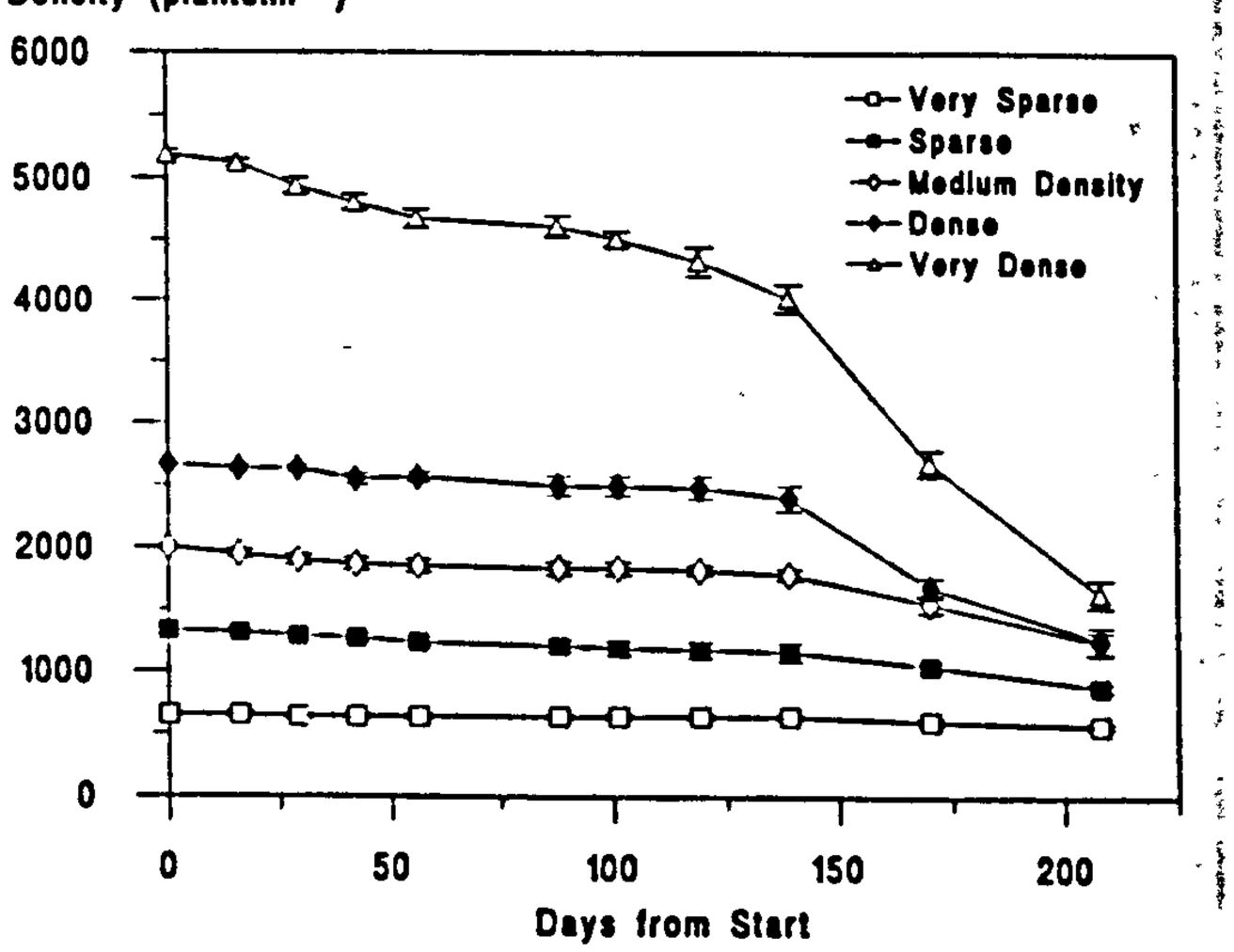
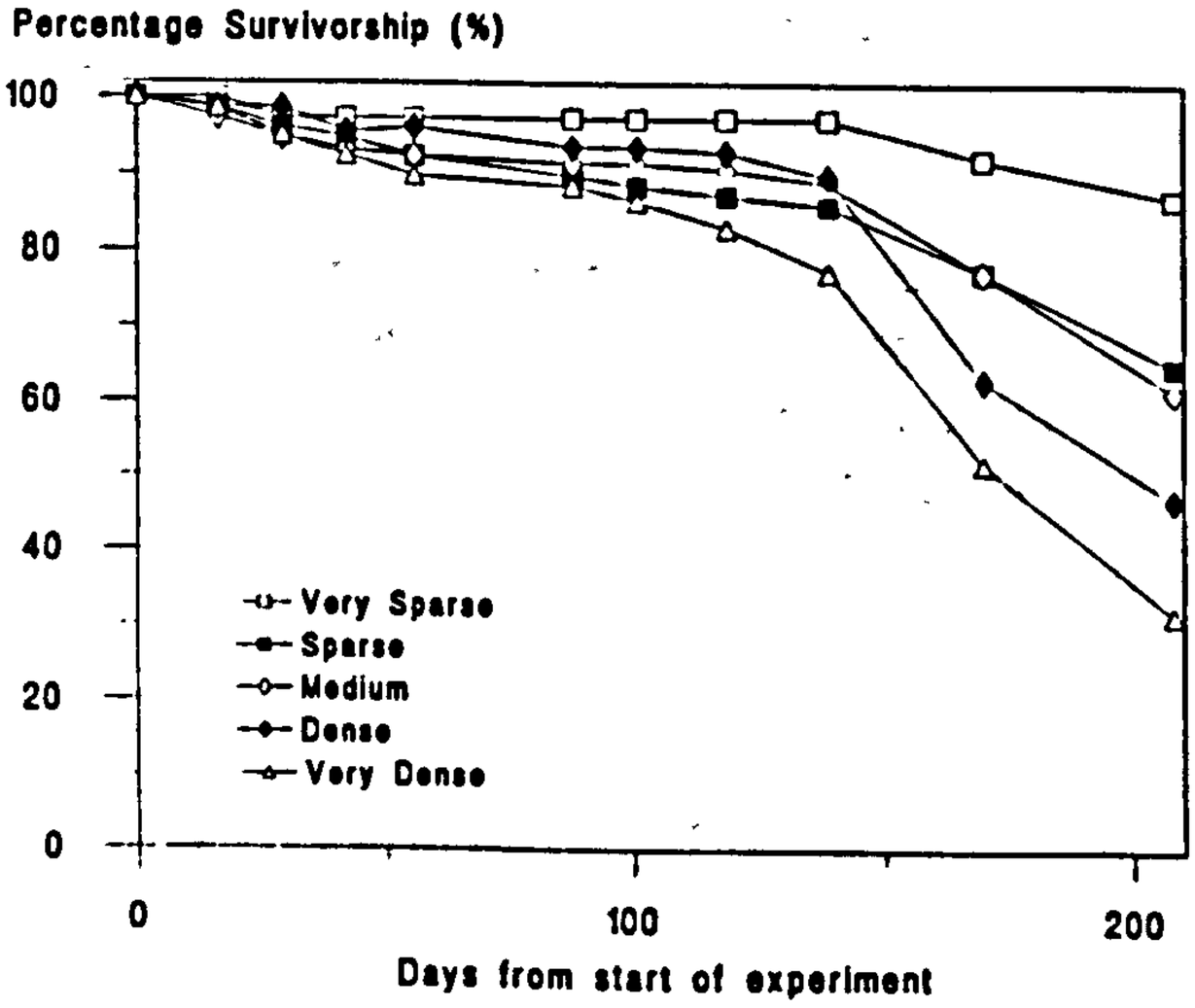


Figure 5.24 Standardised survivorship in populations of *Laminaria digitata* at different densities



between days 170 and 208 densities became more similar as density dependent mortality took place (Table 5.19). Density was positively correlated with skewness, and negatively correlated with mean plant length (Table 5.13).

Table 5.19 Analysis of Variance (and Tukey Tests) of initial density on subsequent density in *Laminaria digitata* at different time periods.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	12184954	7469.68	<0.001	All different
	Residuals	15	1631			
Day 16	Density	4	11862966	3999.75	<0.001	All different
	Residuals	15	2966			
Day 29	Density	4	11025239	1443.61	<0.001	All different
	Residuals	15	7637			
Day 42	Density	4	10326763	1031.64	<0.001	All different
	Residuals	15	10010			
Day 56	Density	4	9739510	826.11	<0.001	All different
	Residuals	15	11790			
Day 88	Density	4	9437431	474.92	<0.001	All different
	Residuals	15	19872			
Day 101	Density	4	8986980	533.93	<0.001	All different
	Residuals	15	16832			
Day 119	Density	4	8169831	269.39	<0.001	All different
	Residuals	15	30327			
Day 139	Density	4	6870977	197.58	<0.001	All different
	Residuals	15	34776			
Day 170	Density	4	2466131	99.88	<0.001	All different except
	Residuals	15	24691			M and D
Day 208	Density	4	663774	18.38	<0.001	VS≠M, D, or VD
	Residuals	15	36110			S≠VD

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

5.3.2.5 Standing Crop

Standing crop as dry weight increased in all density populations until day 139 (Figure 5.25). Standing crop subsequently continued to increase in the two lowest density population sets until the end of the experiment, but at a lesser rate, and decreased in the three highest density population sets (Figure 5.25). The mean standing crop was initially highest in the highest density treatment, and lowest in the very sparse population (Table 5.20). However, by the end of the experiment, there was no significant difference in standing crop between densities (Table 5.20). The standing crop increased by an order of magnitude in the lowest density population, fivefold in the medium density population and threefold in the most dense population during the course of the experiment. Standing crop was positively correlated with time and maximum length (Table 5.13).

Figure 5.25 Standing crop in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.

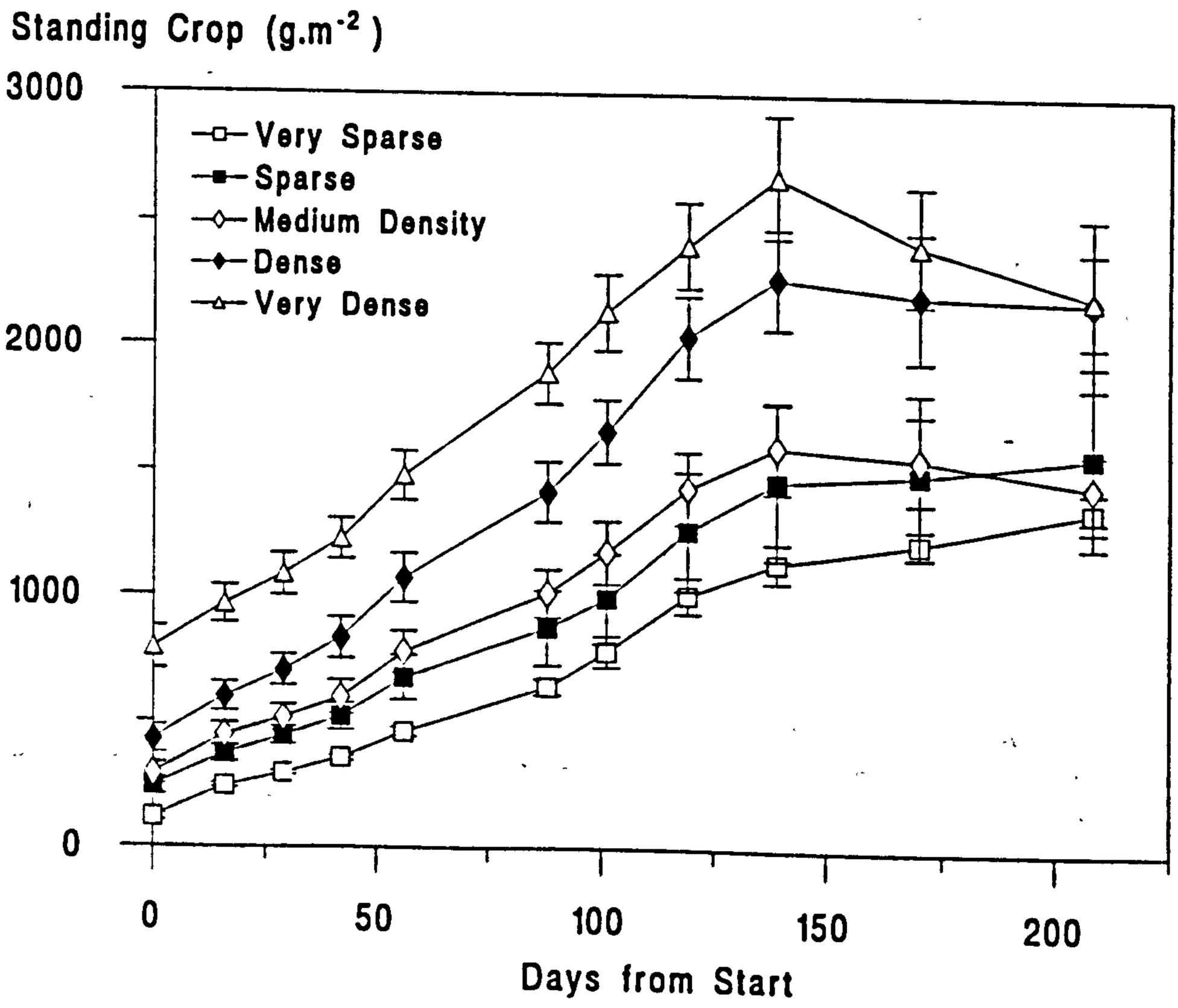


Table 5.20 Analysis of Variance (and Tukey Tests) of initial density on standing crop in *Laminaria digitata* at different times.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0	Density	4	267173	19.59	<0.001	VD≠D, M, S or VS
	Residuals	15	13638			D≠VS
Day 16	Density	4	305851	23.86	<0.001	VD≠D, M, S or VS
	Residuals	15	12819			D≠VS
Day 29	Density	4	368076	23.73	<0.001	VD≠D, M, S or VS
	Residuals	15	15511			D≠VS
Day 42	Density	4	454299	20.64	<0.001	VD≠D, M, S or VS
	Residuals	15	22010			D≠VS
Day 56	Density	4	621936	17.26	<0.001	VD≠M, S or VS
	Residuals	15	36030			D≠VS
Day 88	Density	4	968182	15.04	<0.001	VD≠M, S or VS
	Residuals	15	64368			D≠VS
Day 101	Density	4	1188942	12.35	<0.001	VD≠M, S or VS
	Residuals	15	96297			D≠VS
Day 119	Density	4	1322294	8.89	0.001	VD≠M, S or VS
	Residuals	15	148674			D≠VS
Day 139	Density	4	1573249	6.28	0.004	VD≠S or VS
	Residuals	15	250494			D≠VS
Day 170	Density	4	1012807	3.62	0.029	VD≠VS
	Residuals	15	279612			
Day 208	Density	4	662072	2.05	0.139	NA
	Residuals	15	323746			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

5.3.2.6 Growth rates

The five treatments exhibited similar patterns in mean relative growth rate (RGR) throughout the course of the study (Figure 5.26). The mean RGR in all treatments increased from the first period (day 0-16) of the experiment to the second (days 16-29) after which time it generally fell until the end of the experiment (Figure 5.26). The highest RGRs were always found in the lowest density population and the lowest RGRs found in the highest density population (Figure 4.26). ANOVA revealed that though there was no difference between RGR amongst the densities during the first 29 days, and the end of the experiment, between days 29 and 119 RGR was significantly higher in the lowest densities (Table 5.21).

Figure 5.26 Relative Growth Rates in *Laminaria digitata* at different densities over time. Bars = ± 1.S.E.

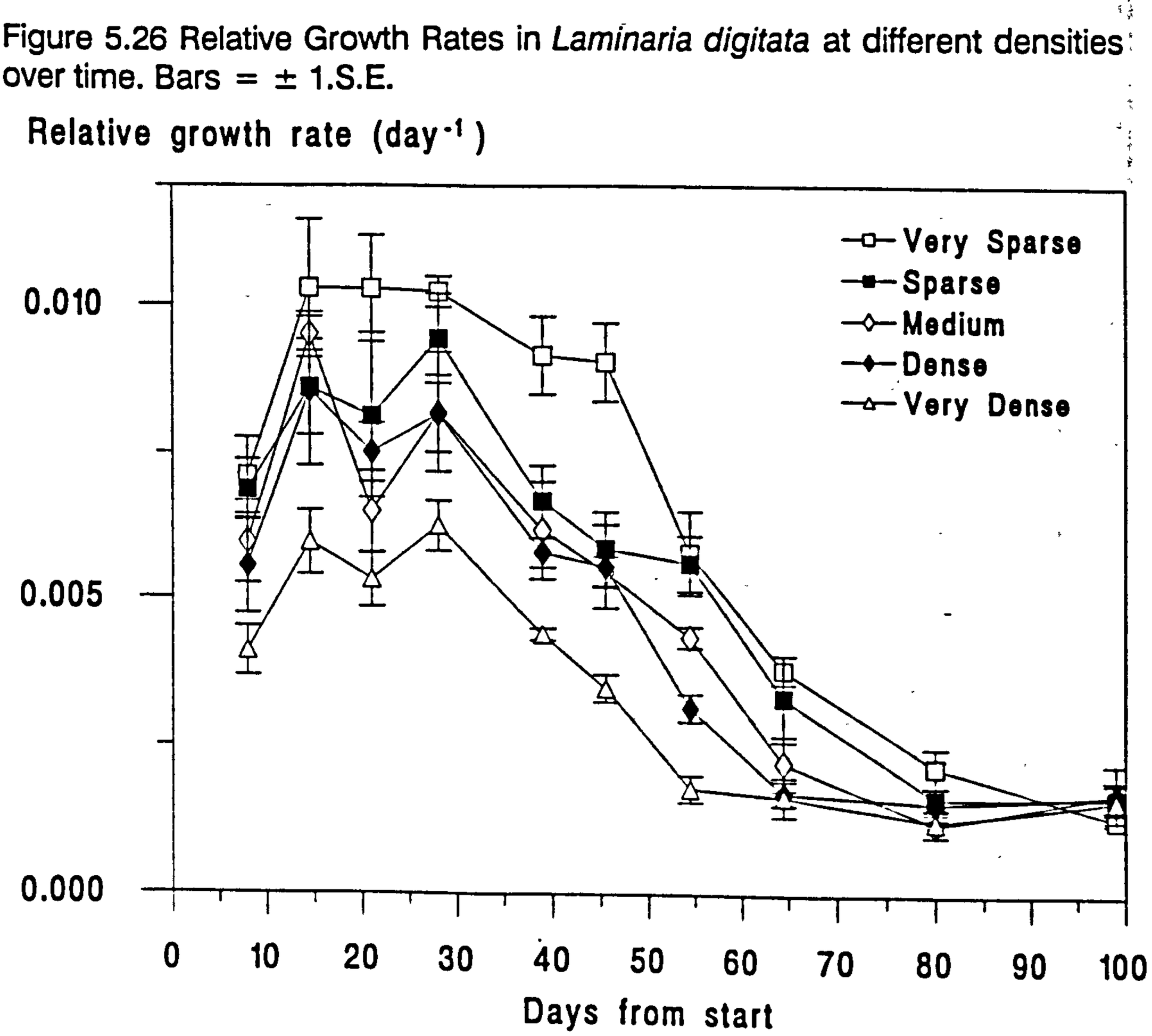


Table 5.21 Analysis of Variance (and Tukey Tests) of initial density on Relative Growth Rate in *Laminaria digitata* at different time periods.

		D.F.	M.S.	F.	p	Tukey Test*
Day 0-16	Density	4	5.6887E-06	2.61	0.078	NA
	Residuals	15	2.1834E-06			
Day 16-29	Density	4	1.0696E-05	2.47	0.090	NA
	Residuals	15	4.3331E-06			
Day 29-42	Density	4	1.3914E-05	3.48	0.033	VD≠VS
	Residuals	15	3.9963E-06			
Day 42-56	Density	4	9.2652E-06	3.77	0.026	VD≠VS
	Residuals	15	2.4594E-06			
Day 56-88	Density	4	1.2200E-05	7.29	0.002	VS≠VD, D or M
	Residuals	15	1.6745E-06			
Day 88-101	Density	4	1.6140E-05	10.48	<0.001	VS≠VD, D, M or S
	Residuals	15	1.5406E-06			
Day 101-119	Density	4	1.1409E-06	12.59	<0.001	VD≠VS, S or M
	Residuals	15	9.0648E-07			D≠VS or S
Day 119-139	Density	4	3.7749E-06	3.68	0.028	Insufficiently sensitive
	Residuals	15	1.0256E-06			
Day 139-170	Density	4	6.0890E-07	1.86	0.169	NA
	Residuals	15	3.250E-07			
Day 170-208	Density	4	1.2752E-07	0.33	0.850	NA
	Residuals	15	3.8)81E-07			

* NA - Not applicable (no difference). VD - Very Dense. D - Dense. M - Medium. S - Sparse. VS - Very Sparse. ≠ signifies difference between these densities, others not different.

5.3.2.7 Density biomass relationships

Until the last three sample times the boundary condition had not been reached (Figures 5.27 and 5.28). Slopes fitted by principal component analysis on the last three times for all data pooled (Figures 5.27 and 5.28) were performed for both biomass and mean plant weight. Neither the $\log_{10}$ *m*-$\log_{10}$ *N* or $\log_{10}$ *B*-$\log_{10}$ *N* plots conformed to the expected thinning trajectories, and significantly departed from them. (Table 5.22).

Table 5.22 The relationship between Density, Biomass and Mean Plant Weight in artificial *Laminaria digitata* populations grown in tanks. Slopes were fit by PCA.

β	Constant	Confidence Limits	r (p = 0.05)	Significance*
Density-Mean Plant Weight (Expected β = -1.5)				
-0.74	2.40	-0.929, -0.574	-0.743	S
Density-Biomass (Expected β = -0.5)				
0.533	1.56	0.360, 0.735	0.609	S

*S indicates that the slope *is* different from the expected

Figure 5.27 Density-biomass relationship in artificial *Laminaria digitata* populations grown at different densities in tanks

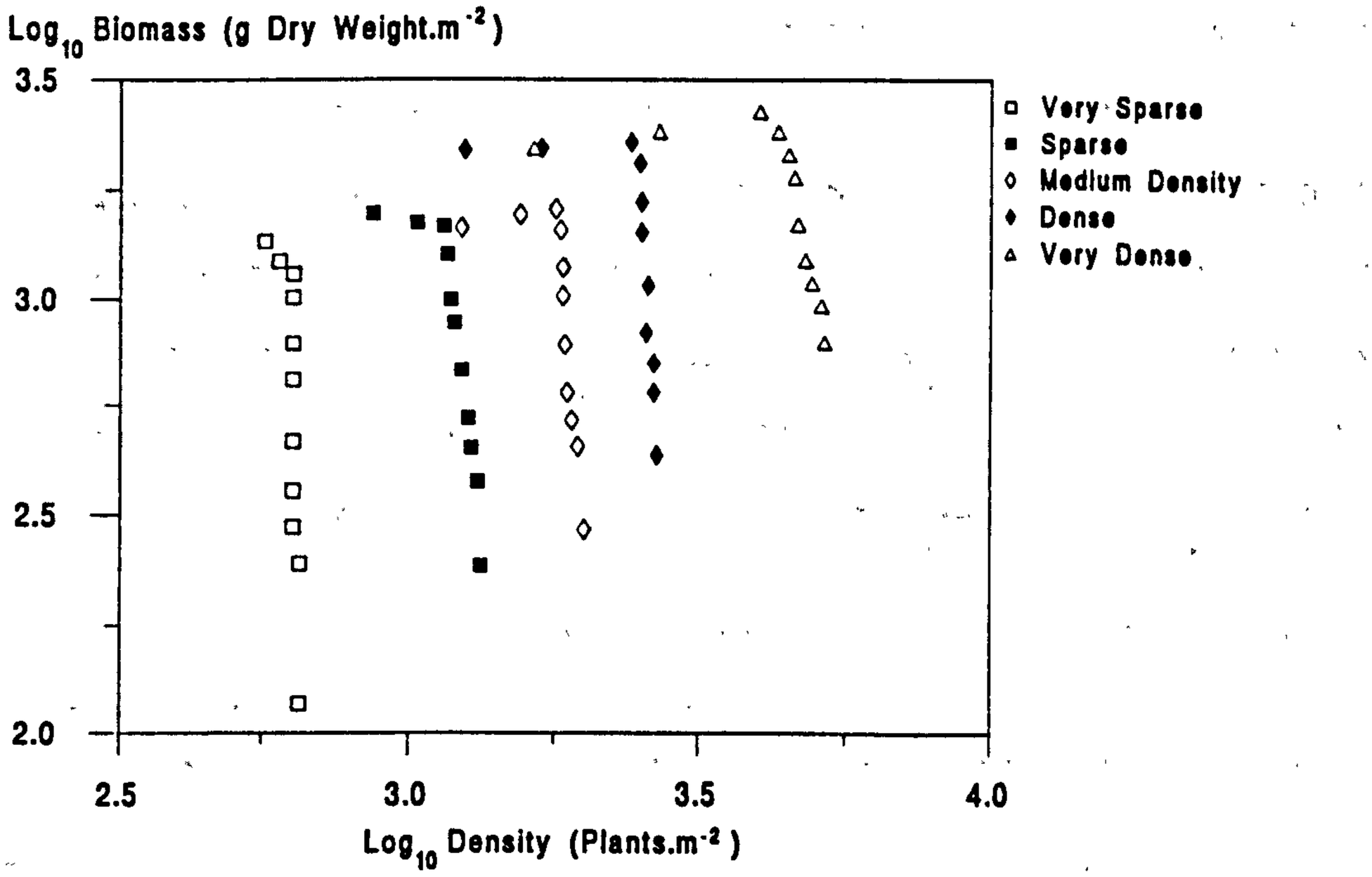
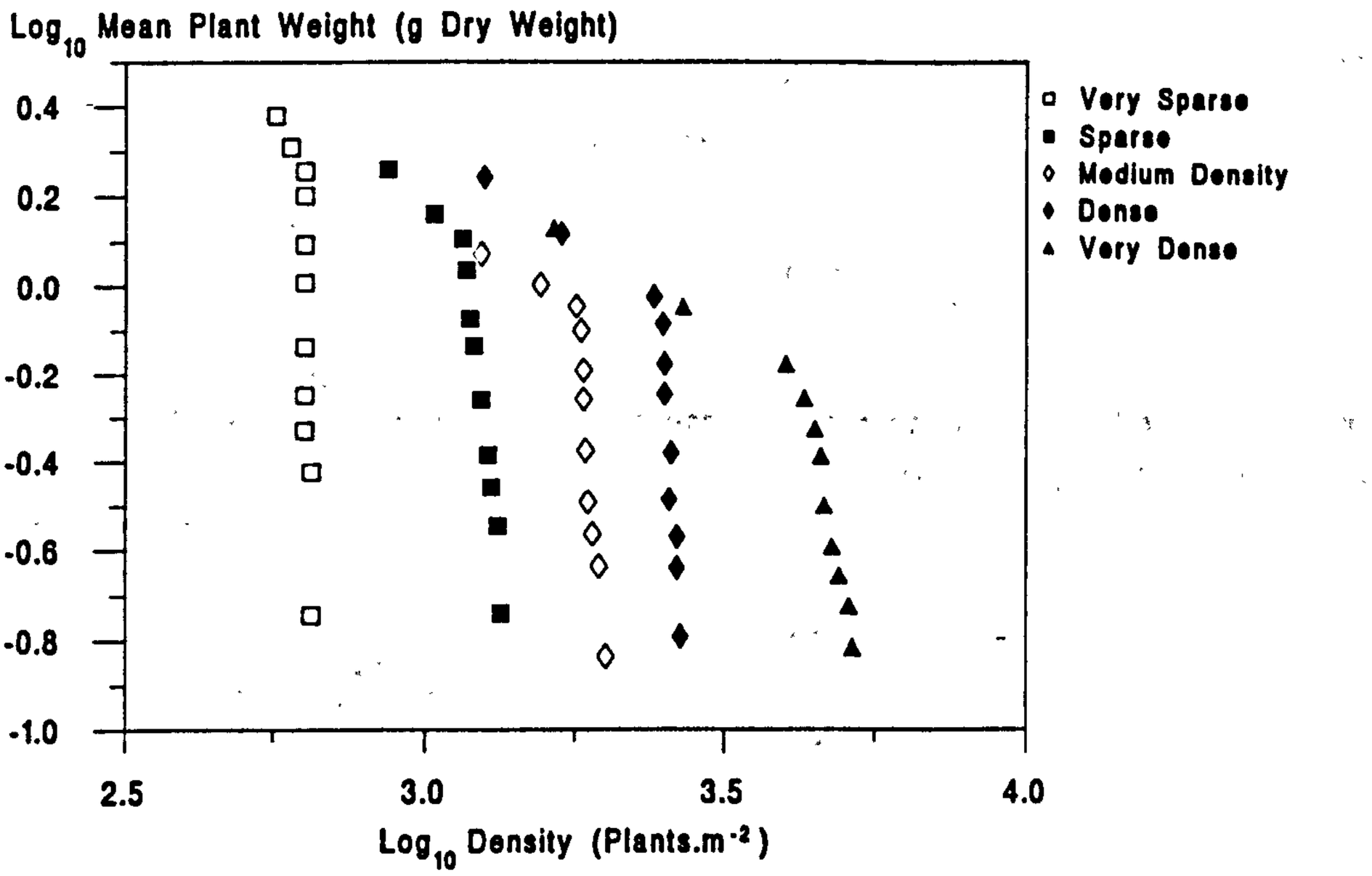


Figure 5.28 Density-mean plant weight relationship in artificial *Laminaria digitata* populations grown at different densities in tanks

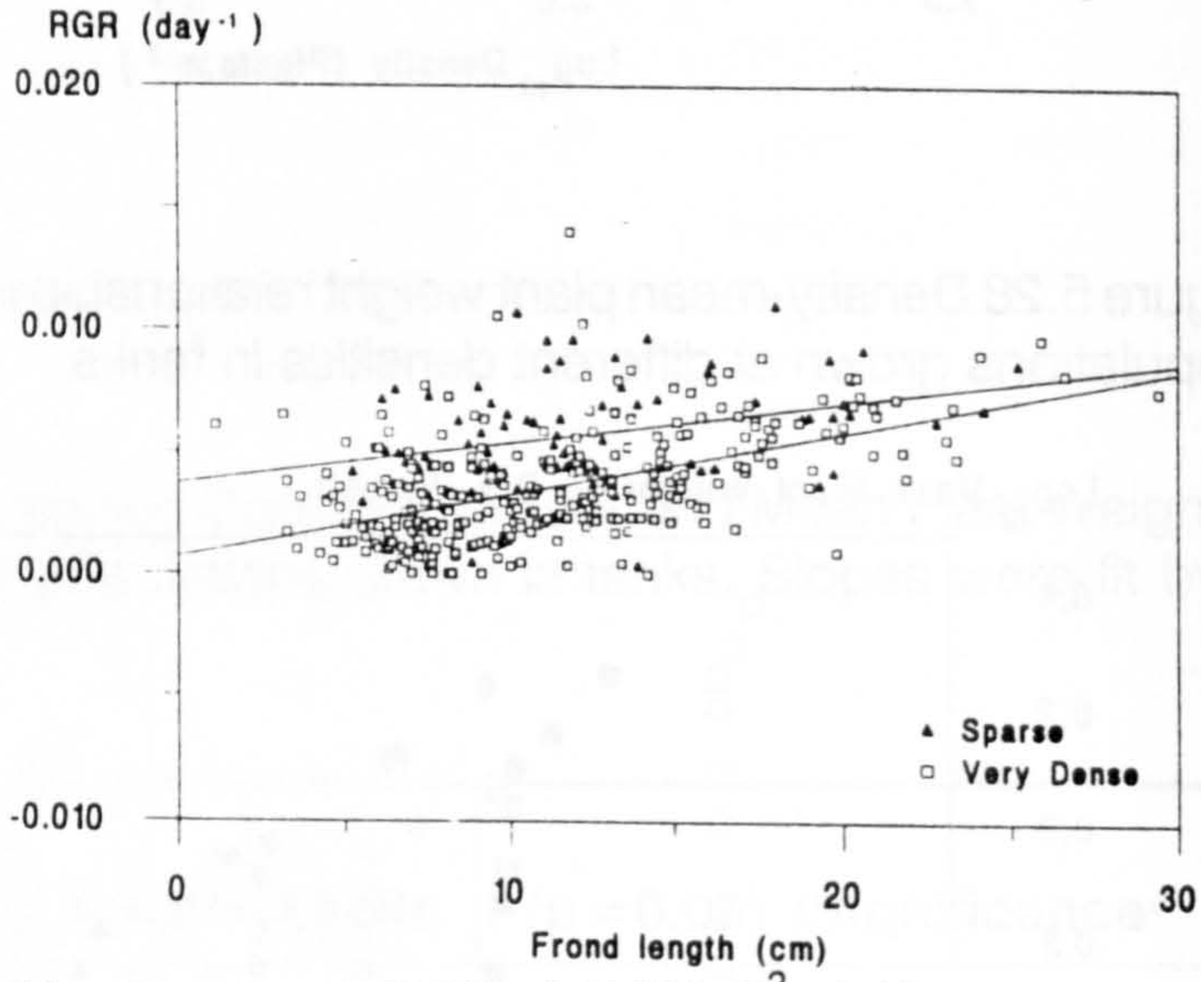


5.3.3 Size and density dependent growth

A test for dominance and suppression is to compare the relationship between relative growth rates of individual plants with plant size. At higher densities slopes should become more positive under dominance and suppression (Schmitt *et al*., 1987). Both *F. serratus* and *L. digitata* exhibited different slopes with different densities (Figure 5.29*a* and *b*). In both species higher density populations showed greater differences in relative growth rate between different sized plants (*ie* steeper slopes) than low density populations.

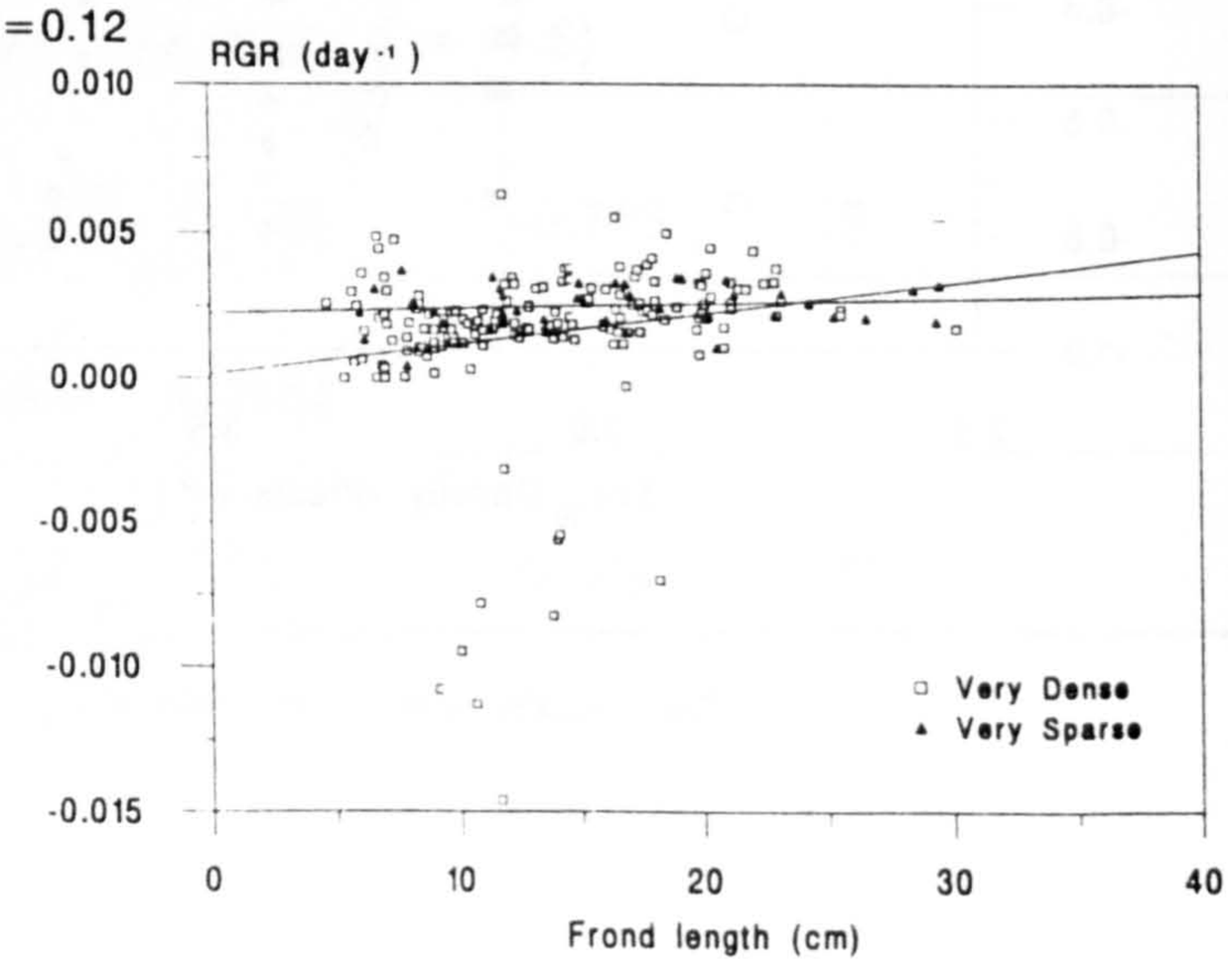
Figure 5.29 Relative growth rate - length relationships in (a) *Laminaria digitata* and (b) *Fucus serratus*.

a)



Lines fit by simple linear regression:Very Dense $y = 0.00070 + 0.00028x$ $R^2 = 0.30$.
Sparse $y = 0.00374 + 0.00017x$ $R^2 = 0.12$

b)

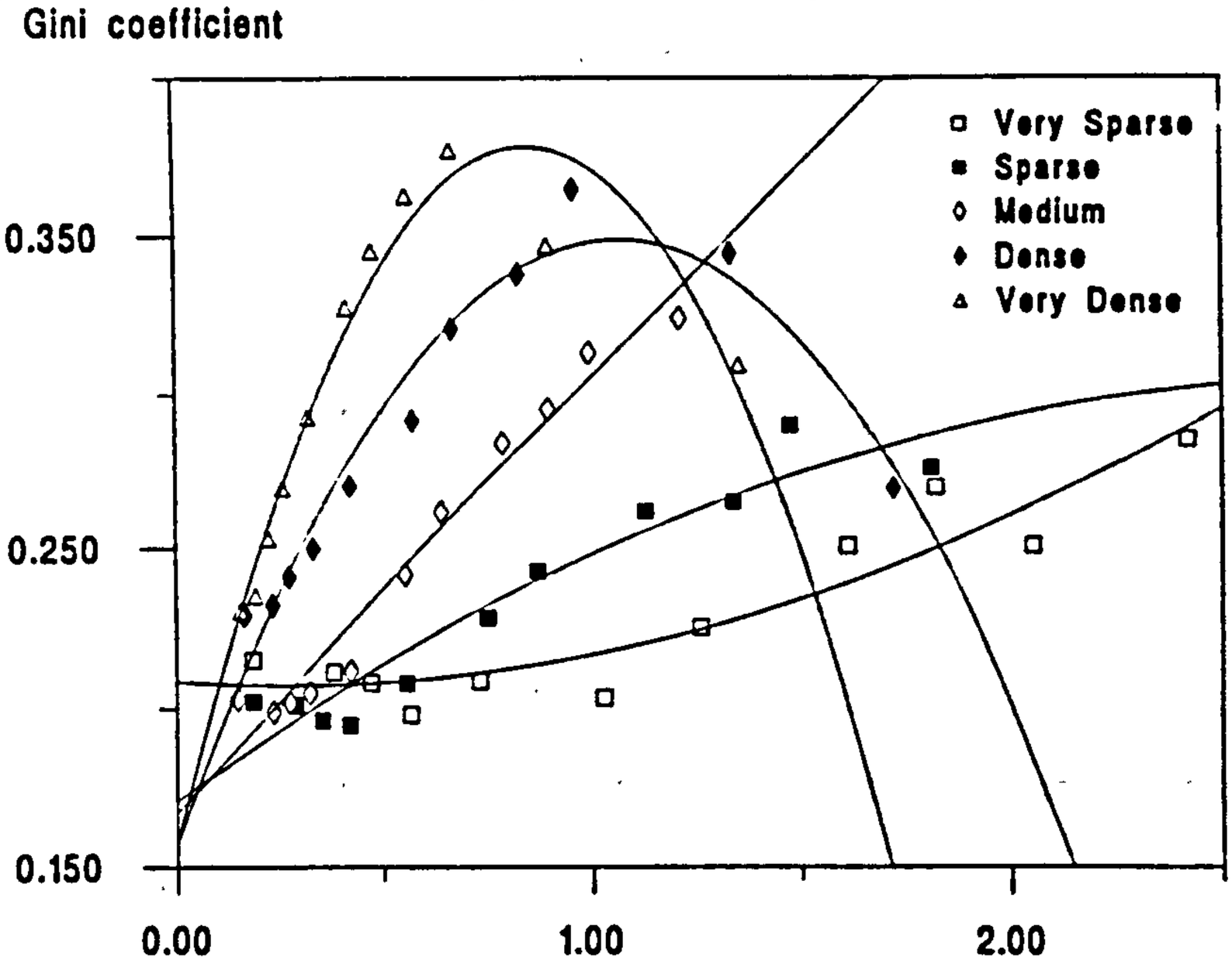


Lines fit by simple linear regression:Very Dense $y = 0.00016 + 0.00011x$ $R^2 = 0.03$.
Very Sparse $y = 0.00229 + 0.00002x$ $R^2 = 0.02$

Another test for dominance and suppression is to compare size distributions at equal mean mass of plant populations grown at different densities; denser populations should be more hierarchical (Schmitt *et al*., 1987). In fact in *L. digitata* and *F. serratus* relationships were rather more complicated (Figures 5.30 and 5.31). Certainly at any given weight the highest Gini coefficient (*ie* most unequal size distribution) was found in the highest density populations (Figure 5.30*a*) in *L. digitata*. However, the two highest density populations exhibited a subsequent decrease in Gini coefficient (increase in equality of sizes) later on in the experiment. Similarly higher density populations were more positively skewed (had more small plants) than lower density populations, but again the two highest density populations became less positively skewed later on in the experiment (Figure 5.31*a*). *F. serratus* populations gave rather similar results. The Gini coefficient increased gradually with increasing mean plant weight in the lowest density populations (Figure 5.30*b*). However, the most dense population never became more unequal than the dense population, though both these populations exhibited increasing equality later on. The relationship between skewness and mean plant dry weight was also complex (Figure 5.31*b*). There was little change in skewness in the most sparse population with increasing mean plant dry weight. However, the three highest density populations all became increasingly less positively skewed with increasing mean plant dry weight.

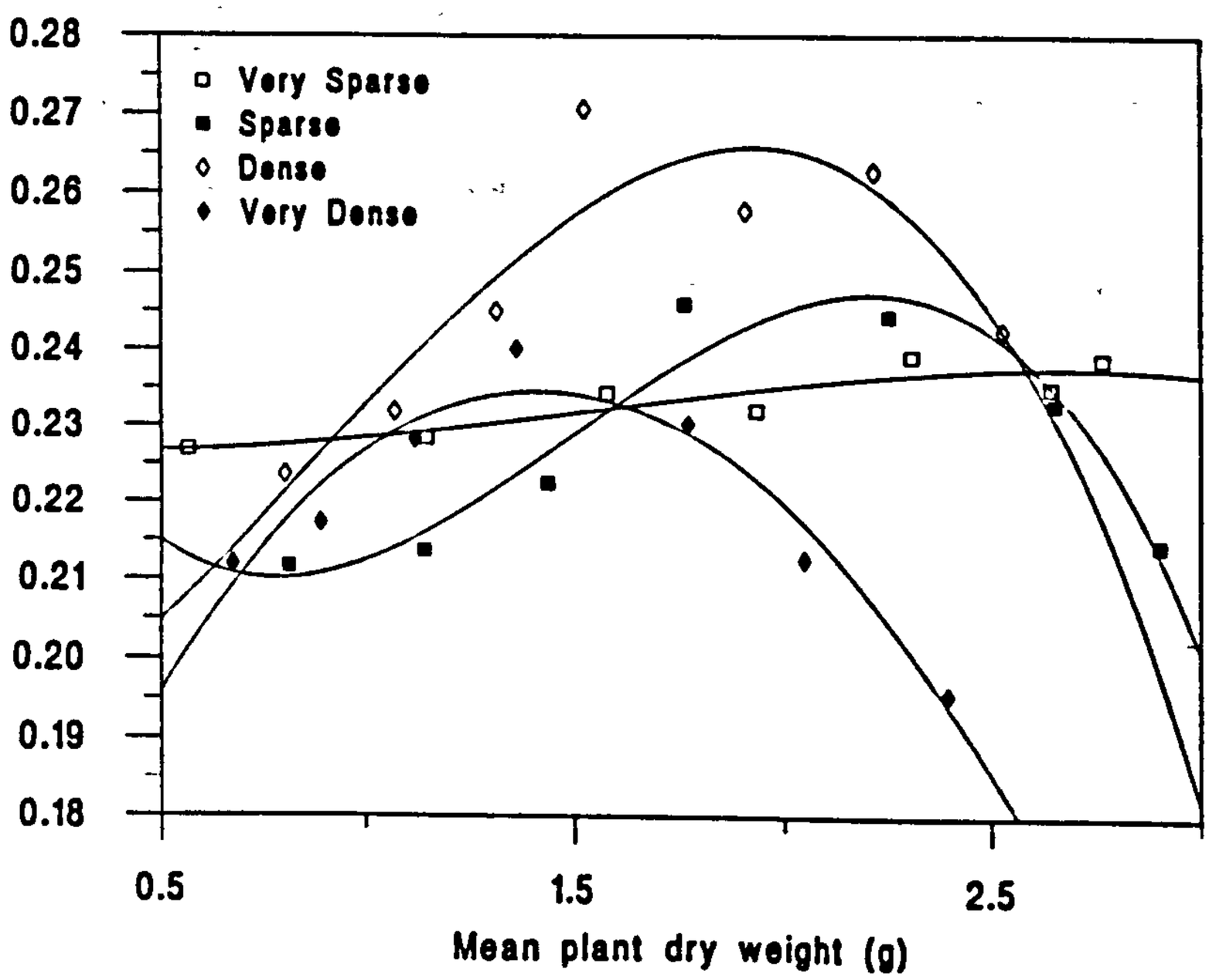
Figure 5.30 Relationship between mean plant dry weight and population size variability at different densities (a) *Laminaria digitata* (b) *Fucus serratus*

a)



Lines fit by second order polynomial: VS $y = 0.20824 - 0.00923x + 0.01769x^2$ $R^2 = 0.88$.
S $y = 0.17132 + 0.09279x - 0.01599x^2$ $R^2 = 0.92$. M $y = 0.16759 + 0.14060x - 0.00265x^2$ $R^2 = 0.96$.
D $y = 0.15791 + 0.35890x - 0.16859x^2$ $R^2 = 0.95$. VD $y = 0.15794 + 0.51934x - 0.30594x^2$ $R^2 = 0.94$..

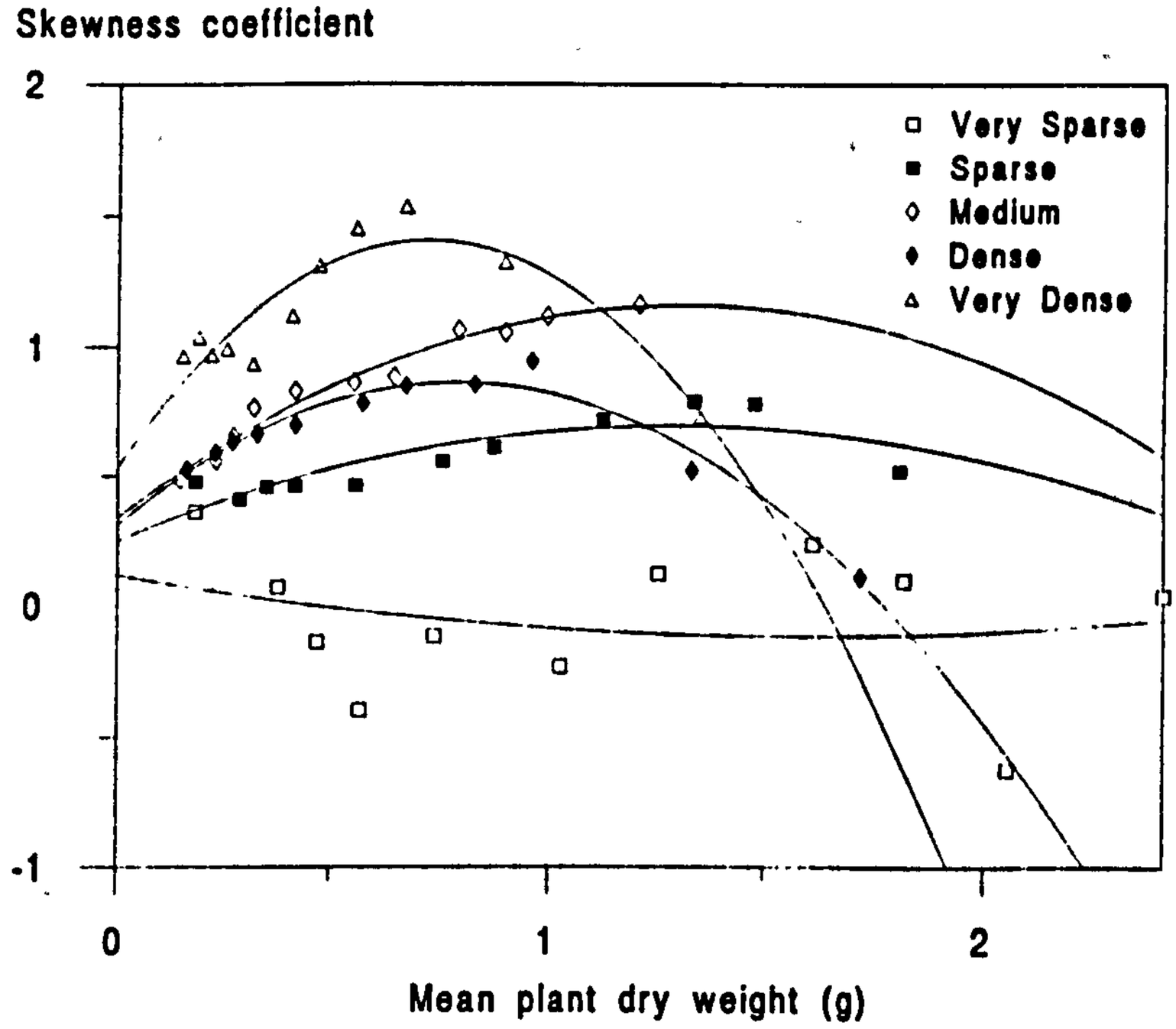
b)



Lines fit by third order polynomial: VS $y = 0.22833 - 0.00737x + 0.00937x^2 - 0.00198x^3$ $r^2 = 0.81$.
S $y = 0.25529 - 0.13121x + 0.11367x^2 - 0.02531x^3$ $r^2 = 0.93$.
D $y = 0.18665 + 0.01791x + 0.04536x^2 - 0.01729x^3$ $r^2 = 0.85$.
VD $y = 0.13951 + 0.13949x - 0.05478x^2 + 0.00254x^3$ $r^2 = 0.93$.

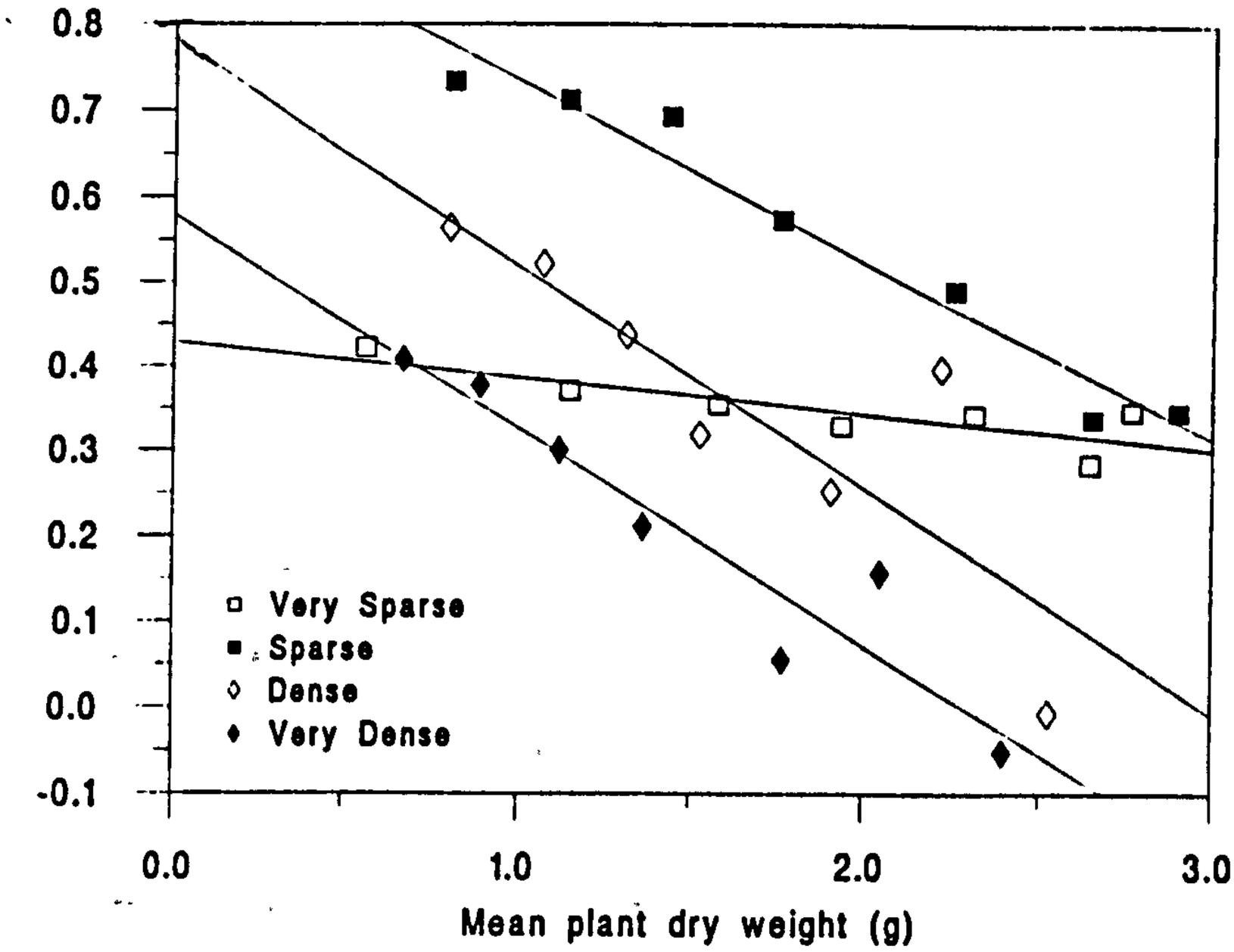
Figure 5.31 Relationship between mean plant dry weight and population size skewness at different densities (a) *Laminaria digitata* (b) *Fucus serratus*

a)



Lines fit by second order polynomial: VS $y = 0.535 + 2.415x - 1.676x^2$ $R^2 = 0.83$.
S $y = 0.309 + 1.397x - 0.887x^2$ $R^2 = 0.96$. M $y = 0.339 + 1.250x - 0.477x^2$ $R^2 = 0.97$.
D $y = 0.250 + 0.688x - 0.268x^2$ $R^2 = 0.70$. VD $y = 0.116 - 0.298x + 0.093x^2$ $R^2 = 0.05$.

b)

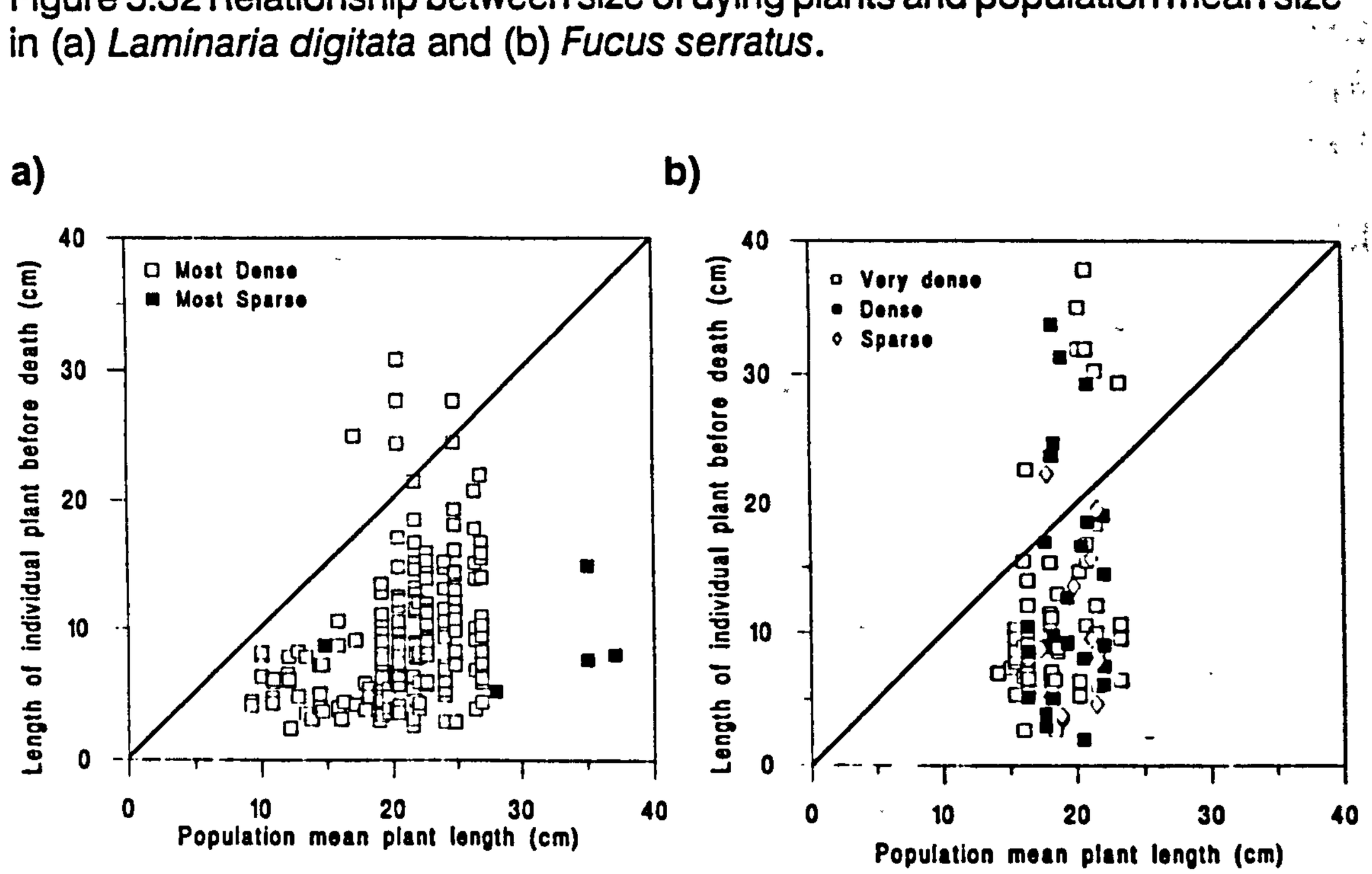


Lines fit by simple linear regression: VS $y = 0.430 - 0.043x$ $R^2 = 0.68$. S $y = 0.944 - 0.210x$ $R^2 = 0.96$.
D $y = 0.783 - 0.263x$ $R^2 = 0.73$. VD $y = 0.580 - 0.253x$ $R^2 = 0.90$.

5.3.4 Size dependent mortality

By relating mean population plant length to the length of individual plants before they die, it was found that dying plants were, on average, smaller in both *F. serratus* and *L. digitata* (Figure 5.32).

Figure 5.32 Relationship between size of dying plants and population mean size in (a) *Laminaria digitata* and (b) *Fucus serratus*.



Diagonal lines represent: population mean length = dying plant length.

If mortality is size independent equal numbers of points should fall above and below the diagonal line.

5.4 Discussion

The manipulation of density is of fundamental importance in the study of intraspecific competition (Antonovics and Levin, 1980). Unfortunately, while a number of population studies of marine plants have been carried out, little consideration has been given to the underlying mechanisms which structure populations. That few such studies have been carried out in the marine environment is understandable; such an environment is often difficult to visit regularly and to manipulate. But only recently have terrestrial plant population ecologists conducted experiments to test preconceptions held for many years (*eg* Turner and Rabinowitz, 1983; Schmitt *et al*., 1987).

5.4.1 The effect of density on population structure

Population structure is dictated by two components: both the variability and the hierarchy of plant sizes are important in the description of a population structure. While the positive skewness of *L. digitata* populations was higher at higher density, in *F. serratus* there was little difference between the skewness of different density populations. Also, while there was a clear trend of increased variability in higher density populations of *L. digitata*, variability in size of *F. serratus* populations did not differ much between population densities. For *L. digitata* not only the degree of variation in sizes increased with increased density, but the rate of increase was also greater in high density stands.

5.4.2 Growth rate and density interference

When mean relative growth rate (calculated including negative values) was compared between densities in *F. serratus*, in the least dense populations there was a trend of higher rates at lower density. In *L. digitata* mean relative growth rate was found to be significantly higher in the lowest density populations. Black (1974) found density dependent growth rates in thinned and natural populations of *Egregia laevigata*, as did Reed (1990a) for *Pterygophora californica*. Hurtado-Ponce (1990) found that the greater the spacing of fragments of

Gracilaria on rope cultures, the faster the growth rate. North (1971) on the other hand found that growth rates in *Macrocystis pyrifera* at high density were higher than those at lower densities, though he attributed this result to localised factors.

5.4.3 Dominance-suppression or conserved inherent growth rates?

The development of a population structure is influenced by many variables, however some generalities have previously been found. Plant populations grown in (dense) monocultures often develop a size hierarchy from an essentially normal distribution (Harper, 1967; Ford, 1975; Harper, 1977; Turner and Rabinowitz, 1983; Schmitt *et al.*, 1986, 1987). Two explanations have been put forward as to why this could be so. One hypothesis recognises that individual plants often grow exponentially in early life, and if a number of plants have different growth rates then over time plant masses or sizes will diverge (Turner and Rabinowitz, 1983). The implication is that plants have inherent genetically derived growth rates. Alternatively, the dominance and suppression hypothesis recognises that an interaction of larger and smaller individuals will result in larger individuals becoming dominant over smaller suppressed individuals (Schmitt *et al.*, 1987). This hypothesis has been particularly associated with competition for light, which is asymmetric. A large plant can shade a smaller one, but not *vice versa*. In such a case the ability to compete is not simply proportional to a plants size (as may be the case for instance in nutrient competition), as small plants have far less influence than their size would merit.

The literature relating to terrestrial plant populations has usually supported the dominance and suppression hypothesis, the mechanism being driven by light competition (see reviews by Weiner and Thomas, 1986; Schmitt *et al.*, 1986) though Turner and Rabinowitz (1983) supported the growth rate hypothesis. In seaweed populations only two studies have considered the theoretical basis for population dynamics. Dean *et al.* (1989) reviewed studies on a number of seaweed populations for evidence of dominance and suppression, and con-

cluded that their own study species *Macrocystis pyrifera*, which exhibited density dependent survival and growth was an exception in seaweeds by virtue of its deep (so low light) distribution and its canopy forming nature. Reed (1990*a*) found that growth was density dependent in experimental populations of *Pterygophora californica* but survival was not. There was some evidence that size variability was greater in higher density stands, and that smaller plants showed greater growth in low density stands, and he concluded that dominance and suppression was the mechanism operating in these populations (Reed, 1990*a*).

If dominance and suppression are important, the more dense a population, the more hierarchical the population structure (Scmitt *et al.*, 1987) and therefore in dense populations small plants will have lower relative growth rates than large ones. The data for *L. digitata* populations studied here would appear to confirm the notion that as a population develops it gets more unequal and more positively skewed. For *F. serratus* the evidence was less clear. However, another important factor in shaping populations structures has not yet been considered - mortality. If mortality selectively removed small plants and mortality pressure was variable with time and density then the more complex relationships between population size variability and mean plant weight found in my study can be explained.

5.4.4 Density dependent mortality

Density dependent mortality or survival has been found in some seaweed species (Black, 1974; Schiel and Choat, 1980; Chapman and Goudey, 1983; Chapman, 1984; Schiel, 1985*b*; Dean *et al.*, 1989). Studies of my two species confirmed that density dependent mortality (self-thinning) was taking place. Furthermore, mortality was size specific. In *L. digitata* for instance, in the highest density populations 97 % of plants which died were smaller than the average plant size for the population. Chapman (1984) found that mortality in *Laminaria longicruris* was greatest in large plants, and in *L. digitata* there was no

association between mortality and plant size in a natural kelp forest. There was no length to mortality association in *Laminaria longicruris* in the same area a few years later however (Chapman, 1986a). De Wreede (1986) found that older plants of *Pterygophora californica* survived longer than younger ones. All these data were collected from natural populations subject to numerous stresses which did not occur in the tanks. Smaller plants survived less well than larger plants in my experiments. This is further important evidence that the dominance and suppression hypothesis applies to these species.

That selective mortality was taking place in these populations may help to explain why in populations of both species there was an initial increase in hierarchy followed by a decrease. It seems likely that the influence of mortality on population size hierarchy can be quite strong, and the result of size specific mortality is to normalise a skewed distribution of plant sizes. In terrestrial plant populations too, the onset of self-thinning has been associated with decreased population size variability (Ford, 1975; Mohler et al., 1978; Kohyama and Fujita, 1981; Weiner and Thomas, 1986).

5.4.5 Density-Biomass relationships - the ultimate outcome

The combined outcome of mortality and the dominance and suppression of plants in a population is the self-thinning trajectory. The species studied here exhibited different trajectories, and they merit some consideration. *F. serrratus* exhibited trajectories not significantly different from those expected from the self-thinning rule. The *L. digitata* populations exhibited thinning trajectories different from the expected. For *L. digitata* trajectories indicated that population biomass stayed constant as density decreased. This type of trajectory is often associated with a population of senescent plants, though in this case is unlikely as plants were healthy throughout . The populations were grown from January to August, but only data from June to August was used to fit slopes by PCA, and this coincided with decreasing natural light levels. If light competition was the factor limiting growth in *L. digitata*, which seemed to be the case, then

decreasing light levels from June onwards may put all populations under successively greater intraspecific competition in the absence of substantial growth.

In conclusion, the growth of monospecific seaweed populations in tank culture verified that density dependent growth and mortality was taking place, and population structure was dictated by dominance and suppression and selective mortality in these two species. One sided or asymmetric competition for light seemed the most likely factor limiting growth. Tank culture, similar to glass-house experiments in terrestrial plant demography, is a useful tool available to the seaweed ecologists, as it enables certain variables to be controlled, most importantly by reducing density independent mortality by such vectors as herbivory and storm damage. Also tank culture of this kind enables the creation of population densities of even staged plants in far higher densities than those found naturally. However, in this study uncontrolled fluctuations in natural light levels resulted in seasonal variability in self-thinning trajectories. Future experiments of this kind should be carried out under light-constant conditions. One problem encountered in these studies was the necessity of taking repeated measures. Such populations take considerable time to create. An ideal experimental design would employ destructive harvests rather than repeated measures, as this would allow the use of more powerful statistical analysis. However, such an experiment would require a large number of tanks, and as light levels would have to be controlled, this would probably be impracticable without enormous resources being available to the investigator.

Chapter 6

The effect of density on Fucus vesiculosus propagules

6.1 Introduction

"Propagules are the mainspring of algal life" (Norton, 1992*b*). However algal propagules of canopy species must spring from obscurity to canopy. As seaweed propagules settle into an area they are probably not alone. Maybe hundreds of thousands of equivalently sized neighbours may be within a very small distance of them. However, because of the small size of algal propagules rather little work has been carried out in the field or laboratory into the influence of conspecific, equivalent sized neighbours on one another at the early post-settlement stage.

Early post-settlement has been defined as a period from settlement to 15 mm length (Vadas *et al.*, 1992). Mortality and growth rates are dictated by numerous physical, chemical and biological variables at this stage, many of which are little understood because of the scale on which they operate (Amsler *et al.*, 1992). A typical spore may increase in size by two orders of magnitude in the early post-settlement stage.

The importance of density on subsequent growth and survivorship has been studied in visible and microscopic seaweed populations (Black, 1974; Chapman and Goudey, 1983; Chapman, 1984; Schiel, 1985*b*; Reed, 1987; Dean *et al.*, 1989; Chapman, 1990*b*; Reed, 1990*a* and *b*; Ang and De Wreede, 1992). The results of such studies have demonstrated that at higher densities there are reduced growth rates (Black, 1974; Schiel, 1985*b*; Reed, 1990*a*), greater mortality (Chapman and Goudey, 1983; Reed, 1990*b*), reduced recruitment (Black, 1974; Reed, 1990*a*) or reduced reproductive potential (Reed, 1987). However, Schiel and Choat (1980) and Schiel (1985*b*) presented evidence that sometimes growth is positively density dependent in seaweeds (but see Brawley and Adey, 1981*b*, who suggest this an effects of grazer interactions). There is some evidence to suggest that crowding confers certain advantages

on microscopic populations. Reed (1990*b*) and Reed *et al.* (1991) found that kelp spores needed a minimum density for subsequent fertilisation and sporophyte production, and that gametophyte growth and reproduction were negatively related to density. Vadas *et al.* (1990) found that density was implicated in spore dislodgement experiments. 'Safety-in-numbers' factors may be responsible for other reports of higher survival at higher densities (Schonbeck and Norton, 1978; Hruby and Norton, 1979) and similarly in turfs (Hay, 1981). Ang and De Wreede (1992) found that survivorship was better in high density populations of early stage *Fucus distichus* germlings, but that mortality was positively density dependent after two months. Black (1974) found that mortality was positively density dependent only for the first three months in populations of *Egregia laevigata*. Yoshida (1972) found that initially yield was positively density dependent in cultivated *Porphyra tenera*.

In terrestrial plants seed and seedling sizes are widely recognised to be normally distributed (Harper, 1977; Bonan, 1988), and we may expect spore sizes of seaweeds to be equally so, though the little evidence is unconvincing (Mshigeni, 1976; Destombe *et al.*, 1992). This initial size structure is the base on which dominance and suppression may operate to produce skewed plant size distributions. However little is known of propagule size distribution pre- or post-settlement. What is also little comprehended, is that the first few weeks of growth of seaweed propagules may confer crucial advantages to larger plants if dominance and suppression take place at this early stage. In essence, the first week in a propagule's life may dictate its future existence. This chapter investigates the development of different densities of *Fucus vesiculosus* at this crucial time in a laboratory study which minimises other confounding factors found on rocky shores.

6.2 Material and Methods

Material was collected from a small area of Port St Mary ledges, Isle of Man on the low tide of 15th August 1991. Twenty female and ten male reproductive *Fucus vesiculosus* plants were collected in plastic bags and returned to the laboratory.

6.2.1 Preparation of material

All receptacles were excised from the plants of each gender using a scalpel. The receptacles of all the plants of a gender were pooled and spread out on two plastic trays so that each tray had the receptacles of one gender. The trays were left outside and the receptacles sun-dried for five hours. After this time, the receptacles of each tray were quickly washed in fresh water, which was subsequently drained and replaced with filtered sea-water to a level half covering the receptacles. Within twenty minutes egg and sperm release was taking place. After one hour the water containing gametes was removed from the receptacles.

The water containing oogonia was passed through a 100μm filter to remove egg packets and other dross, but allow single eggs to pass. The filtrate was passed through a 60μm filter which retained eggs but allowed the mucus-thick water to pass. The eggs were washed out of the filter with fresh filtered sea-water into a one litre measuring cylinder. The cylinder and contents were vigorously shaken to suspend the eggs before they were allowed to settle at the bottom of the column. After settlement most of the water was decanted, fresh sea-water added, spores resuspended, and once more allowed to settle. This process was repeated once more, to remove smaller, slower sinking propagules of other species of algae.

The water containing sperm was passed through a 40μm filter to remove dross and the filtrate kept.

6.2.2 Spore settlement

Glass slides were washed in detergent before being rinsed for one day in fresh water and one day in sea-water. Small glass settlement tanks were treated in the same way. Fourteen slides were laid out in two rows of seven in three glass tanks. The slides were laid contiguously and in the centre of the tanks. The tanks were filled to a depth of 2 cm with filtered sea-water.

The egg suspension was mixed with a small portion of the sperm suspension and shaken. Aliquots were taken to make 100%, 10% and 1% solution of the original suspension, and all the solutions were made up to 500 ml. Each suspension was trickled onto the water surface of one of the three tanks in a zigzag pattern. The three tanks were left in a constant temperature room for one day.

6.2.3 Experimental design and culture details

Four fresh tanks, filled with 3 l of filtered sea-water, were placed on a shelf of a constant temperature room adapted for algal culture work. Three slides from each of the three densities (tanks) were randomly taken with forceps, numbered with sticky micromarkers on the underside and placed into each of the four tanks. Within each tank slides were randomly distributed spatially, while the tanks were linearly arranged along the shelf.

The spores/embryos were grown under 24hr light at 200μmol Photons $m^{-2}s^{-1}$ supplied from three Thorn EMI 58W polylux 4000 light tubes in filtered sea-water at a constant temperature of 15°C. The water was changed every two days.

Three slides, one bearing each density, were randomly taken from each of the four tanks at each sample time. Therefore four replicate slides were used at each time for each density (Figure 6.1).

6.2.4 Measurements

Using one of the spare sparsely settled slides, the number of plants needed to adequately describe a slide was assessed, and it was found that 12 fields of view of 5.3 mm diameter were necessary (Figure 6.2).

In order to randomise viewing of slides, a slide was painted white, and 12 permanent-marker dots, corresponding to randomly generated coordinates, were drawn on the white slide. This slide was inserted under the slide to view as a target slide and a fibre-optic light source was used to provide incident light. A *camera lucida* was attached to the stereo microscope. The microscope had an eyepiece with a cross on. Sheets of paper with a circle and cross target were prepared for drawing images (Figure 6.3). When viewed, the cross on the paper was aligned with the eyepiece cross to centre the drawing area. The slide was then moved until the cross was in the centre of the first dot (Figure 6.3).

Spore/embryo outlines of twelve fields of view for each slide were traced using the *camera lucida*. In order to prevent potential bias of the observer, the slides were drawn before the number of the slide was noted, as this was face down. For each sample time a total of 144 fields of view were drawn. After being drawn the slides were carefully soaked in fresh water for five minutes before being oven dried at 60°C for one day. Slides were then dry weighed on a balance accurate to 0.0001g before being cleaned, rinsed, redried and reweighed, the difference in weights being a rough estimate of the total weight of spores/embryos on a slide.

6.2.5 Image analysis

The images were digitised using a Graf/Bar Mark II sonic digitiser (Science Accessories Corporation) run in conjunction with an IBM PC and DesignCAD 2-D v4.2 software. Each plant was simplified to a line of maximum plant length

and the image was saved as an ASCII text file. The images were imported into a bespoke Lotus 123 macro which sorted images, removed unnecessary data and calculated plant lengths, before calculating various population parameters in the standard way (Chapter 1).

Figure 6.1 The experimental design for culture of *Fucus vesiculosus* propagules.

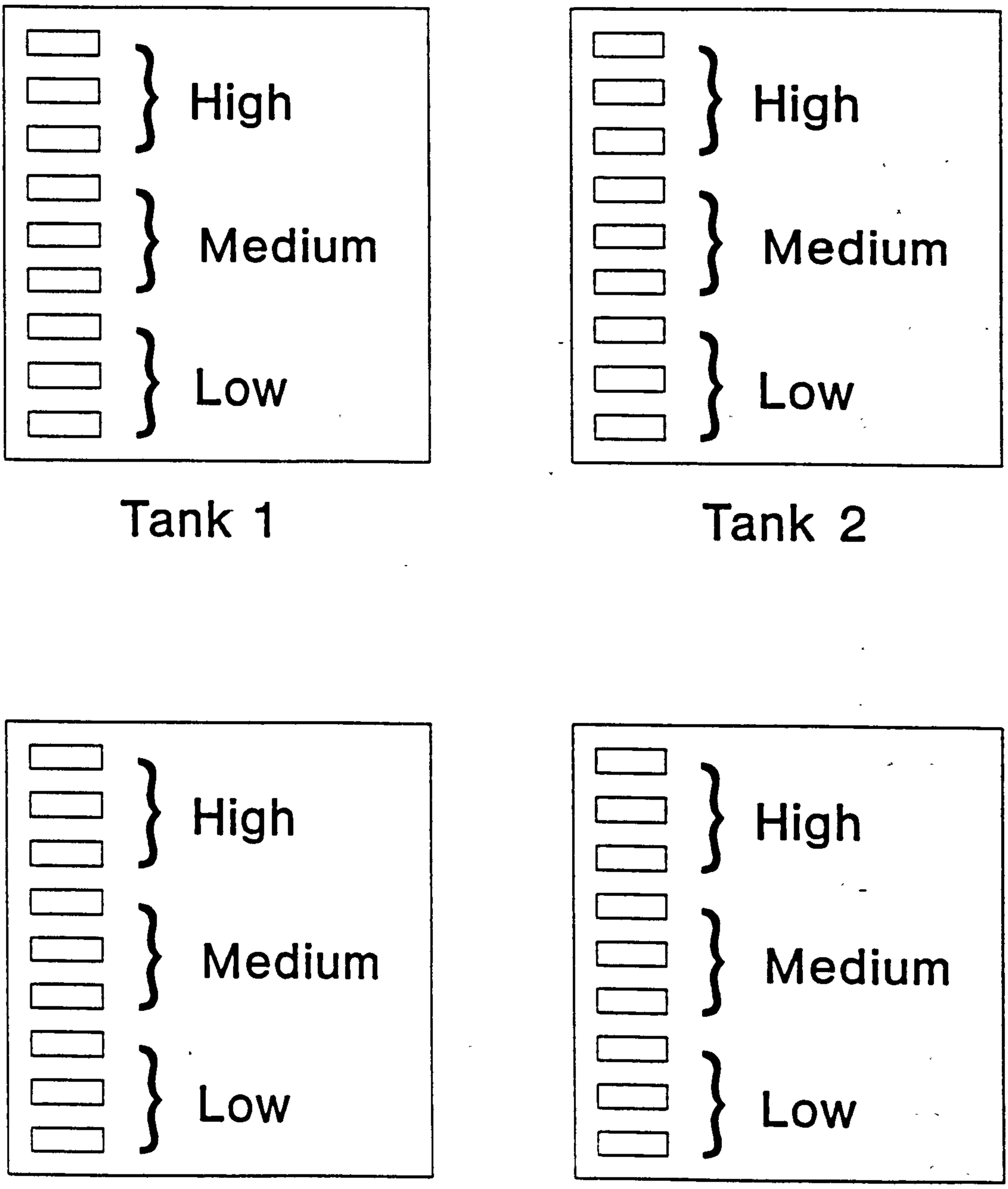


Figure 6.2 The number of fields of view needed adequately to describe a slide of *Fucus vesiculosus* propagule density.

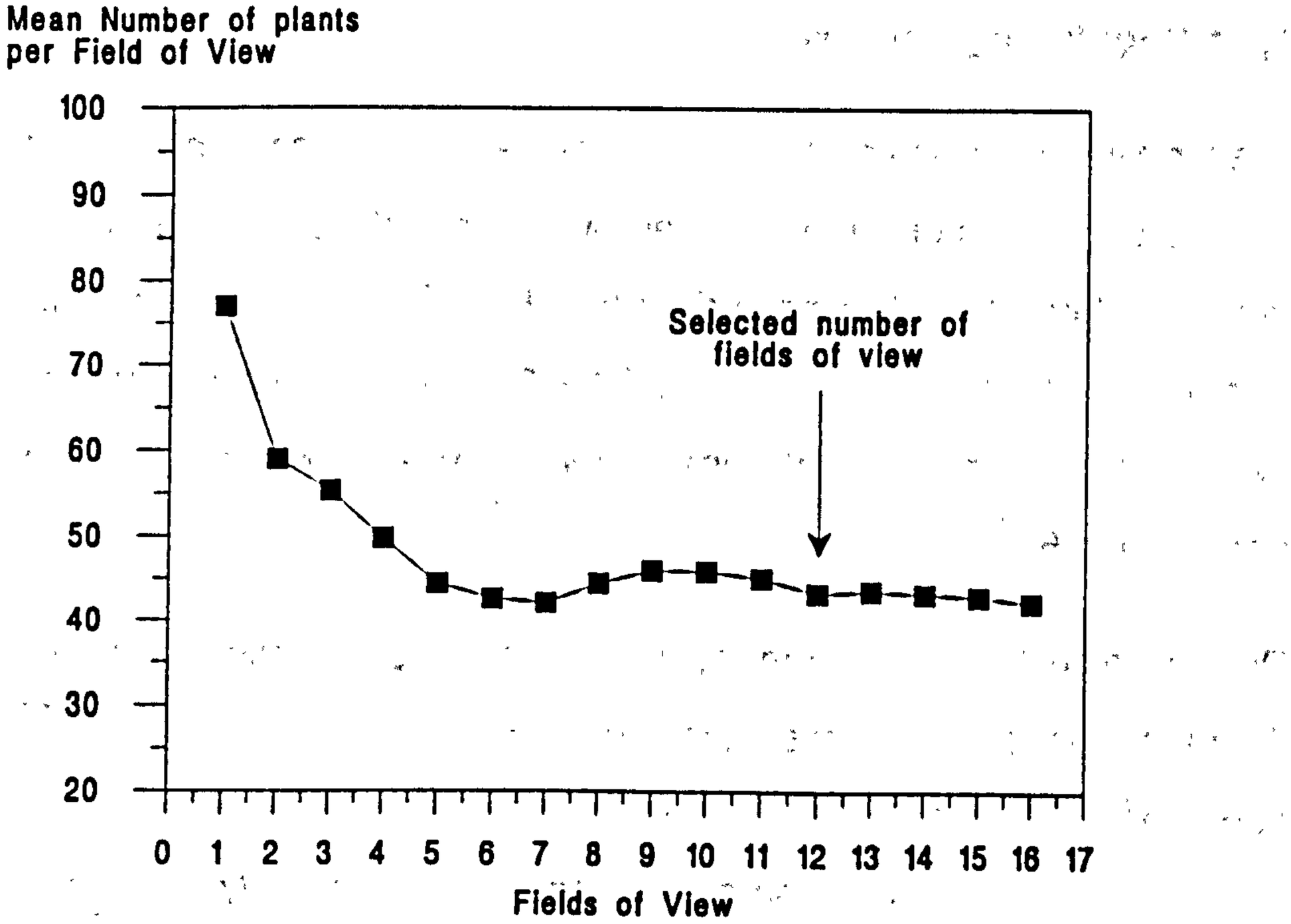
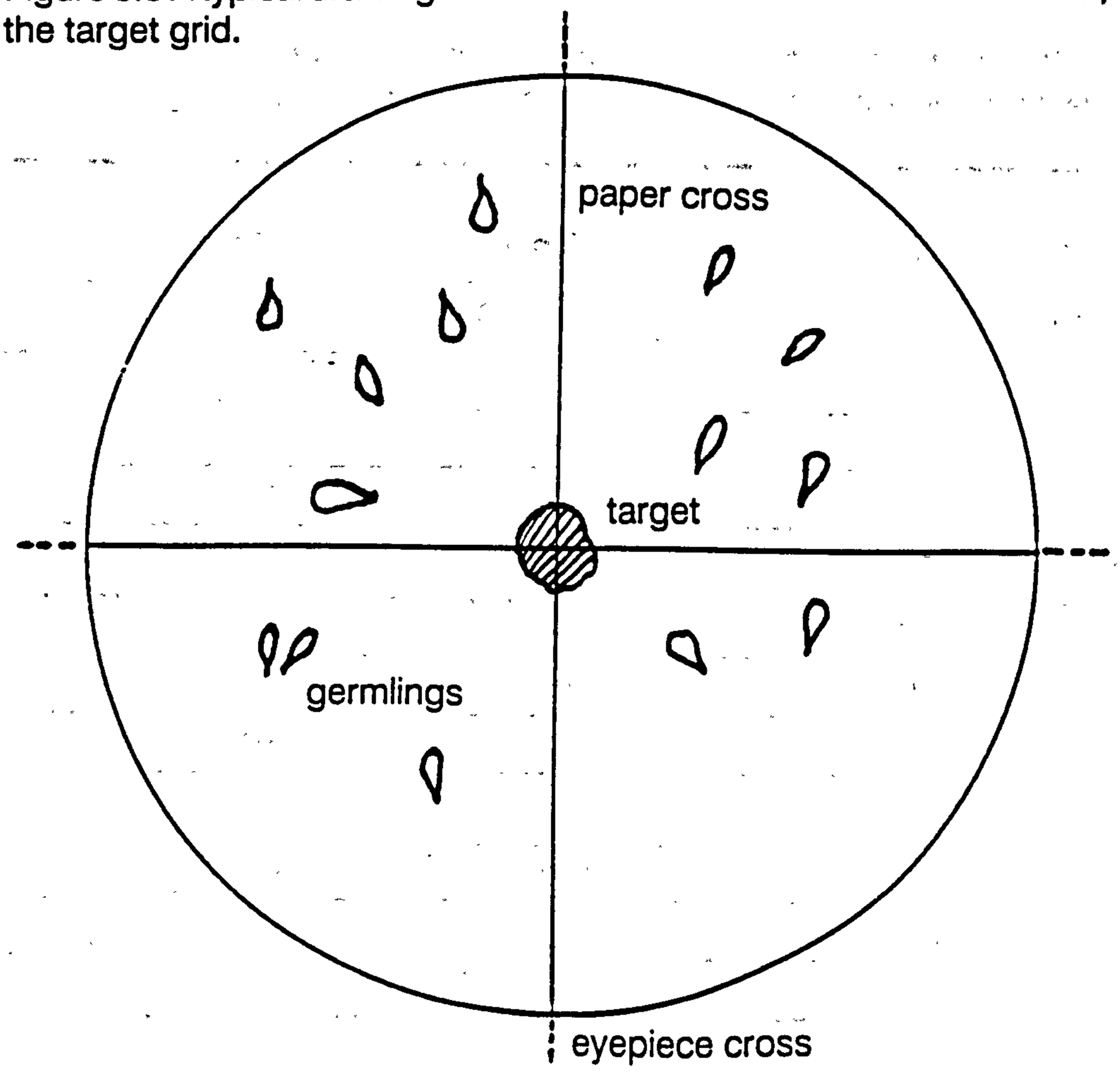


Figure 6.3 A typical drawing of one field of view from the *camera lucida*, showing the target grid.



6.3 Results

6.3.1 Population structure

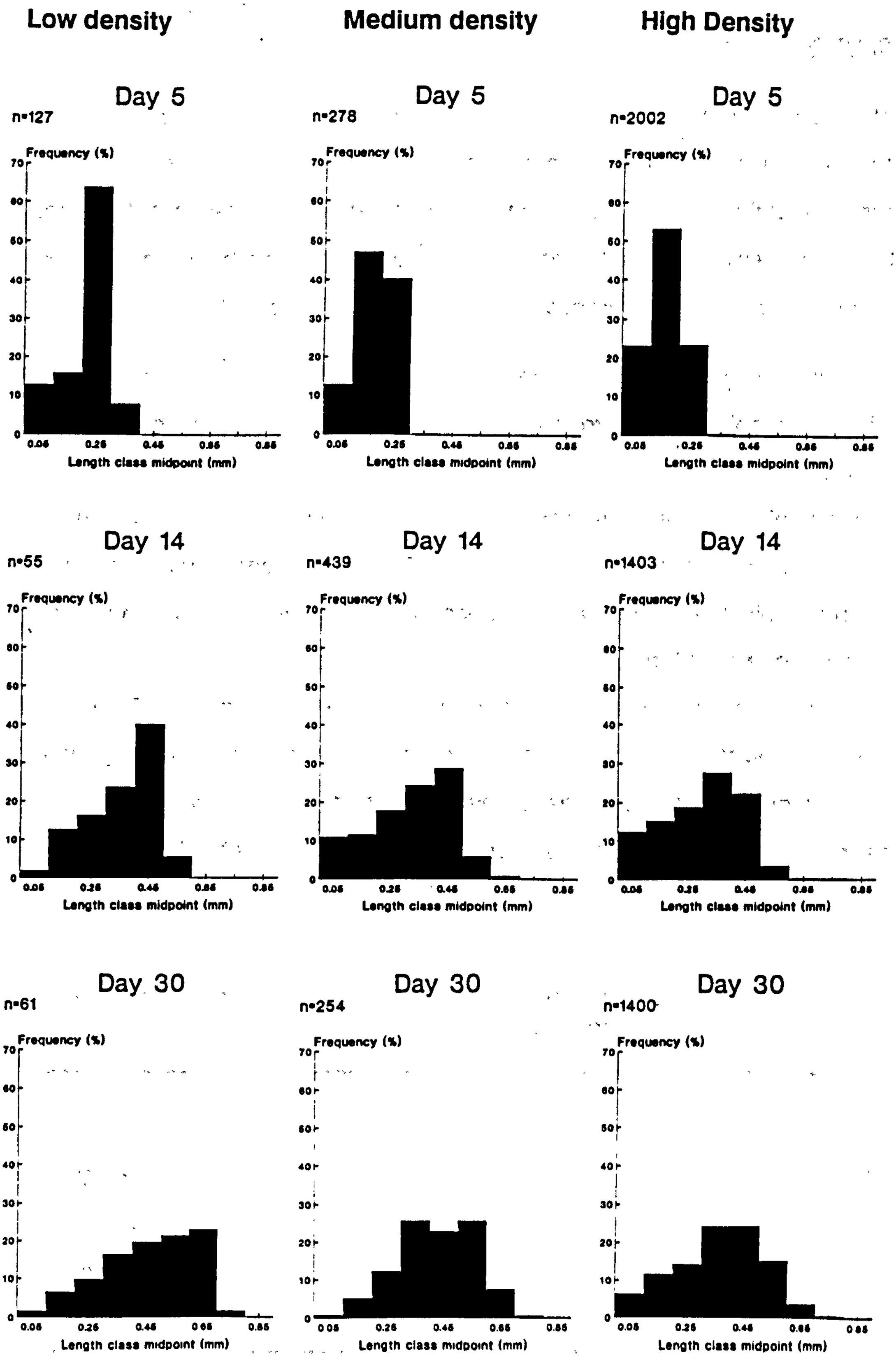
Even only 5 days after settlement important differences between the three density population development had taken place (Figure 6.4). Negative skewness was higher the lower the density, while the highest density populations were essentially normal (Figure 6.4, Table 6.1). However variability and inequality were highest in the most dense populations and lowest in the least dense ones (Table 6.1).

During the next 25 days all the populations remained negatively skewed, though the most dense populations were only slightly so and the least dense populations became most negatively skewed (Table 6.1). The variability/inequality in plant size increased in all the populations, but only slightly in the least dense

Table 6.1 Coefficient of variation, Gini coefficient and skewness in *Fucus vesiculosus* propagule populations over thirty days after settlement at three densities.

	5 Days	14 Days	30 Days
Coefficient of variation			
High Density	0.373	0.457	0.424
Medium Density	0.331	0.433	0.315
Low Density	0.324	0.342	0.355
Gini coefficient			
High Density	0.213	0.261	0.241
Medium Density	0.189	0.246	0.179
Low Density	0.176	0.192	0.199
Skewness			
High Density	-0.020	-0.168	-0.186
Medium Density	-0.229	-0.314	-0.277
Low Density	-0.786	-0.419	-0.505

Figure 6.4 Size frequency histograms of population structure of different density populations of *Fucus vesiculosus* propagules over 30 days post-settlement. Scales are identical.



populations. By the end of the experiment, variability/inequality was higher in the most dense populations than in the least dense ones.

6.3.2 Plant length

Mean plant length was higher after 5 days in the lowest density populations than in the higher density ones (Figure 6.5). This feature was preserved throughout the experiment, though mean plant length increased over time too. There was a significant difference in mean plant length both between densities and over time, but no interaction between the two (Table 6.2).

Maximum plant length was calculated as a mean of the largest plant from each of the four replicate slides for any one density and time. Maximum plant length was similar after five days in all the three density populations (Table 6.3). There was a significant difference between times as maximum plant size increased in all density populations (Table 6.3). There was also a significant difference in maximum plant length between densities, with the highest density populations having the largest big plants. There was also an interaction between density and time, with the medium density population increasing similarly to the high density population until day 14, but after that time hardly increasing so that at the end of the experiment the largest plants found in the low and medium density populations were of a similar size (Figure 6.6 and Table 6.3).

Table 6.2 Analysis of Variance of mean plant length on time and density in *Fucus vesiculosus* propagule populations.

Factor	D.F.	M.S.	F.	p
Time	2	0.171500	100.77	< 0.001
Density	2	0.023794	13.98	< 0.001
Time x Density	4	0.000796	0.47	0.759
Residuals	27	0.001702		

Figure 6.5 Plant length in three population densities of *Fucus vesiculosus* propagules over three times. Bars = ± 1S.E.

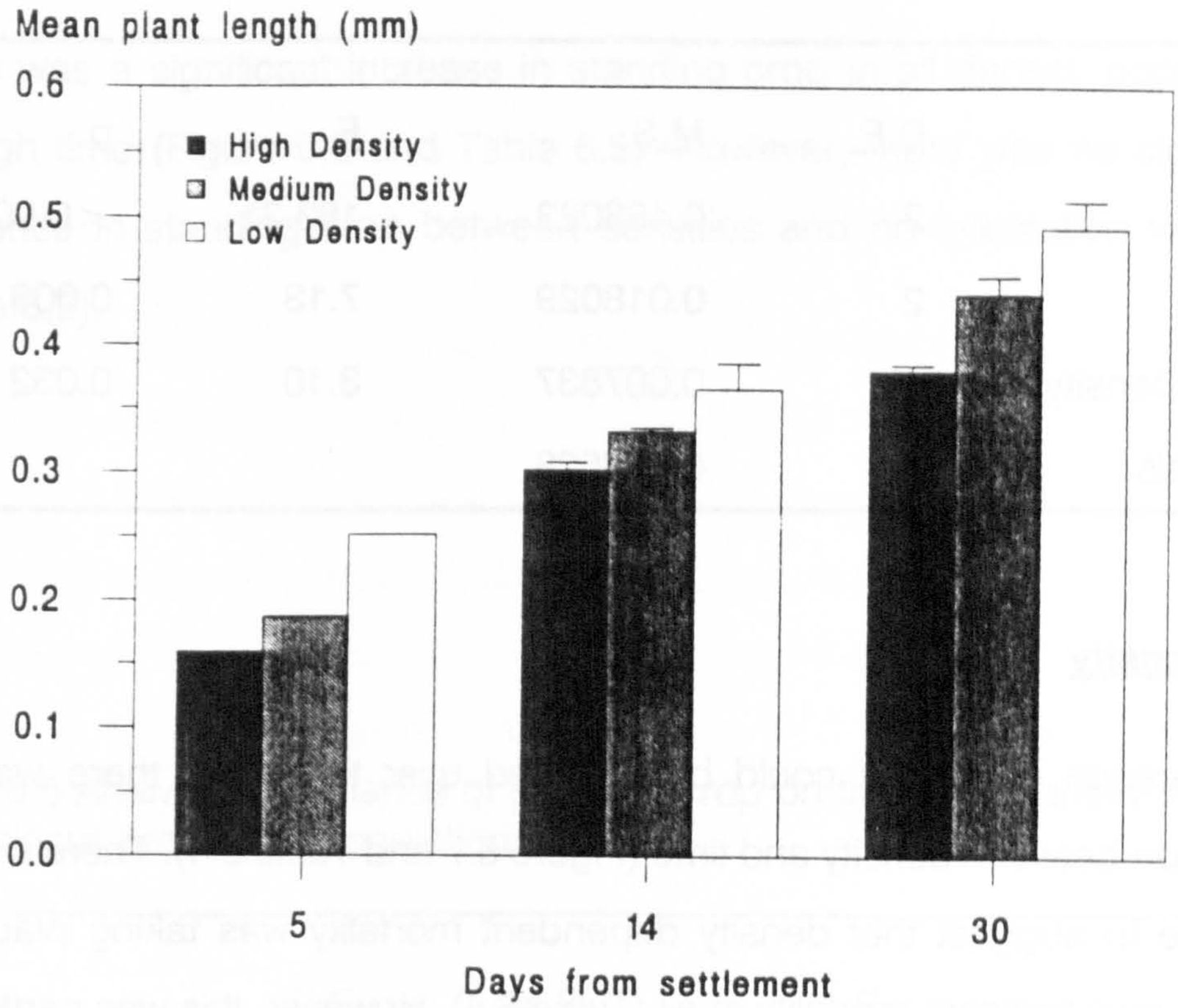


Figure 6.6 Maximum plant length in three population densities of *Fucus vesiculosus* propagules over three times. Bars = ± 1S.E.

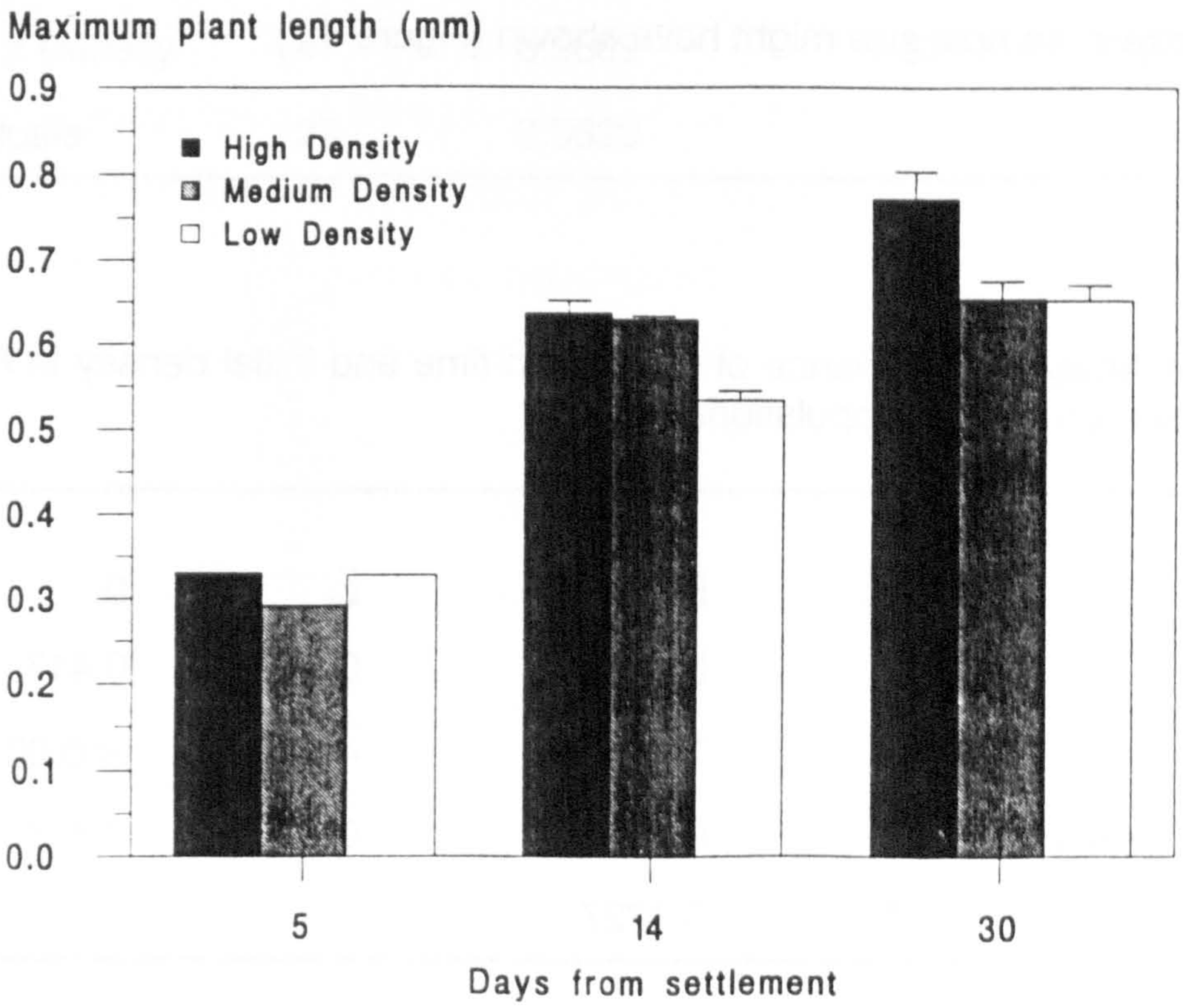


Table 6.3 Analysis of Variance of maximum plant length on time and density in *Fucus vesiculosus* propagule populations.

Factor	D.F.	M.S.	F.	p
Time	2	0.463083	183.21	<0.001
Density	2	0.018029	7.13	0.003
Time x Density	4	0.007837	3.10	0.032
Residuals	27	0.002528		

6.3.3 Density

No difference in density could be detected over time, and there was no interaction between density and time (Figure 6.7 and Table 6.4). There was no evidence to suggest that density dependent mortality was taking place, or indeed any significant mortality at all (Table 6.4). However, this was partly due to the high variability in density, and there seemed to be a trend of far more substantial decrease in high density populations than low density ones which an increase in sample size might have shown (Figure 6.7).

Table 6.4 Analysis of Variance of density on time and initial density in *Fucus vesiculosus* propagule populations.

Factor	D.F.	M.S.	F.	p
Time	2	0.1559	0.90	0.417
Density	2	7.1611	41.46	<0.001
Time x Density	4	0.1618	0.94	0.458
Residuals	27	0.1727		

6.3.4 Standing Crop

There was a significant increase in standing crop in all density populations through time (Figure 6.8 and Table 6.5). However, there was no significant difference in standing crop between densities and no interaction with time (Table 6.5).

Table 6.5 Analysis of Variance of standing crop on time and density in *Fucus vesiculosus* propagule populations.

Factor	D.F.	M.S.	F.	p
Time	2	11.7660	32.50	<0.001
Density	2	0.8893	2.46	0.105
Time x Density	4	0.5669	1.57	0.212
Residuals	27	0.3620		

Figure 6.7 Density change in three population densities of *Fucus vesiculosus* propagules over three times. Bars = ± 1S.E.

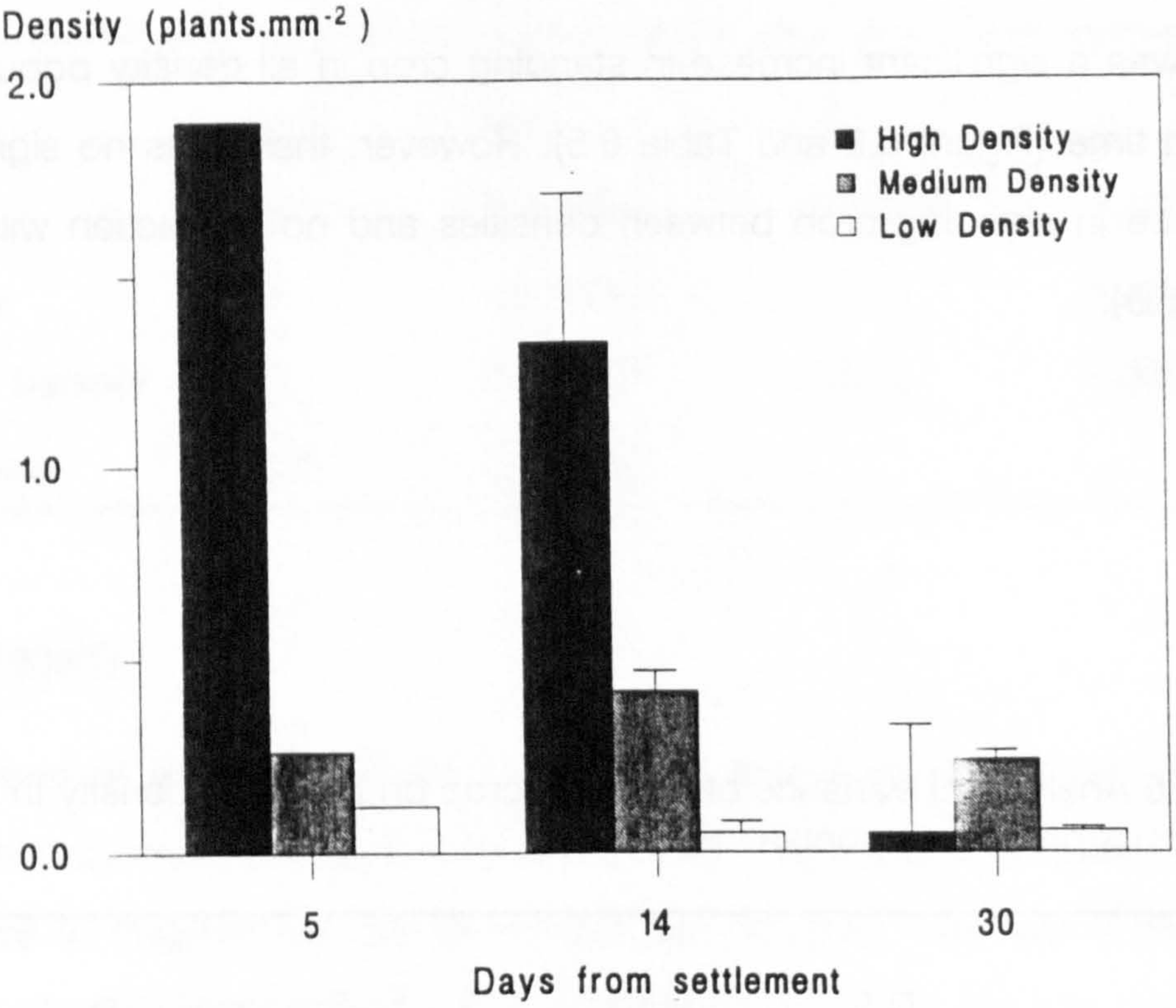
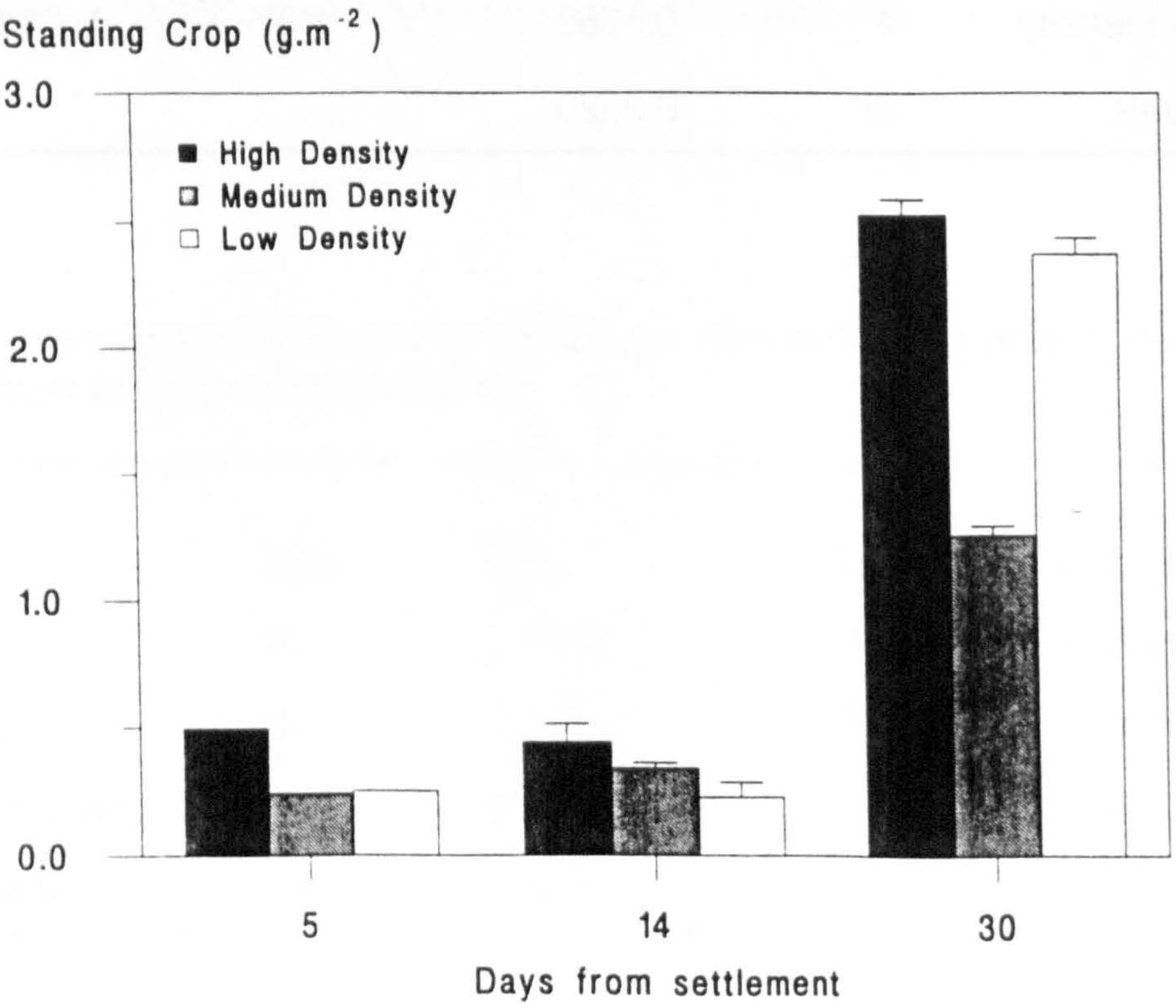


Figure 6.8 Standing crop in three population densities of *Fucus vesiculosus* propagules over three times. Bars = ± 1S.E.



6.4 Discussion

This experiment examined the first month in the growth and survival of *Fucus vesiculosus* propagules. Even the most dense populations were not closely packed, but two major differences were found between the different densities.

The rate of growth as mean plant length was highest in the lowest density population after only five days. This continued to be a feature of the populations throughout the experiment. As the propagules were not closely packed, and certainly never multi-layered, it is difficult to believe that shading of smaller plants could be taking place at this early stage. It seems more likely that nutrient limitation was taking place in these populations. Only filtered sea-water was used in the experiment, and with no water movement propagules may have suffered nutrient depletion near the slide surface. Ward (1982) found the growth rate in *Fucus serratus* germlings was negatively density dependent in laboratory culture, as did Ang and De Wreede (1992) in outplanted *Fucus distichus*. Black (1974) found that growth was density dependent in very small *Egregia laevigata* plants.

While densities were significantly different at the start of the experiment, no density dependent mortality could be detected by ANOVA throughout the experiment, though a trend was evident, and density dependent mortality may have been detected if the sample size had been increased. Ang and De Wreede (1992) did find density dependent mortality in populations of *Fucus distichus* sporelings, and Black (1974), Reed (1990*b*) and Reed *et al*. (1991) detected density dependent mortality in kelps.

There were important differences in population structure between densities. Plant sizes in high density populations were more variable than in low density populations, and a strong negative skewness developed in the low density ones. Ang and De Wreede (1992) found that high size inequality soon developed in high density germling stage populations of *Fucus distichus*, and suggested dominance and suppression.

The limiting factor of intraspecific competition in this experiment (nutrients?) may have been different from those in other chapters conducted on larger plants (light). Indeed, it is very difficult to envisage competition for light occurring in very young even-aged sporelings unless they are physically stacked on one another. Even then, while those on top get more light, they have no substratum to attach to. Indeed there is some evidence to suggest that very high densities of spores may experience high mortality because large chunks of spores break away from the surface. Another very real threat to high densities of spores is disease, particularly bacterial (personal observation with *Himanthalia elongata* spores), which may be transmitted in a density dependent fashion, and be equivalent to "damping-off" of seeds at high densities (Harper, 1977).

Probably the earliest signs of negative density dependence are reduced growth rates, and only at a later stage does mortality start to take a toll. Differential growth is of fundamental importance in any population. The largest plants not only outcompete smaller ones, but in the absence of other factors (*eg* wave action) are less likely to die and more likely (eventually) to reproduce first. The factors which limit growth in microscopic populations are therefore very important, and the interaction between density, light and nutrients will be the subject of the next chapter.

Chapter 7

The importance of light and nutrients as determnants of early stage population development

7.1 Introduction

In the last chapter we looked at density as a factor effecting the growth and survival of *Fucus vesiculosus* germlings. I concluded that while competition for light was not important in those laboratory populations, nutrient limitation might have been taking place, and that intraspecific competition certainly occurred. While early post settlement propagules in the field are subjected to numerous factors which may precipitate mortality (Vadas *et al*., 1992), laboratory culture reduces the number of these variables and a reasonable experimental design negates the effects of those remaining. Of those factors thought to be respon-

sible for limiting growth and causing mortality light and nutrients are usually considered potentially the most important. While density is obviously an important factor in influencing the growth and survival of propagules, the limiting factors in intraspecific competition are something of a puzzle.

The experiment detailed in this chapter was designed to elucidate the importance of some of the physical influences which may limit growth and survivorship. *Fucus serratus* was used, a species reproductive at the time of the experiment and similar to *Fucus vesiculosus* of the previous experiment.

7.2 Materials and Methods

Fertile plants of *Fucus serratus* were collected from a small area of rocky shore near Poyllvaaish on the eastern side of Bay ny Carrickey, Isle of Man (Chapter 2). Ten female and three male plants were collected in separate plastic bags on a low tide on 4th February 1992, and returned to the laboratory for preparation of gamete release.

7.2.1 Preparation of material

The preparation of material was identical to those methods detailed in Chapter 6 for *Fucus vesiculosus*, except that rather than being sun-dried for a few hours, the *F. serratus* plants were given thermal shock (5 hours at 6°C) to release gametes.

7.2.2 Preparation of settlement plates

Glass slides were thought to be atypically smooth, and in an effort to create a substratum more akin to the texture of rock, and of convenient size, artificial settlement plates were constructed. Glass slides were taken and scored with a diamond pen, once lengthways and four times widthways, and slides were snapped to produce eight rectangular glass pieces. A large number of glass pieces were created in this way. Sikadur 31 Rapid (Sika Ltd., Welwyn Garden City, UK), a two part thixotropic epoxy adhesive was made up and spread over the glass pieces. Then the settlement plates were gently tapped and the thixotropic properties of the material settled it. The adhesive consisted of resin and fillers, and the fillers ensured a rough texture to the settlement plates on a similar scale to fine sand. The settlement plates were left at room temperature for 24 hours to harden, before being numbered with micromarkers and colour coded with a permanent marker. The plates were soaked in fresh water and filtered sea-water for a day each.

7.2.3 Settlement

The aim was to create five different densities of settled spores. Five small glass tanks were thoroughly cleaned and rinsed. Sixty four settlement plates were placed face up in each of the five tanks and the tanks were filled to 2 cm depth with filtered sea-water.

A suspension of *F. serratus* eggs was mixed with a small portion of sperm suspension and shaken. Aliquots were taken to make 50 %, 10 %, 5 % and 1% suspensions of the original suspension, these being chosen to cover two orders of magnitude and half way between each. Each suspension was trickled onto the water surface of one of the five tanks in a zigzag pattern, and the tanks left undisturbed in a constant temperature room for 24 hours.

7.2.4 Experimental design, treatments and culture details

A fully factorial experimental design with four replicates was used to assess the relative roles of density, time, light and nutrients on survival and growth of propagules of *F. serratus*.

One plate of each density was transferred to a Petri dish using forceps. Sixty four Petri dishes, each with five plates (one of each density) were constructed in this way. Four light levels were created by using chiffon or black plastic netting (with approx 1 mm holes) sold for clothing. These materials were cut into Petri dish diameter circles and Sellotaped onto the Petri dish lids in different proportions to create four light intensities (Table 7.1). Each set of four different light level Petri dishes was assigned either a high or low nutrient status. Low nutrient status was achieved by culturing the plants in filtered sea-water changed every 15 days, while high nutrient status was created by using F/2 enriched sea-water medium (Appendix 1) changed weekly. All other conditions were as those described in Chapter 6.

In order to minimise any difference in conditions along and across the constant temperature room shelf, different treatments were laid out in a specific pattern.

Table 7.1 The creation of four light levels

Material	**Photon irradiance**	Percentage incident light
No cover	180μmol photons.$m^{-2}s^{-1}$	100
2 layers net	110μmol photons.$m^{-2}s^{-1}$	61
4 layers net	60μmol photons.$m^{-2}s^{-1}$	33
1 layer chiffon	10μmol photons.$m^{-2}s^{-1}$	5.5

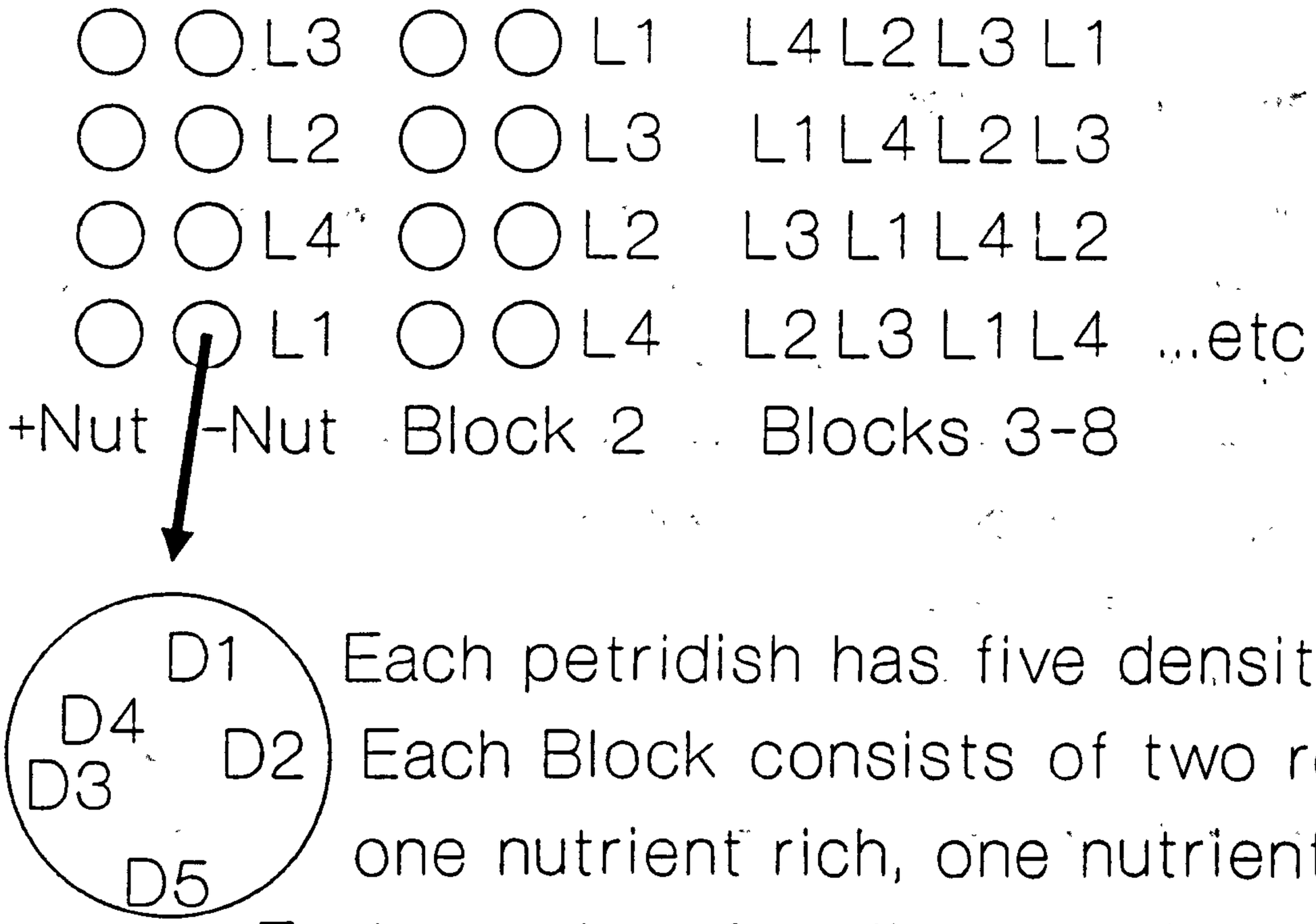
At the start of the experiment, a block of four light levels of low nutrients was laid across the shelf in a row, with light levels randomly placed within the row. A row of four light levels with high nutrients was laid out next to this with corresponding light levels adjacent (Figure 7.1). These two rows were termed a block. The next block only differed in that the light levels were altered so that the back row light level of the first block was the same as the first row of the second block, the other levels being moved back. This was carried out down all the subsequent blocks (Figure 7.1). Every seven days the blocks were randomly assigned new positions along the shelf, and the two light levels at the back of each block moved to the front.

7.2.5 Measurements

After setting up the experiment four blocks were immediately (destructively) harvested in order to check for any differences between treatments resulting from the method. A second (destructive) harvest was carried out after 76 days, at the end of the experiment.

At the start of the experiment, counts were made of the number of propagules in four random 22.1 mm^2 areas of each of the four replicate slides for each treatment and level for the three highest densities. In the two lowest densities whole plate counts were made. The plates of the two lowest densities were placed on acetate sheets and photocopied so that area and thus density (Plants mm^{-2}) could be determined later. At the end of the experiment counts were made of all the germlings on each plate, and all the plates were photocopied

Figure 7.1 The experimental design



as above. Furthermore, a *camera lucida* was used to draw the outlines of germlings in order to determine lengths and thus population structures. Where there were more than ten germlings on a plate, a sample of at least ten were drawn, while where there were less all were drawn. As in Chapter 6 drawings were digitized with DesignCAD software and sorted using a bespoke Lotus 123 macro on an IBM personal computer. The digitizer and DesignCAD software were also used to measure the areas of plates from the photocopies.

7.3 Results

7.3.1 Checking the methods

ANOVA of actual density of propagules at the start of the experiment found a significant difference between density treatments (Table 7.2). However, a Tukey test revealed that only the two highest density treatments were significantly different from all the others, the three lowest densities being statistically similar (Table 7.2, Figure 7.2). Consequently, the three lowest densities were pooled and subsequent analyses were carried out between 'high' (100 % original suspension of spores), 'medium' (50 %) and 'low' (10 %, 5 %, 1 %) densities. A second ANOVA revealed differences, and a Tukey test demonstrated that the three densities were statistically different at the start of the experiment (Table 7.3)

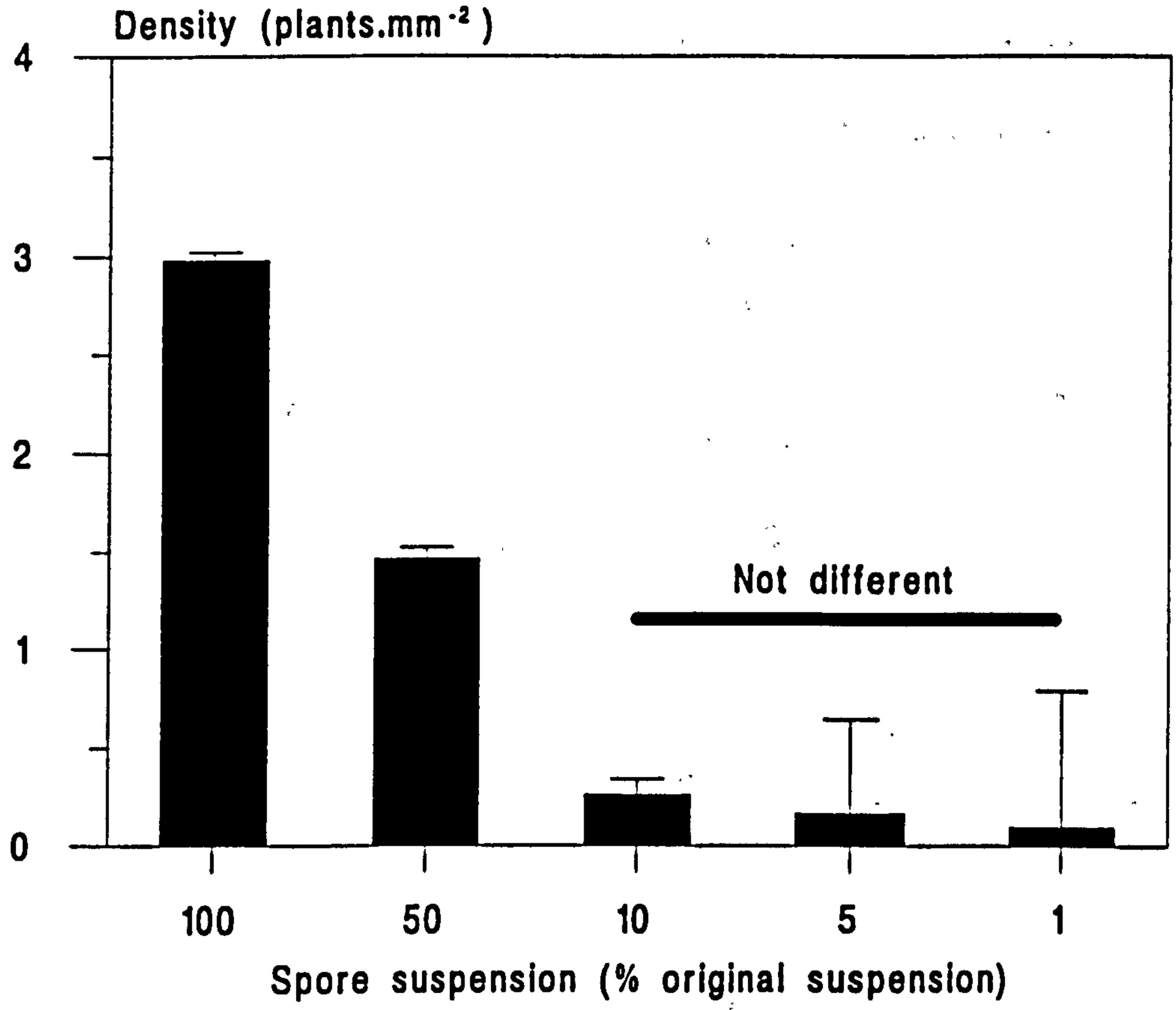
Table 7.2 Analysis of variance of actual density between initial density levels - a test of methods for the five density treatments.

Factor	D.F.	M.S.	F.	p
Density	4	49.635	352.58	<0.001
Residuals	155	0.141		

Table 7.3 Analysis of variance of actual density between initial density levels with the three smallest density treatments pooled

Factor	D.F.	M.S.	F.	p
Density	2	99.049	698.56	<0.001
Residuals	157	0.142		

Figure 7.2 Mean densities at the beginning of the experiment. The three smallest densities were not statistically different. Bars = ±1 Standard deviation.



7.3.2 Population structures

The most striking feature of the population structures was the difference in growth between high and low nutrients treatments. The high nutrient treatment obviously stimulated the growth of plants substantially (Figure 7.3a and *b*, note scales). Coefficients of variation and Gini coefficients indicated a higher variability and inequality in plant size in the populations grown under higher nutrient conditions (Tables 7.4 and 7.5). In general terms the populations grown under low nutrients were closer to normality than those grown under high nutrient conditions, which tended to be positively skewed (Table 7.6 and Figure 7.3a and *b*). However, differences between density and light levels were minor for these three population measures (Tables 7.4, 7.5 and 7.6).

Figure 7.3a The population structure of *Fucus serratus* populations after 76 days cultured under four light conditions, three densities and high nutrient levels.

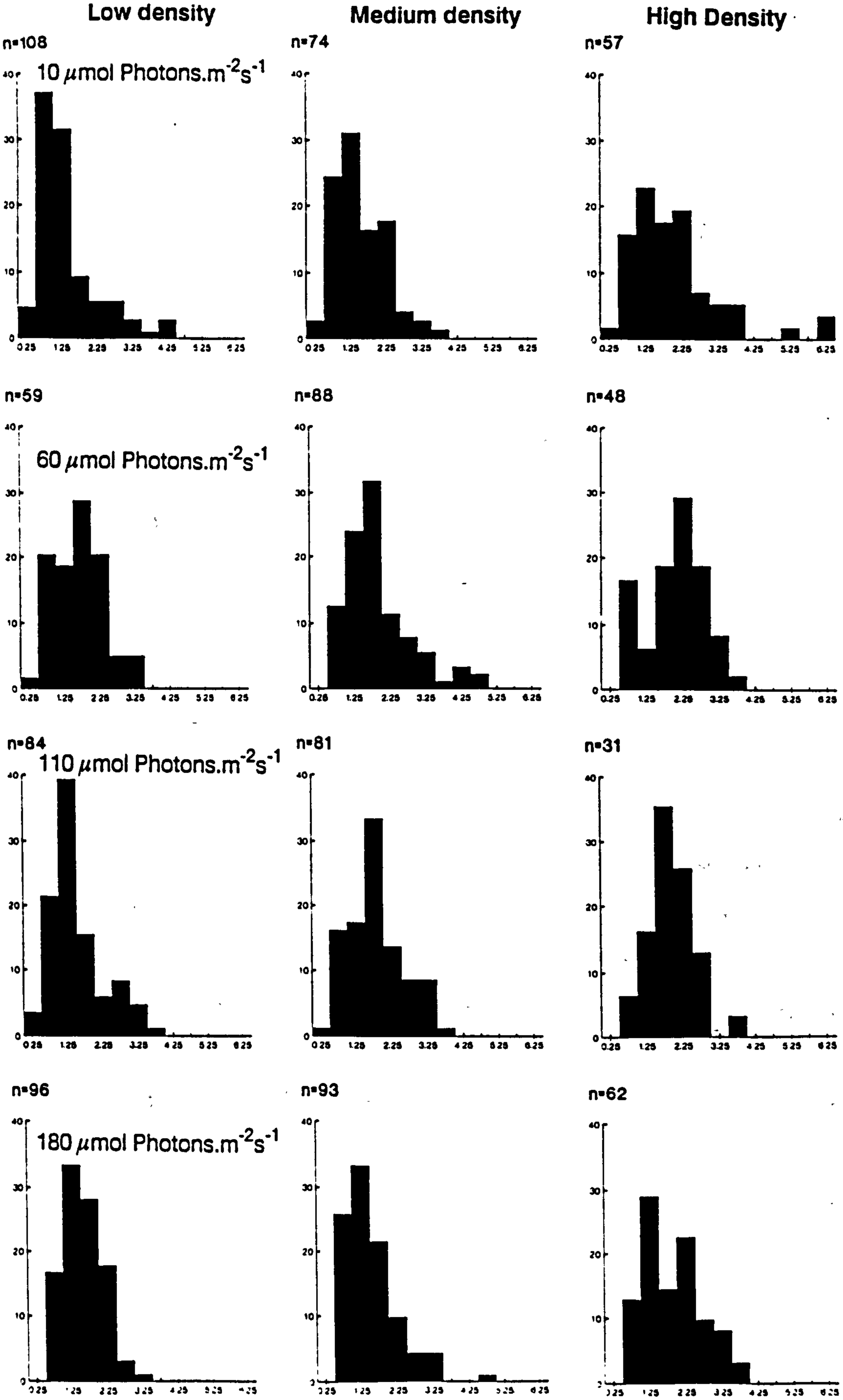


Figure 7.3*b* The population structure of *Fucus serratus* populations after 76 days cultured under four light conditions, three densities and low nutrient levels. (Note the different scale from 7.3*a*).

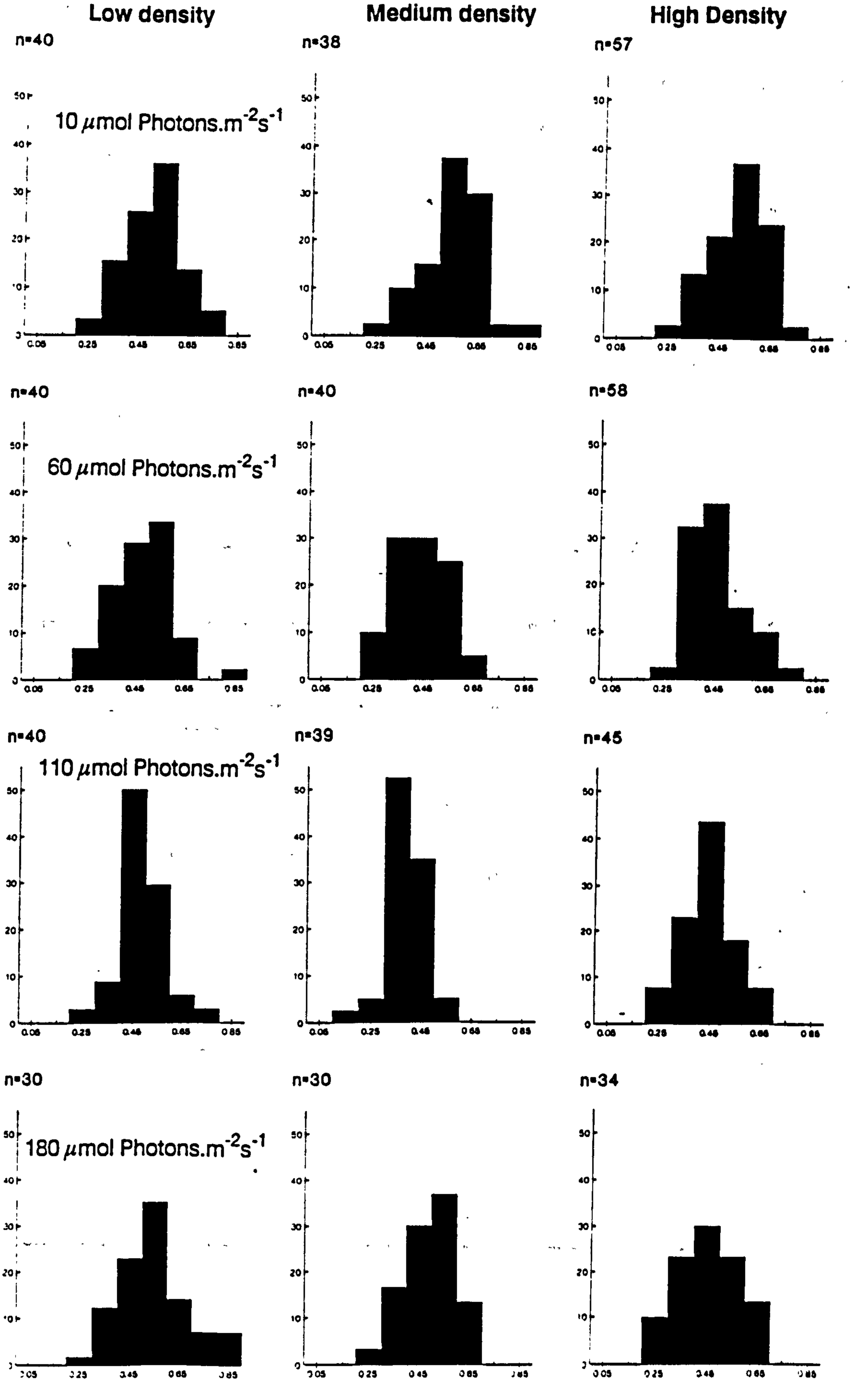


Table 7.4 Coefficient of variation in length of *Fucus serratus* populations grown for 76 days post settlement under various light, nutrient and density regimes

Nutrient Level	Light Level (μmol.phot. $m^{-2}s^{-1}$)	High Density	Medium Density	Low density
High	180	0.49	0.42	0.43
	110	0.35	0.49	0.33
	60	0.41	0.47	0.37
	10	0.62	0.47	0.61
Low	180	0.22	0.26	0.19
	110	0.21	0.24	0.25
	60	0.25	0.23	0.22
	10	0.21	0.22	0.25

Table 7.5 Gini coefficient of length of *Fucus serratus* populations grown for 76 days post settlement under various light, nutrient and density regimes

Nutrient Level	Light Level (μmol.phot. $m^{-2}s^{-1}$)	High Density	Medium Density	Low density
High	180	0.26	0.24	0.24
	110	0.20	0.26	0.18
	60	0.23	0.25	0.21
	10	0.31	0.26	0.31
Low	180	0.12	0.14	0.10
	110	0.12	0.13	0.14
	60	0.14	0.13	0.12
	10	0.12	0.12	0.14

Table 7.6 Skewness in length of *Fucus serratus* populations grown for 76 days post settlement under various light, nutrient and density regiemes

Nutrient Level	Light Level (μmol.phot. $m^{-2}s^{-1}$)	High Density	Medium Density	Low density
High	180	1.05	0.46	0.62
	110	0.44	1.37	0.39
	60	0.35	1.27	-0.11
	10	1.67	0.70	1.71
Low	180	-0.46	0.15	0.04
	110	0.00	0.18	0.42
	60	0.14	0.65	0.10
	10	-0.02	-0.35	0.51

7.3.3 Effects of time, nutrients, light and initial density on subsequent density

A four-way ANOVA showed that initial density, light, nutrients and time interacted (Table 7.7). All densities at the end of the experiment were significantly lower than at the beginning (Figure 7.4*a-d*).

At the start of the experiment under nutrient enriched conditions Tukey tests found there were no differences in spore density between light levels for each initial density level, though of course there were significant differences in density between initial density levels at any light level (Figure 7.4*a*). Very similar results were found under low nutrient conditions, except at the medium initial density level where inexplicably the density at 60μmol photons.m^{-2}.s^{-1} was significantly higher than the other light levels (Figure 7.4*b*).

At the end of the experiment, under high nutrient conditions, there was no difference in final density between the four light levels of any of the three initial

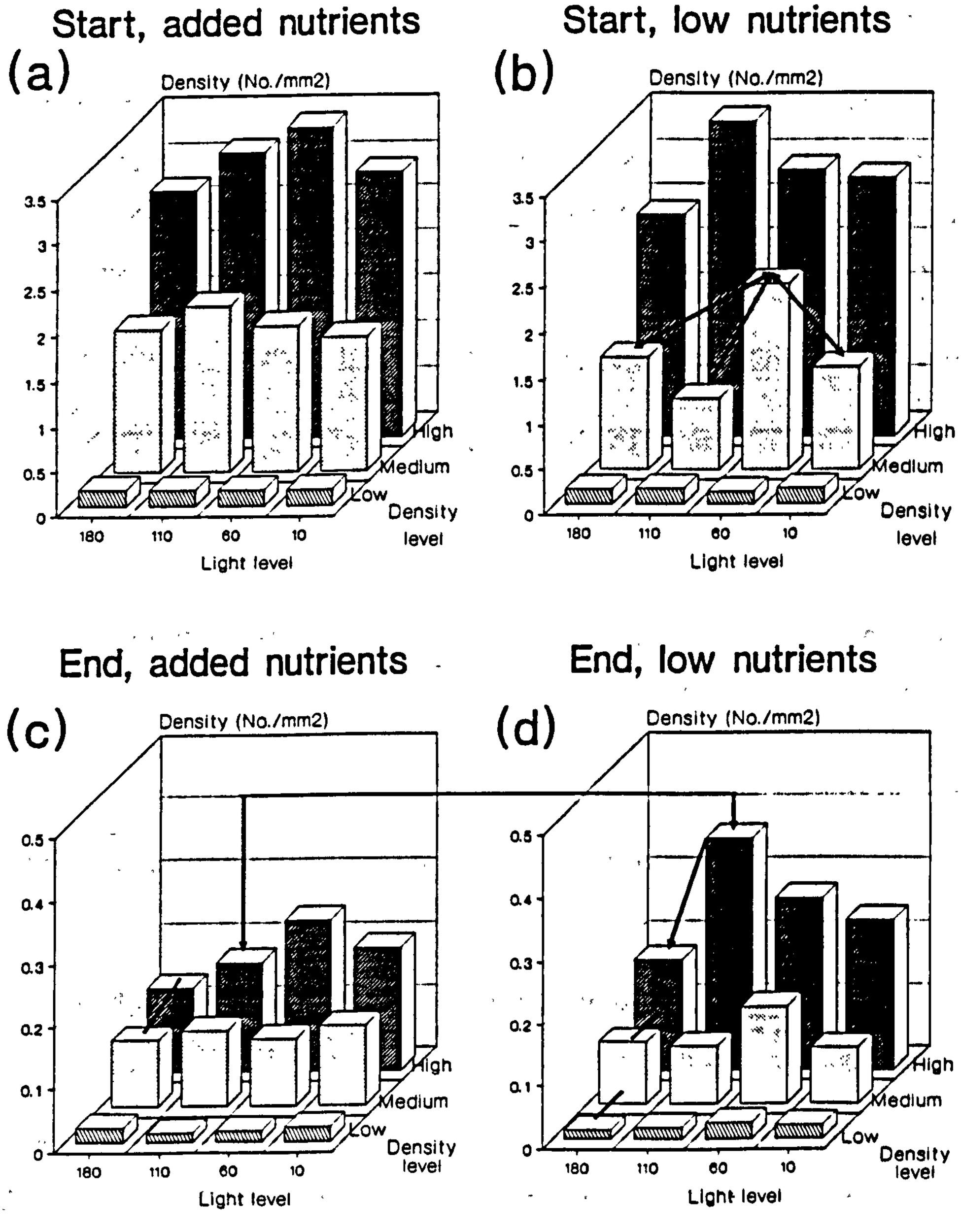
density levels (Figure 7.4c). There was a significant difference in final density between initial density levels at each light level except under 180μmol photons.m^{-2}.s^{-1} light. At this light level, the medium and high initial density levels showed no difference in final density, though both were higher than the low initial density level (Figure 7.4c). There was no difference between light levels at any initial density level.

Under low nutrient conditions at the end of the experiment there was no difference in final density between light levels at low and medium initial density levels. However, at the high initial density level the final density of sporelings at the 110μmol photons.m^{-2}.s^{-1} light level was significantly higher than at 180μmol photons.m^{-2}.s^{-1}, though both these light levels were not different from the two lower light levels (Figure 7.4d). At the 180μmol photons.m^{-2}.s^{-1} light level no

Table 7.7 Four-way Analysis of Variance of initial density, light, nutrients and time on subsequent density in *Fucus serratus* propagules in culture

Factor	D.F.	M.S.	F.	p
Density (D)	2	57.1055	1065.56	<0.001
Light (L)	3	0.4385	8.18	<0.001
Nutrients (N)	1	0.2804	5.23	0.023
Time (T)	1	124.8404	2329.46	<0.001
D x L	6	0.3274	6.11	<0.001
D x N	2	0.1435	2.68	0.071
D x T	2	42.4830	792.71	<0.001
L x N	3	0.0308	0.57	0.632
L x T	3	0.2664	4.97	0.002
N x T	1	0.5201	9.71	0.002
D x L x N	6	0.2789	5.20	<0.001
D x L x T	6	0.2068	3.86	0.001
D x N x T	2	0.1532	2.86	0.059
L x N x T	3	0.0383	0.71	0.544
D x L x N x T	6	0.1910	3.56	0.002
Residuals	272	0.0536		

Figure 7.4 The density of propagules of *Fucus serratus* in culture under different density, light and nutrient regimes at the start and end of the experiment



All densities were significantly lower at the end of the experiment than at the beginning. All densities levels were different for each light-nutrient-time combination unless joined with a bridging bar, signifying no difference. There was no significant difference between different light levels of each density level under any time or nutrient levels unless marked with a double arrow signifying a difference. There were no differences for any cell across low/high nutrient graphs unless indicated. —links two bars not significantly different, ↔ shows a difference between two bars.

difference in final density was found between the medium and high or medium and low initial density levels, though there was a difference between high and low initial density levels (Figure 7.4*d*).

At the end of the experiment there were no differences when comparing corresponding factors and levels between the two nutrient levels except at high initial density and 110μmol photons.m^{-2}.s^{-1} light level when propagule density was significantly higher under nutrient poor conditions (Figure 7.4*c* and *d*).

7.3.4 Effects of time, nutrients, light and initial density on survivorship

Survivorship was calculated by taking mean density of replicates at the end of the experiment from the mean density of replicates at the beginning and finding the percentage decrease.

A three-way ANOVA on arcsin transformed data revealed that only density significantly affected survivorship (Table 7.8) so data were pooled and a one-way ANOVA of initial density on survivorship was carried out (Table 7.9). Tukey tests showed that survivorship was significantly lower at the high initial density level than the low one, though there was not a statistical difference between the medium and high or low initial density levels (Figure 7.5).

7.3.5 Effects of time, nutrients, light and initial density on subsequent plant length

A three-way ANOVA showed that density and nutrients were important factors influencing the growth of young sporelings of *Fucus serratus* (Table 7.10), while light levels had no effect on growth as indicated by mean plant length at the end of the experiment (Table 7.10).

Tukey tests showed that there was no difference in mean plant size between the three initial density levels under nutrient poor conditions, while the highest initial density level had, on average, significantly smaller plants than the low density level (Figure 7.6).

Table 7.8 Three-way Analysis of Variance of initial density, light and nutrients on survivorship (arcsine transformed) in *Fucus serratus* propagules in culture

Factor	D.F.	M.S.	F.	p
Density (D)	2	0.01549	5.41	0.016
Light (L)	3	0.00153	0.53	0.666
Nutrients (N)	1	0.00907	3.17	0.094
D x L	6	0.00173	0.60	0.723
D x N	2	0.00100	0.35	0.711
L x N	3	0.00262	0.91	0.456
D x L x N	6	0.00240	0.84	0.559
Residuals	16	0.00287		

Table 7.9 One-way Analysis of Variance of initial density on survivorship (arcsine transformed) in *Fucus serratus* propagules in culture

Factor	D.F.	M.S.	F.	p
Density	2	0.01549	5.07	0.011
Residuals	37	0.00306		

Figure 7.5 The effect of different initial densities of settled propagules of *Fucus serratus* on subsequent survivorship 76 days later. Bars = ± standard deviation.

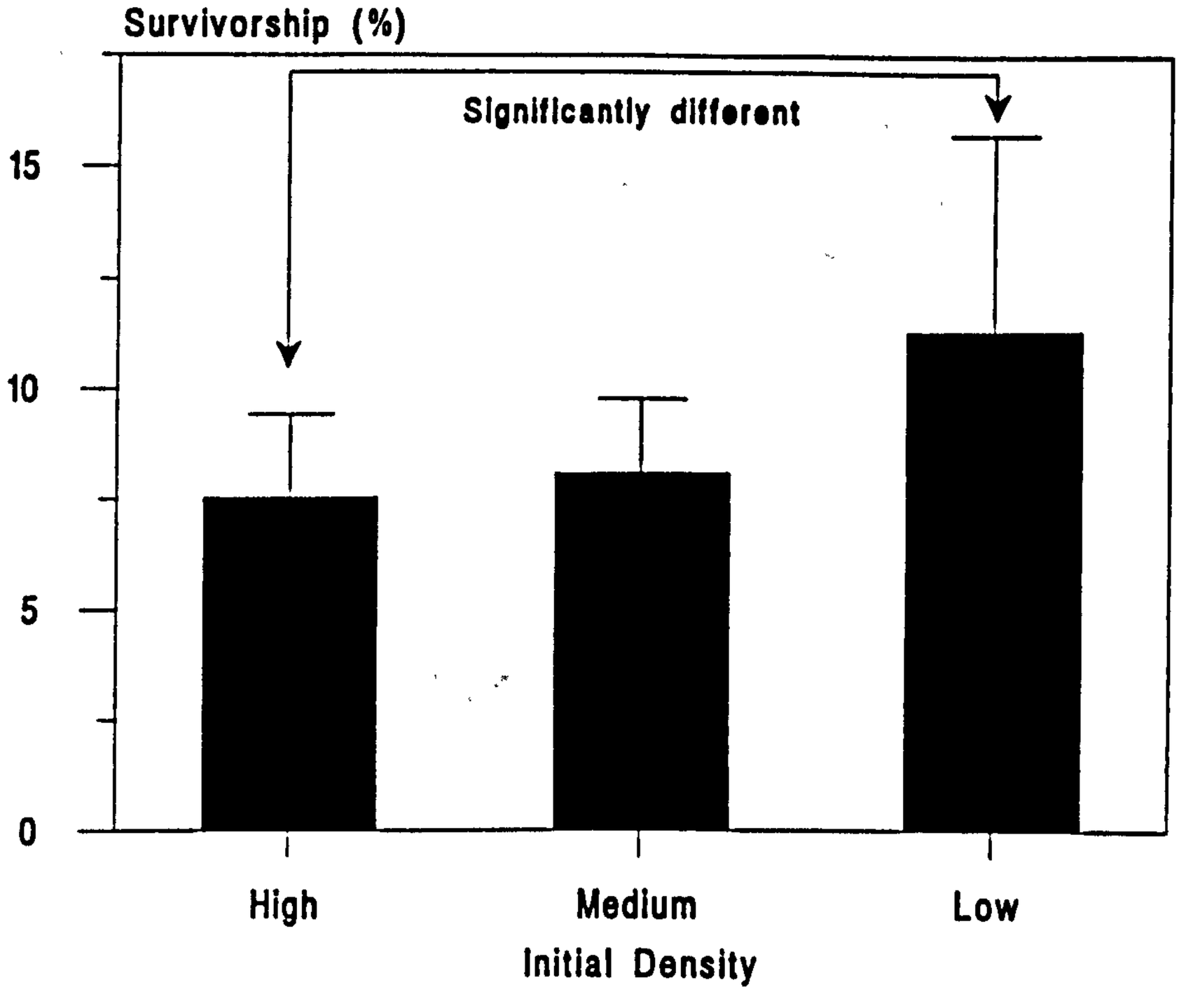
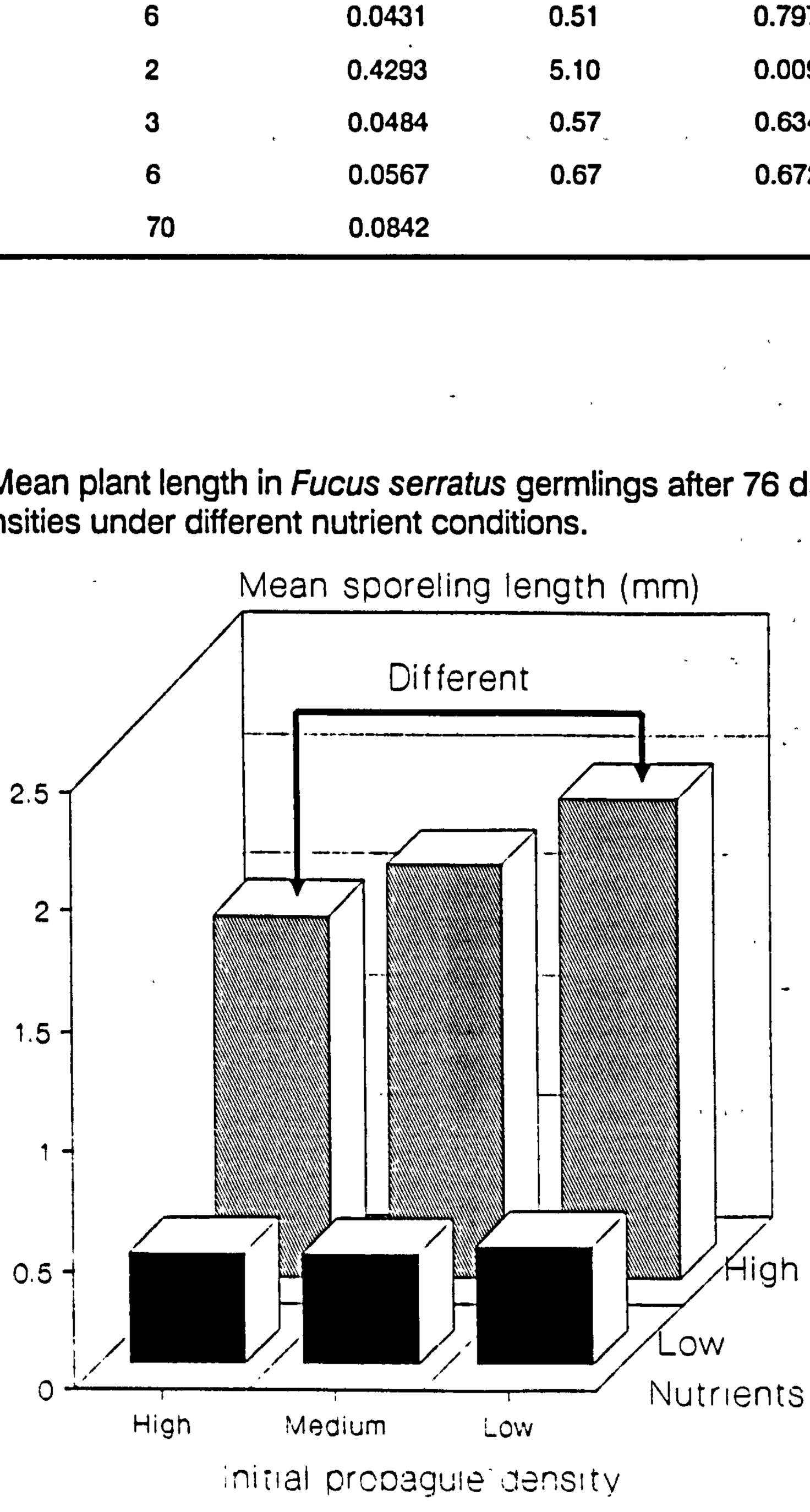


Table 7.10 Three-way Analysis of Variance of initial density, light and nutrients on mean plant length (arcsine transformed) in *Fucus serratus* propagules in culture

Factor	D.F.	M.S.	F.	p
Density (D)	2	0.5524	6.56	0.002
Light (L)	3	0.0391	0.46	0.708
Nutrients (N)	1	36.9417	438.74	<0.001
D x L	6	0.0431	0.51	0.797
D x N	2	0.4293	5.10	0.009
L x N	3	0.0484	0.57	0.634
D x L x N	6	0.0567	0.67	0.672
Residuals	70	0.0842		

Figure 7.6 Mean plant length in *Fucus serratus* germlings after 76 days grown at three densities under different nutrient conditions.



7.4 Discussion

There was large-scale plant mortality in all the populations (90 % in 76 days), though the higher the density, the greater the mortality. Plants grown under nutrient rich conditions certainly grew more rapidly than those under nutrient poor conditions, while light did not affect growth at all at the selected levels. It is probable that nutrient limitation of growth was taking place in these populations, and the density dependent nature of this limitation at high nutrient levels was expressed. Essentially, under low nutrient conditions there was little growth, so differences in growth between densities were not expressed, while under high nutrient conditions differences in growth between densities became obvious.

The effect of nutrients on final density was rather less clear. Generally the nutrient level made no difference to the subsequent density of plants. However in high density populations at 110μmol photons.m^{-2}.s^{-1} the final density was higher in populations under low nutrient conditions than those under higher ones. This suggests an interesting interaction involving light and nutrients. One theoretical explanation is that beyond 110μmol photons.m^{-2}.s^{-1} increased light caused mortality. However, this only occurred in the highest initial density level, and therefore must have been a density dependent process. One possibility is that under high nutrient conditions as plants grew quickly their nutrient requirements increased to a point when growth became limited by nutrients once more. This stimulated mortality resulting in lower final densities in high nutrient, high density populations. The lower density populations were not affected by nutrient limitation because of the lower numbers of plants and same nutrient resources. At the same time, under low nutrient conditions, light levels above 110μmol photons.m^{-2}.s^{-1} somehow precipitated mortality in high density populations, maybe because they were most nutrient stressed anyway.

While it is dangerous to extrapolate from culture to field (Russell and Fielding, 1974), some authors have suggested that life history stage determines the

importance of factors limiting growth (Fei *et al.*, 1989, Carpenter, 1990). In Chapter 5 we concluded that competition for light shaped populations of large plants. In this chapter nutrient limitation seemed to be more important. Carpenter (1990) reviewed the relative roles of light and nutrients in competition and it is not in the scope of this discussion to assess in detail the physiological complexities of these factors in determining growth. Suffice it to say that either resource can be limiting, and most importantly density dependence goes hand in hand with nutrient and light availability. The exact mechanisms are far from clear and further experiments may elucidate the interplay of light and nutrients. However, water movement has a profound effect by increasing nutrient supply to seaweeds. The cultures in this experiment had no water movement and were nutrient limited. On the shore however, nutrient limitation is uncommon, probably because of water movement.

Further work must take into account the interaction of density with other factors and realistic experiments assessing propagule competition must be carried out in laboratory culture but with greater mimicry of shore conditions. Unfortunately such an approach would be rather expensive.

Chapter 8

The importance of population structure in developing plant populations

8.1 Introduction

We saw in Chapter five that the way a seaweed population develops can be profoundly influenced by intraspecific competition. In this chapter we will assess the influence that initial population structure itself has on the growth of its component plants, mortality, biomass accumulation and on the subsequent development of the population's structure.

There is much evidence to suggest that settlement by seaweed propagules is not a one-off event resulting in a theoretically perfect, normally distributed population structure. Short term periodicity of seaweed gamete release has been found in many species reliant on lunar, tidal, night-day, saline, pH and thermal prompts to reproduction (reviewed by Brawley and Johnson, 1992). 'Spore clouds' (Norton, 1992*a*), 'recruitment windows' (Reed *et al.*, 1988) and 'mast years' (Vadas *et al.*, 1992) may all promote short term periodic settlement. It is probable therefore that multi-age recruitment takes place in seaweed populations.

Though some authors have assessed the role of population structure on the performance of populations on land (*eg* Westoby and Howell, 1986), no studies have previously looked at the effect of experimentally-creating population structures in seaweeds. Such studies may provide further evidence of the dominance and suppression found in Chapter 5 by approaching the subject from the point of view of the population structure rather than the growth of individual plants. It is the aim of this chapter to investigate that point of view.

Laminaria digitata plants were used because their sizes can be readily standardised (see below) and they grow very well in tanks (Chapter 5).

8.2 Materials and Methods

A range of sizes of small *Laminaria digitata* plants were collected from an area of rocky shore on Port St. Mary Ledges, Isle of Man (see Chapter 2 for study site details). Collection was carried out during a single low spring tide in March 1992, and plants were transferred to the laboratory in plastic bags the same evening and stored in a holding tank of running sea-water overnight. The following two days plants were sorted into three size categories by total length: 5-10 cm, 15-20 cm and 20-25 cm. During sorting a small number of plants were discarded because they had thicker stipes and shorter lamina than their peers and these features suggested that they were atypically short probably because of damage.

In order to reduce size variability to a minimum, plants were cut to standard lengths by removing a portion of the lamina at its tip. The 5-10 cm plants were cut to 5 cm, 15-20 cm plants to 10 cm and the 20-25 cm plants to 15 cm. In order to estimate growth rate and tip loss single holes were cut out of the lamina above the meristematic region using a cork borer (see Chapter 5).

Using the prepared plants three different population structures were created with the rope twine and plate method as in Chapter 5. One population consisted entirely of the smallest (5 cm) plants, another of half 5 cm and half 10 cm plants and the third of equal numbers of all three sizes. The density was kept identical for all three population structures. Three replicates of each population type were constructed.

In addition to the three population types, plates were made up with only a single plant apiece to act as a control not influenced by other plants. Six replicate plates (plants) were made for each of the three sizes of plants used to construct the populations.

All the populations and single plants were grown in an outdoor circular tank with a flow rate of 21 $l.min^{-1}$, and the culture details are identical to those introduced in Chapter 5.

Measurements of rope to hole and hole to tip were made periodically from March until October 1992, a period of 213 days during which the populations were sampled on nine occasions. As plant positions on the plates were known, plants could be followed through time. From these measures changes in population structure and growth rate could be followed. Populations were wet weighed at the time of measurement. Backcalculations were performed based on the relationship between wet and dry weight found from destructive harvests at the end of this and other experiments using the simple linear regression equation:

Dry Weight = -0.287 + 0.144Wet Weight $n=44$, Std=0.001, $p<0.001$ R2=99.6%.

Relative Growth Rate was calculated using the equation:

$$\frac{LnLength_{t1} - LnLength_{t1}}{t_2 - t_1}$$

Kain (1982) reviews the merit of using relative growth rate in the Laminariales.

8.3 Results

8.3.1 Population structure

The three populations types reflected their make-up at the start of the experiment showing one, two or three distinct size groups on length frequency histograms (Figure 8.1). The initial population construction obviously influenced the measures of variability and equality of plant sizes, the coefficient of variation and Gini coefficient. These two measures behaved very similarly to one another (Table 8.1 and compare Figures 8.2 and 8.3). At the start of the experiment the within population variability in plant size was at a minimum for all population types (Figures 8.2 and 8.3). There was also a (significant ANOVA, Table 8.2) difference in variability/equality between population types at the start of the experiment, with the one-size population having least plant size variability/inequality and the three-size population showing most variability/inequality of sizes. However, the difference between the one- and two-size population types was far greater than between the two- and three-size population types (Figure

Table 8.1 Pearson correlation coefficients for various population parameters of the three population types of *Laminaria digitata*.

	1	2	3	4	5	6	7	8
1. Time								
2. Mean frond length	0.92*							
3. Maximum frond length	0.87*	0.96*						
4. Coefficient of Variation	0.46*	0.60*	0.74*					
5. Gini Coefficient	0.45*	0.60*	0.74*	1.00*				
6. Skewness	0.42*	0.37*	0.50*	0.55*	0.51*			
7. Density	-0.82*	-0.83*	-0.74*	0.80*	-0.30*	-0.07		
8. Standing Crop	0.87*	0.96*	0.96*	0.68*	0.68*	0.42*	-0.71*	
9. Relative Growth Rate	-0.78*	-0.85*	-0.86*	-0.84*	-0.84*	-0.55*	0.51*	-0.74*

* = Significant @p = 0.05 .

Figure 8.1 Frond length frequency histograms for the three population types of *Laminaria digitata* throughout the course of the experiment

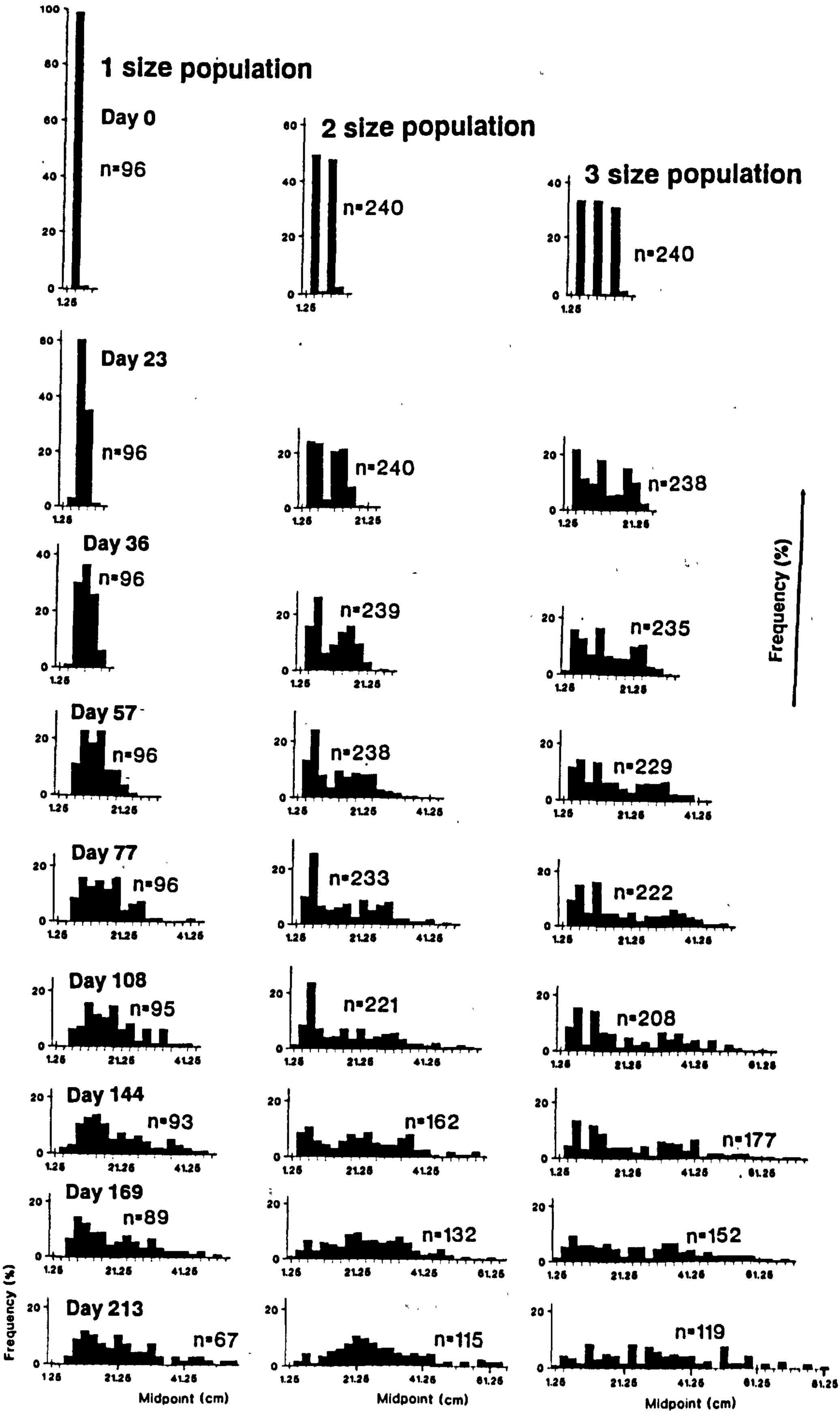


Figure 8.2 Coefficient of variation of frond length in three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

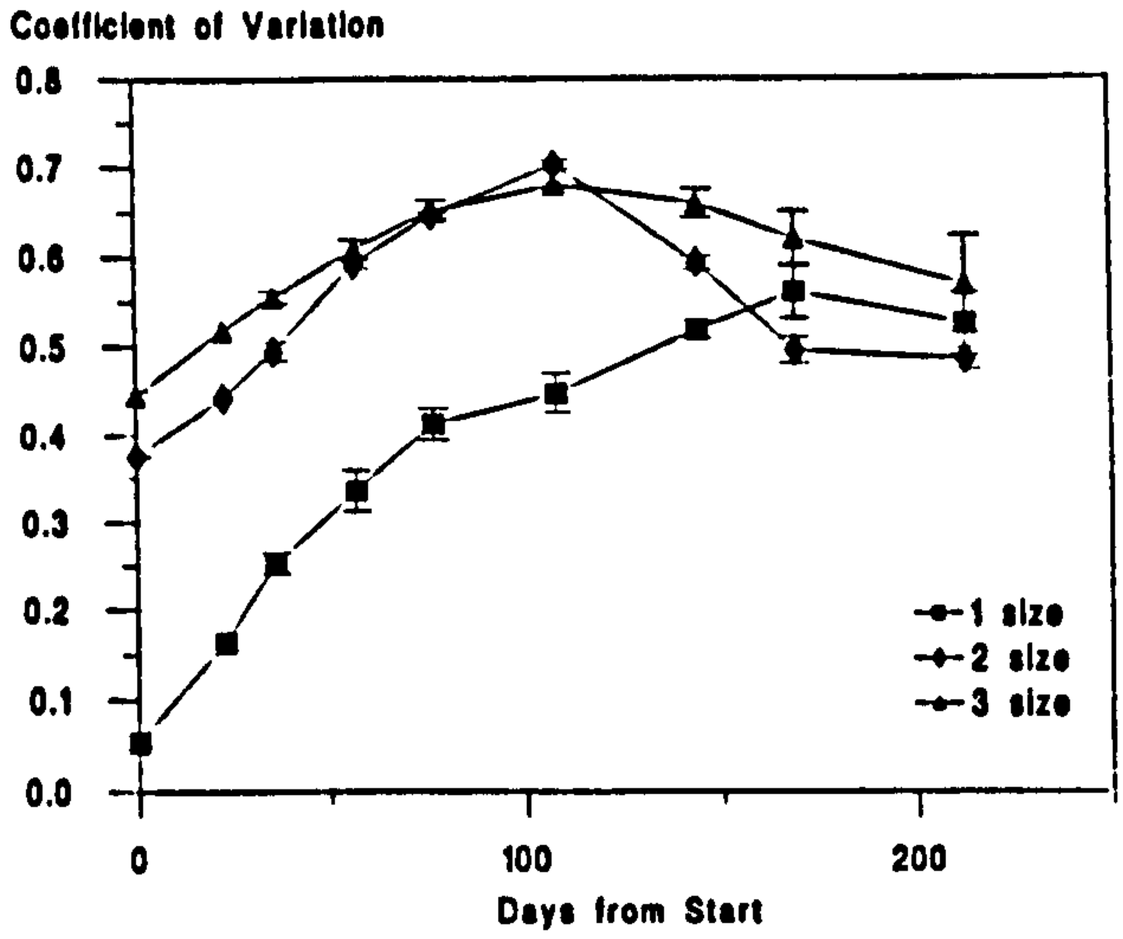


Figure 8.3 Gini coefficient of frond length in three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

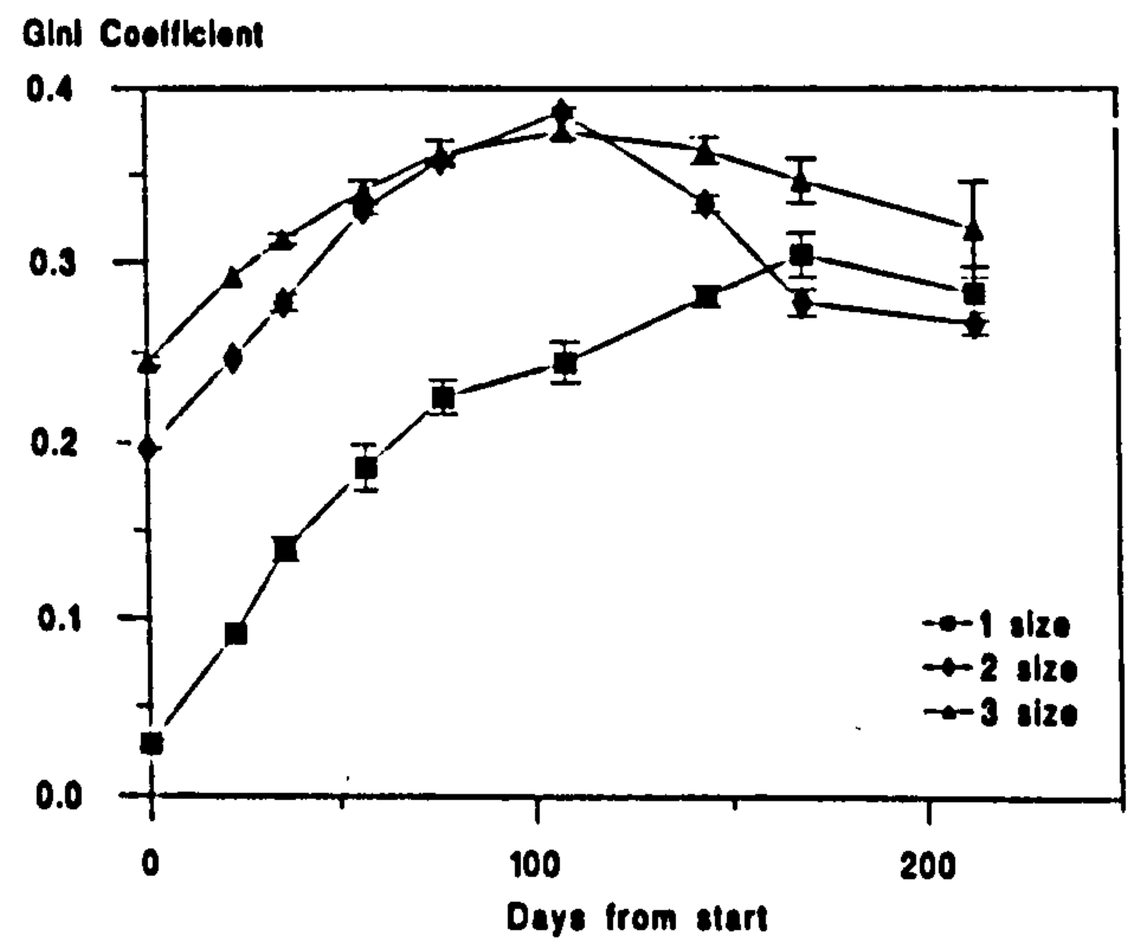


Figure 8.4 Skewness of frond length in three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

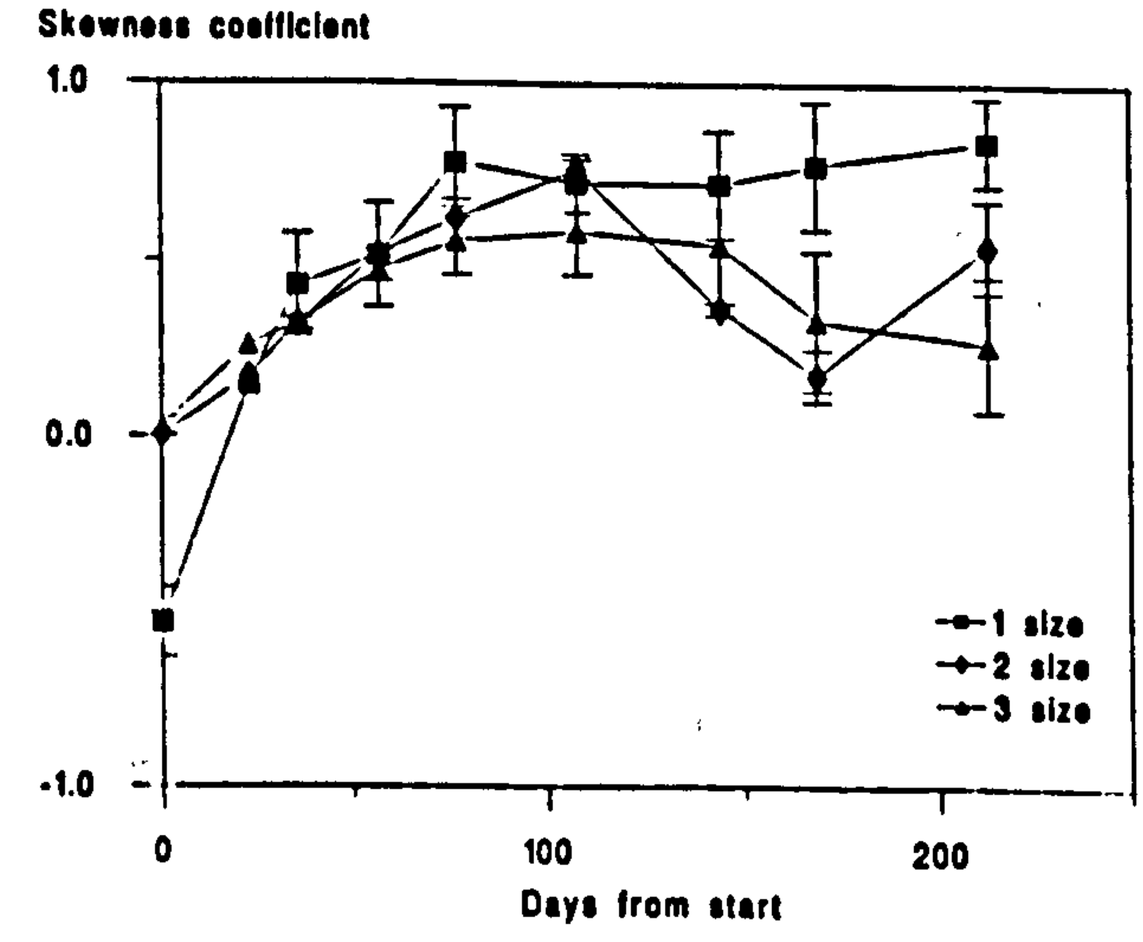


Table 8.2 Analyses of Variance and Tukey tests of coefficient of variation, Gini coefficient and skewness of three different populations of *Laminaria digitata*

	F value	p value	Tukey test
Coefficient of Variation			
Day 0	2193.49	<0.001	All different
Day 23	246.25	<0.001	All different
Day 36	74.97	<0.001	1 size population ≠ 2 or 3 sized population
Day 57	99.64	<0.001	1 size population ≠ 2 or 3 sized population
Day 77	72.71	<0.001	1 size population ≠ 2 or 3 sized population
Day 108	106.09	<0.001	1 size population ≠ 2 or 3 sized population
Day 144	4.80	0.057	1 size population ≠ 2 or 3 sized population
Day 169	1.81	0.242	Not Applicable
Day 213	0.74	0.517	Not Applicable
Gini Coefficient			
Day 0	2235.48	<0.001	All different
Day 23	316.33	<0.001	All different
Day 36	80.52	<0.001	1 size population ≠ 2 or 3 sized population
Day 57	102.53	<0.001	1 size population ≠ 2 or 3 sized population
Day 77	81.15	<0.001	1 size population ≠ 2 or 3 sized population
Day 108	112.40	<0.001	1 size population ≠ 2 or 3 sized population
Day 144	9.68	0.013	1 size population ≠ 3 sized population
Day 169	2.42	0.170	Not Applicable
Day 213	0.94	0.441	Not Applicable
Skewness Coefficient			
Day 0	18.91	0.003	1 size population ≠ 2 or 3 sized population
Day 23	0.32	0.741	Not Applicable
Day 36	0.35	0.715	Not Applicable
Day 57	0.03	0.967	Not Applicable
Day 77	1.17	0.374	Not Applicable
Day 108	0.33	0.729	Not Applicable
Day 144	0.81	0.486	Not Applicable
Day 169	2.80	0.138	Not Applicable

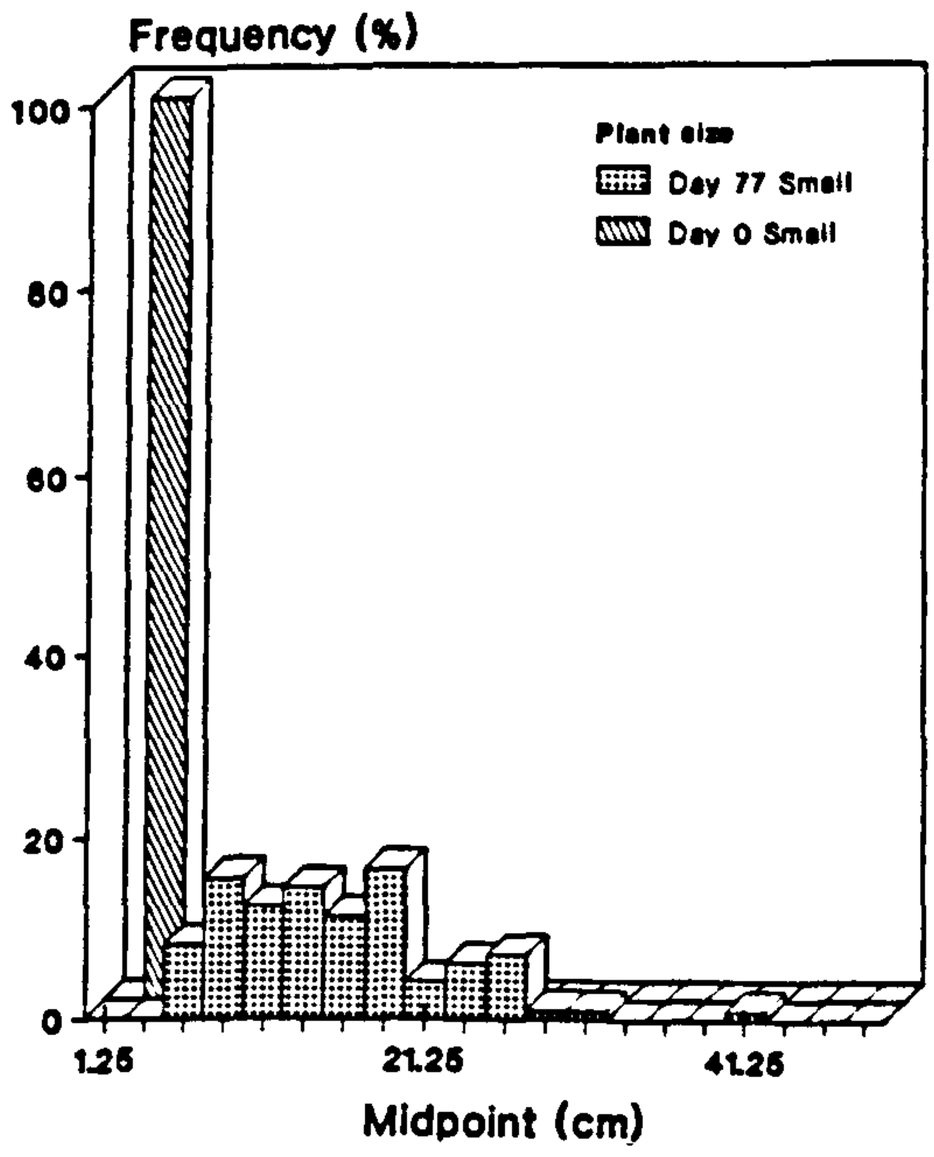
8.2 and 8.3). This was reflected in the fact that after 36 days the two- and three-size populations were not statistically different in population variability/inequality (ANOVA, Table 8.2). The similarity was due to a greater rate of variability/inequality increase in the two-size population (Figures 8.2 and 8.3). After day 36 and until day 144 the one-size population had a plant size variability/inequality significantly lower than the other two population types (Table 8.2). Though all the population types had become more variable/unequal since the start of the experiment, the two- and three-size populations became less variable after day 108 and as the one-size population type continued to become more unequal in plant size, from day 144 to the end of the experiment on day 213 all populations were equally variable (Table 8.2, Figures 8.2 and 8.3). The bi- and tri-modality was preserved although all the populations developed through time as plants moved into larger size classes until (from length frequency histograms) the modes became indistinct after 144 days in the two-size population and 169 days in the three-size population (Figure 8.1).

The skewness of plant lengths was different between populations at the start of the experiment, with the single size population being slightly negatively skewed and the two other population types being approximately normal (Figure 8.4, Table 8.2). The one-size population type became positively skewed very quickly and after only 23 days was as equally skewed as the other two population types. After this time there was no difference between populations in terms of skewness, which generally became more positive over the first 100 days of the experiment (Figure 8.4 and Table 8.2). The correlations between skewness, Gini coefficient, Coefficient of Variation and other population measures are presented in Table 8.1.

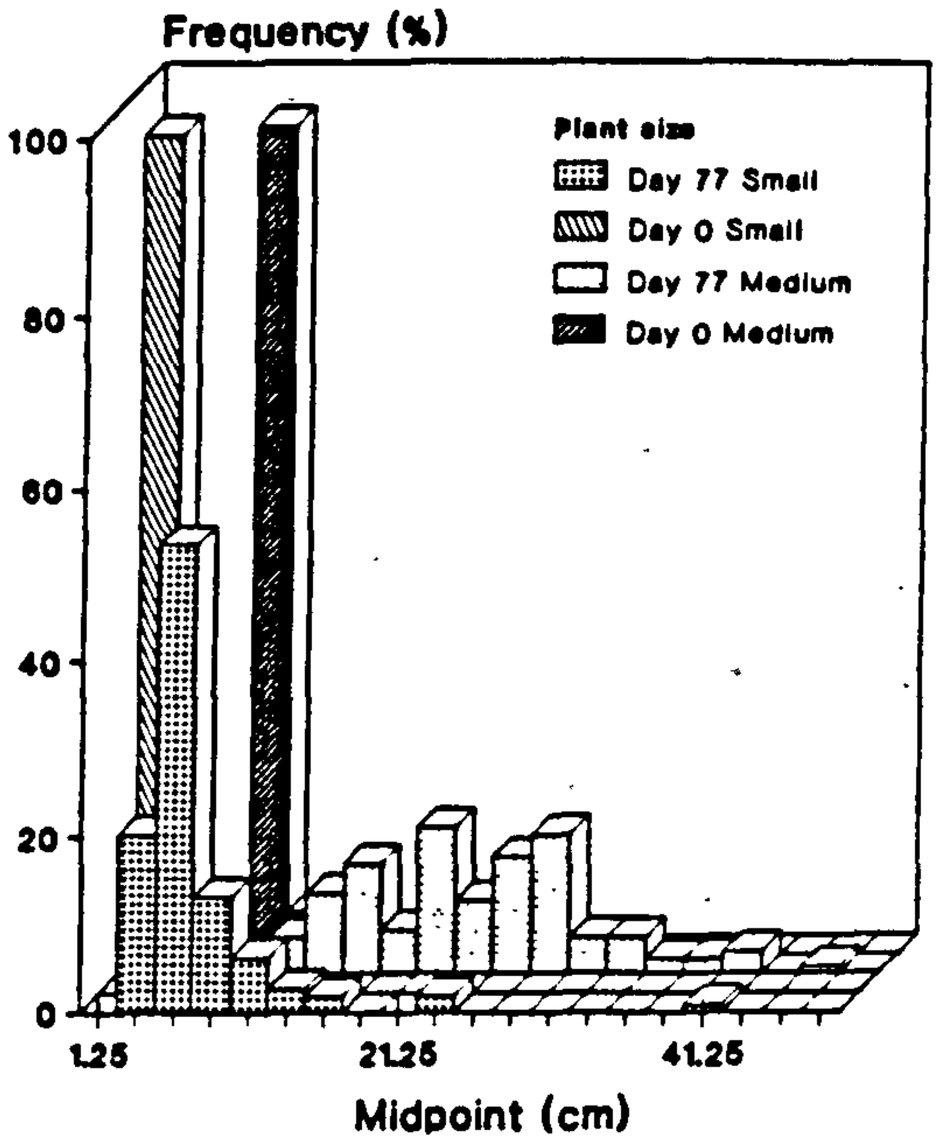
The population types, split into their constituent groups of different sized plants were analysed separately at the start of the experiment and at day 77 (Figure 8.5 and Table 8.3), and this helped to explain the influences of the groups of different sized plants on one another.

Figure 8.5 Frond length frequency histograms of the different initial size groups of three population types of *Laminaria digitata* at the start and after 77 days of the experiment.

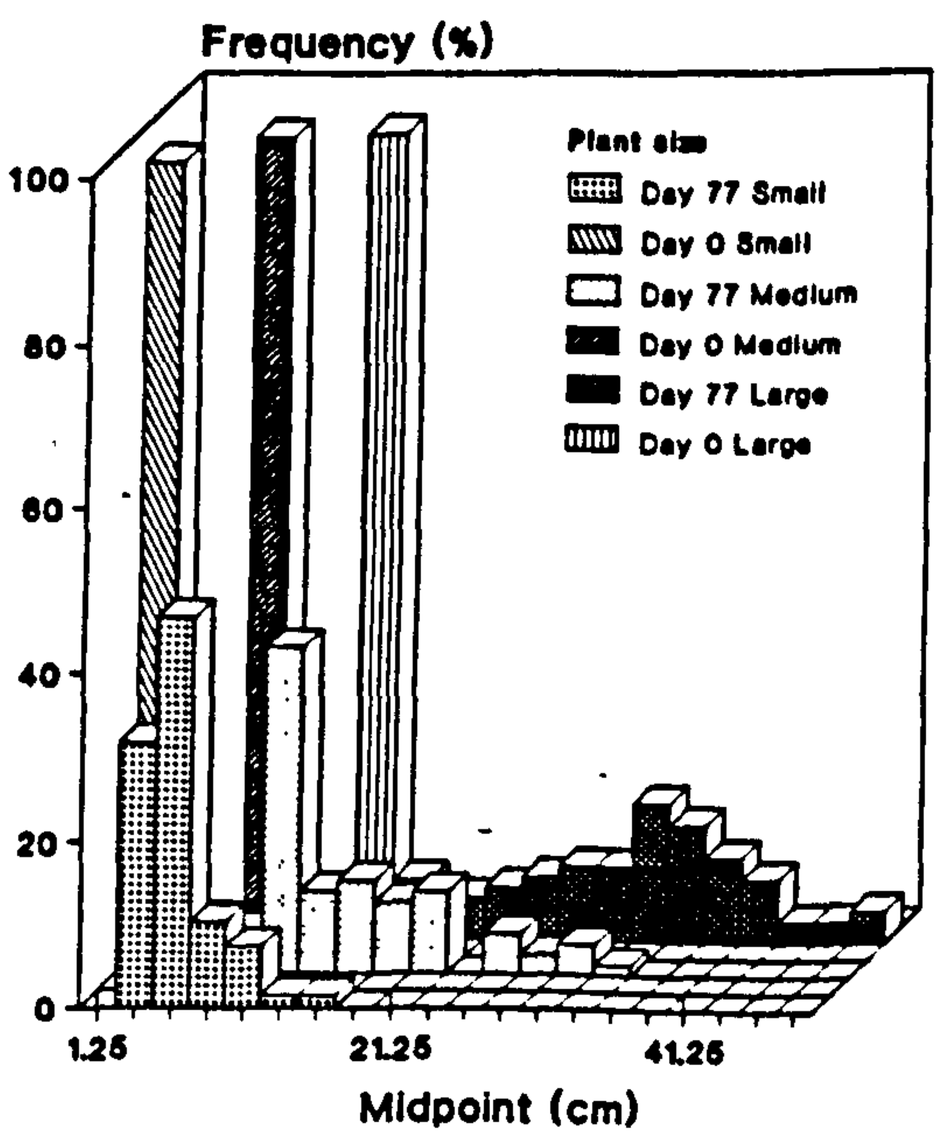
a) 1 size (5 cm) population



b) 2 size (5 and 10 cm) population



c) 3 size (5, 10 and 15 cm) population



In the one-size population the plants had grown so that none were in their original size frequency class. The mean plant size, variability, inequality and standard deviation of plant sizes had increased and the population had moved from being negatively to positively skewed (Figure 8.5a and Table 8.3).

In the two-size population, the initially small sized plants did not increase in mean size or in size standard deviation as much as the plants in the one-sized population (Table 8.3). However small plants were more variable (*CV*), though as equal (Gini), in size than were plants in the one-size population. The small sized plants in the two-size population had become highly positively skewed after 77 days (Table 8.3 and Figure 8.5*b*). A few of the small sized plants had achieved quite a large size (Figure 8.5*b*).

The medium sized plants in the two-size population type grew much larger over the 77 days, and while size standard deviation and skewness were similar to the (small) plants in the one-size population type, size variability and inequality were slightly less (Figure 8.5*b* and Table 5.3). However, size variability and inequality in the medium sized plants were only half as much as in the small plants of the same population type, and the skewness, though positive, was far lower (Figure 8.5*b* and Table 5.3).

In the 3 size population type after 77 days the constituent sizes showed very different distributions (Figure 8.5*c*). The small and medium fractions of the population type were in some ways similar to one another. Both were positively skewed, though not as much as the small plants in the two-size population type (the presence of a few successfully large plants here created a stronger skew, Table 8.3 and Figure 8.5*b* and *c*). The large plants exhibited a negative skew though. The small plants did not increase in mean length as much as the small plants did in the one- or two-size populations types, and the medium sized plants did not increase in mean length as much as the medium sized plants in the two-size population did (Table 8.3). The large plants had size standard deviations similar to the medium size plants in the two-size population type and

the (small) plants in the one-size population type (Table 8.3). The two smaller sizes of plants had size standard deviations lower than those of the largest plants. The large plants were less variable and more equal in size than the medium and small plants, while the small plants were less variable and more equal than the small plants in the other two population types (Figure 8.5c and Table 8.3).

Table 8.3 Mean frond length, standard deviation, coefficient of variation, Gini coefficient and skewness of different initial size fractions of three population types of *Laminaria digitata* at days 0 and 77.

Time and Size	Mean Frond Length	Standard Deviation	Coefficient of Variation	Gini Coefficient	Skewness
1 size population					
Day 0 Small	4.54	0.25	0.054	0.029	-0.545
Day 77 Small	18.33	8.29	0.452	0.252	0.694
2 size population					
Day 0 Small	4.38	0.24	0.062	0.033	0.469
Day 77 Small	7.42	4.68	0.630	0.239	4.552
Day 0 Medium	9.56	0.31	0.032	0.018	0.409
Day 77 Medium	23.61	7.44	0.311	0.174	0.501
3 size population					
Day 0 Small	4.35	0.25	0.057	0.032	-0.451
Day 77 Small	6.53	2.45	0.376	0.184	1.863
Day 0 Medium	9.38	0.28	0.030	0.016	0.276
Day 77 Medium	15.89	6.35	0.400	0.212	1.131
Day 0 Large	14.56	0.27	0.019	0.010	0.448
Day 77 Large	33.02	7.82	0.239	0.132	-0.263

8.3.2 Frond length

Mean frond length increased in all three population types throughout the course of the experiment (Figure 8.6). Understandably, at the start of the study there was a difference in mean frond length between the three population types, but this difference only lasted until day 36 (Table 8.4). After this time, and until day 108 the three-size population type had larger plants on average than the other two population types, which had similar mean plant lengths (Figure 8.6 and Table 8.4). From day 108 until day 169 there was no difference in mean plant length between the population types, though at the final sample time (day 213) the one-size population type mean frond length was significantly lower than the three-size population type mean frond length, due to a slow-down in the rate of frond length increase in the one plant population after approximately day 100 (Figure 8.6). The mean frond lengths of the plants grown singly increased at a much greater rate than the populations, though were subject to some decrease in length later on in the experiment presumably because of frond tip loss (Figure 8.6). The correlations between mean frond length and other population measures are presented in Table 8.1.

Naturally, maximum frond length (as the longest single frond in each replicate) was initially highest in the three-size population type (Figure 8.7 and Table 8.4). All population types showed an increase in maximum frond length throughout the course of the experiment. In the three-size population type this increase was steady throughout the experiment, though the rate of increase in the other two population types lessened after approximately day 100 (Figure 8.7). By day 36 there was no longer any significant difference in maximum frond length between the two- and three-size population types, and after day 144 there was no significant difference between any of the population types (Table 8.4). The correlations between maximum frond length and other population measures are presented in Table 8.1.

Figure 8.6 Mean frond length in three population types and individually grown plants of *Laminaria digitata* over time (bars = ± 1.S.E.).

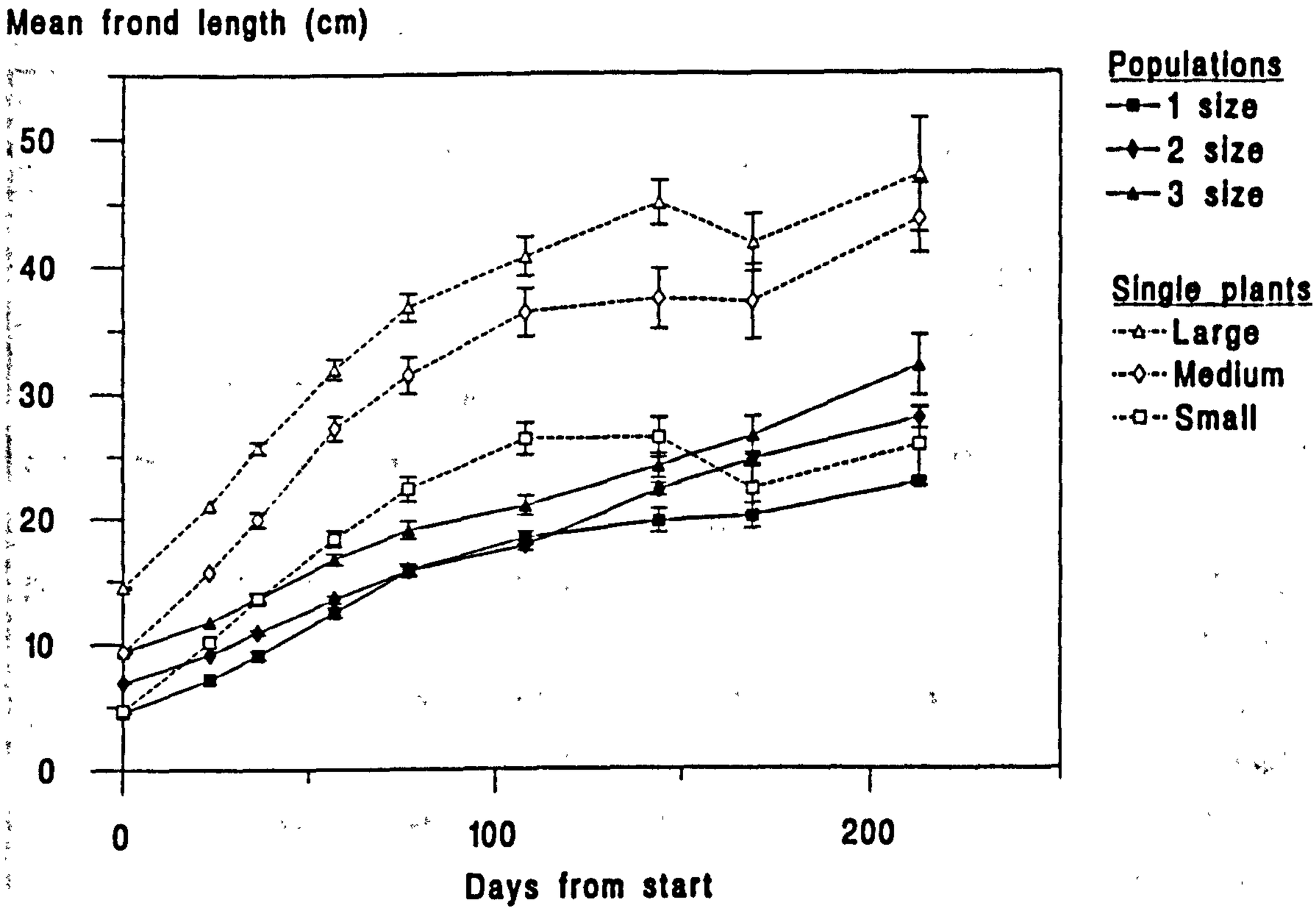


Figure 8.7 Maximum frond length in three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

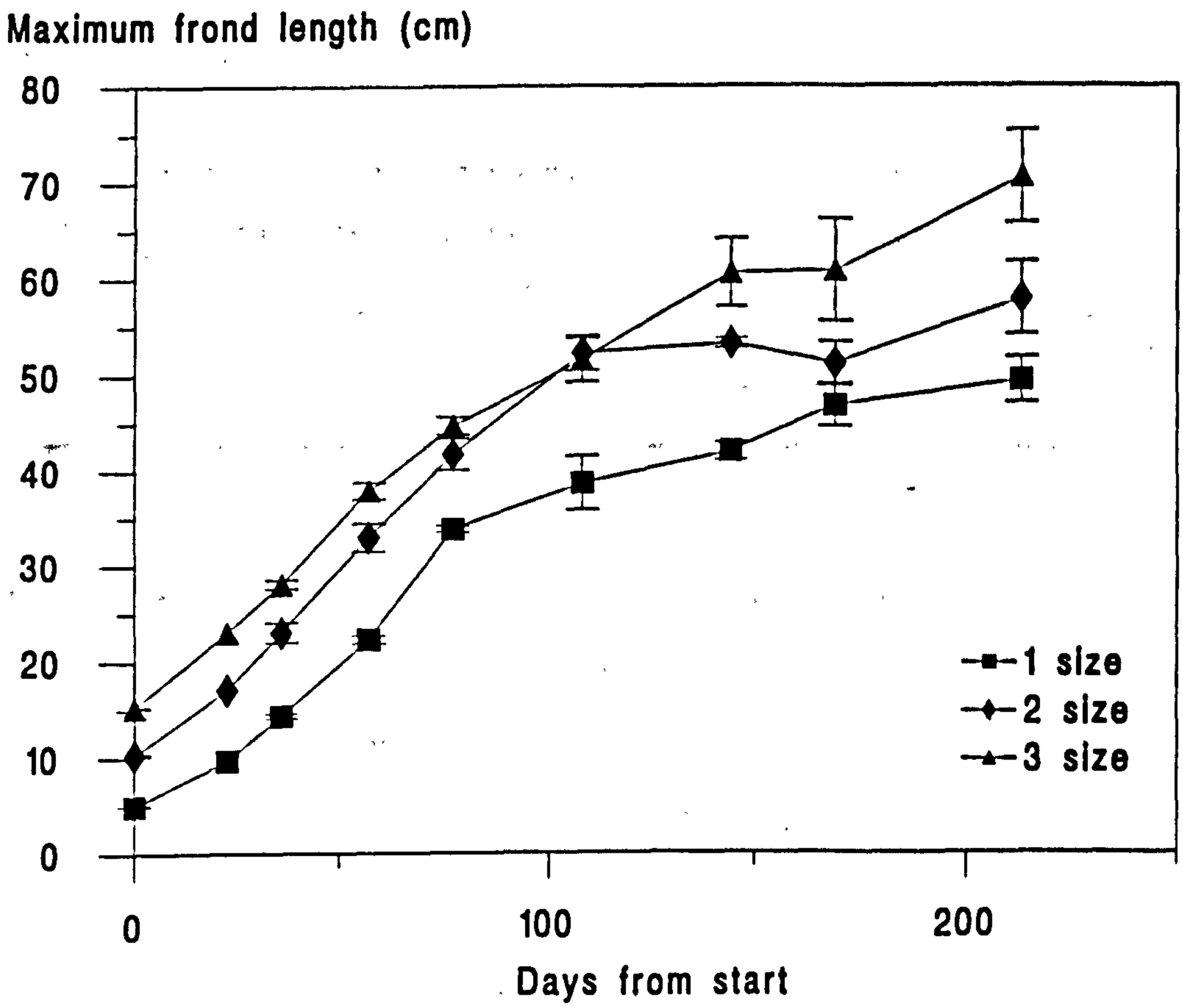


Table 8.4 Analyses of Variance and Tukey tests of mean and maximum frond length in three different populations of *Laminaria digitata*

	F value	p value	Tukey test
Mean frond length			
Day 0	4084.12	<0.001	All different
Day 23	53.02	<0.001	All different
Day 36	25.93	0.001	3 size population ≠ 2 or 1 size populations
Day 57	11.00	0.010	3 size population ≠ 2 or 1 size populations
Day 77	6.54	0.031	3 size population ≠ 2 or 1 size populations
Day 108	2.84	0.136	Not Applicable
Day 144	2.65	0.150	Not Applicable
Day 169	3.28	0.109	Not Applicable
Day 213	7.85	0.021	3 size population ≠ 1 size populations
Maximum frond length			
Day 0	5084.6	<0.001	All different
Day 23	67.92	<0.001	All different
Day 36	30.76	0.001	1 size population ≠ 2 or 3 size populations
Day 57	35.26	<0.001	1 size population ≠ 2 or 3 size populations
Day 77	3.83	0.085	Not Applicable
Day 108	8.35	0.018	1 size population ≠ 2 or 3 size populations
Day 144	4.44	0.065	Not Applicable
Day 169	2.45	0.167	Not Applicable
Day 213	3.22	0.112	Not Applicable

8.3.3 Standing crop

Though standing crop was generally higher in the three-size population type, the other two population types had similar standing crops throughout most of the experiment, except in the first 23 days, when all population types had different standing crops. By the end of the experiment there was no significant difference in standing crop between population types (Figure 8.8 and Table 8.5). Standing crop increased in all population types throughout the course of the experiment, though there was a fundamental change in the rate of biomass accumulation at approximately day 100 (Figure 8.8). The correlations between standing crop and other population measures are presented in Table 8.1.

8.3.4 Density and survivorship

Density decreased throughout the experiment as a result of plant mortality (Figure 8.9). The density of plants was identical in all population types until day 77, when the density of the three-size population type was significantly lower than the one-size population type (Figure 8.9 and Table 8.5). By day 144 both the two- and three-size population types had significantly lower densities of plants than the one-size population type, and this remained the *status quo* until the end of the experiment, with the two- and three-size population types never becoming different (Figure 8.9 and Table 8.5). The survivorship of the populations was essentially similar to density, though ANOVA on arcsine transformed data detected some slight differences in the relationships between the three population types (Figure 8.9 and Table 8.5). After 144 days 97% of plants remained in the single size population type while approximately 70% remained in the other two population types. By the end of the experiment (day 213) 68% of plants remained in the single size population while only 47% remained in the other two population types. The correlations between density, survivorship and other population measures are presented in Table 8.1.

When the survivorship of different fractions of each population type were considered at the end of the experiment, it was found that there was similar

Figure 8.8 Standing crop in three population types and individually grown plants of *Laminaria digitata* over time (bars = ± 1.S.E.).

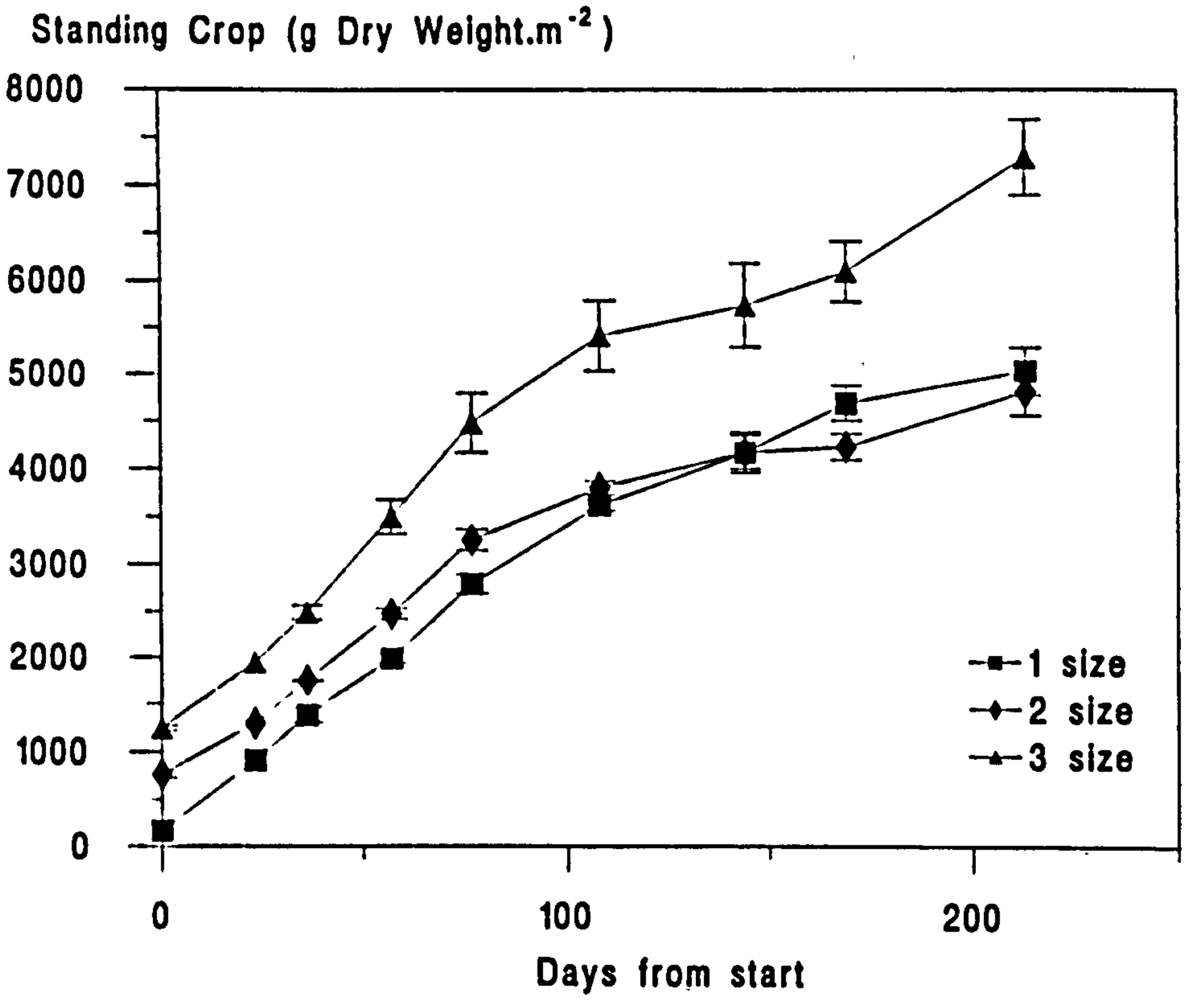


Figure 8.9 Density changes in three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

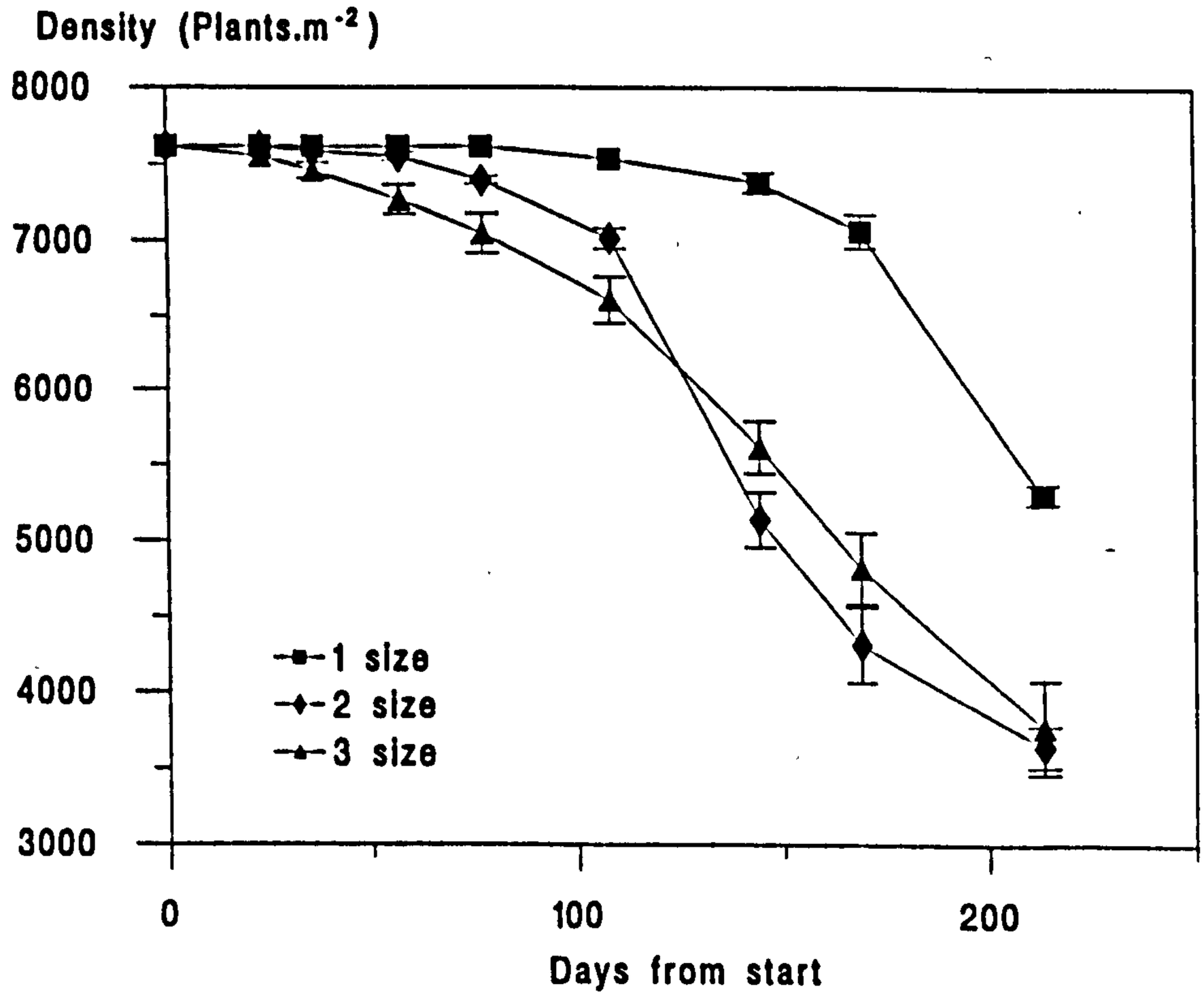
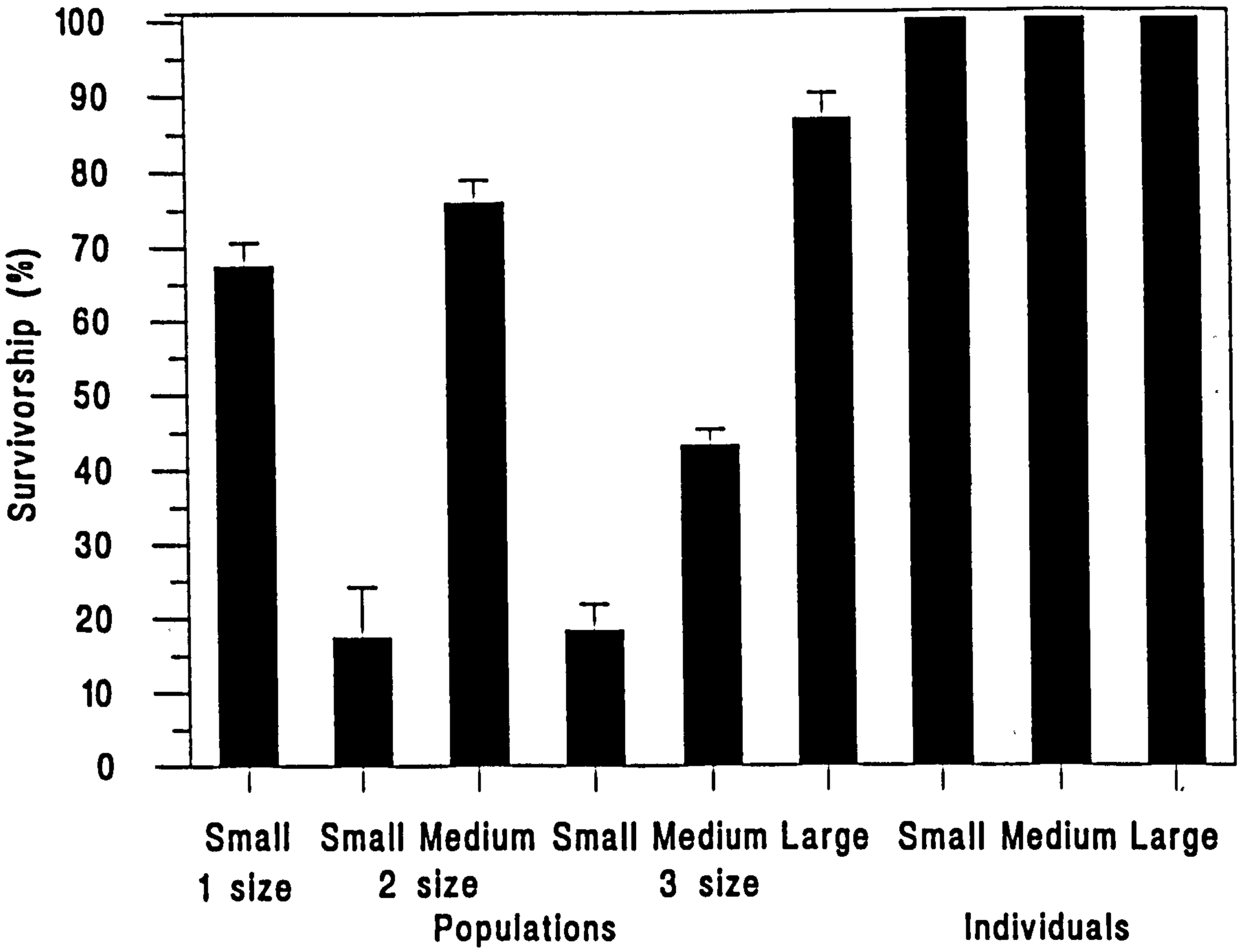


Table 8.5 Analyses of Variance and Tukey tests of standing crop, density and survivorship in three different populations of *Laminaria digitata*

	F value	p value	Tukey test
Standing Crop			
Day 0	253.50	<0.001	All different
Day 23	48.10	<0.001	All different
Day 36	17.00	0.003	3 size population ≠ 1 or 2 size populations
Day 57	10.10	0.012	3 size population ≠ 1 size populations
Day 77	10.10	0.012	1 size population ≠ 2 or 3 size populations
Day 108	6.96	0.027	1 size population ≠ 3 size populations
Day 144	10.43	0.011	3 size population ≠ 1 or 2 size populations
Day 169	6.67	0.030	3 size population ≠ 2 size populations
Day 213	4.65	0.060	Not Applicable
Density			
Day 0	-	-	Not Applicable
Day 23	1.00	0.422	Not Applicable
Day 36	1.50	0.297	Not Applicable
Day 57	3.95	0.081	Not Applicable
Day 77	5.73	0.041	1 size population ≠ 3 size populations
Day 108	6.67	0.030	1 size population ≠ 3 size populations
Day 144	21.14	0.002	1 size population ≠ 2 or 3 size populations
Day 169	36.69	<0.001	1 size population ≠ 2 or 3 size populations
Day 213	11.21	0.009	1 size population ≠ 2 or 3 size populations
Survivorship (Arcsine transformed)			
Day 0	-	-	Not Applicable
Day 23	1.00	0.422	Not Applicable -
Day 36	1.75	0.252	Not Applicable
Day 57	8.99	0.016	1 size population ≠ 2 or 3 size populations
Day 77	13.50	0.006	1 size population ≠ 2 or 3 size populations
Day 108	8.81	0.016	1 size population ≠ 3 size populations
Day 144	20.06	0.002	1 size population ≠ 2 or 3 size populations
Day 169	50.21	<0.001	1 size population ≠ 2 or 3 size populations
Day 213	10.76	0.010	1 size population ≠ 3 size populations

Figure 8.10 Survivorship of different sized parts of three population types and individually grown plants of *Laminaria digitata* over all times (bars = ± 1.S.E.).



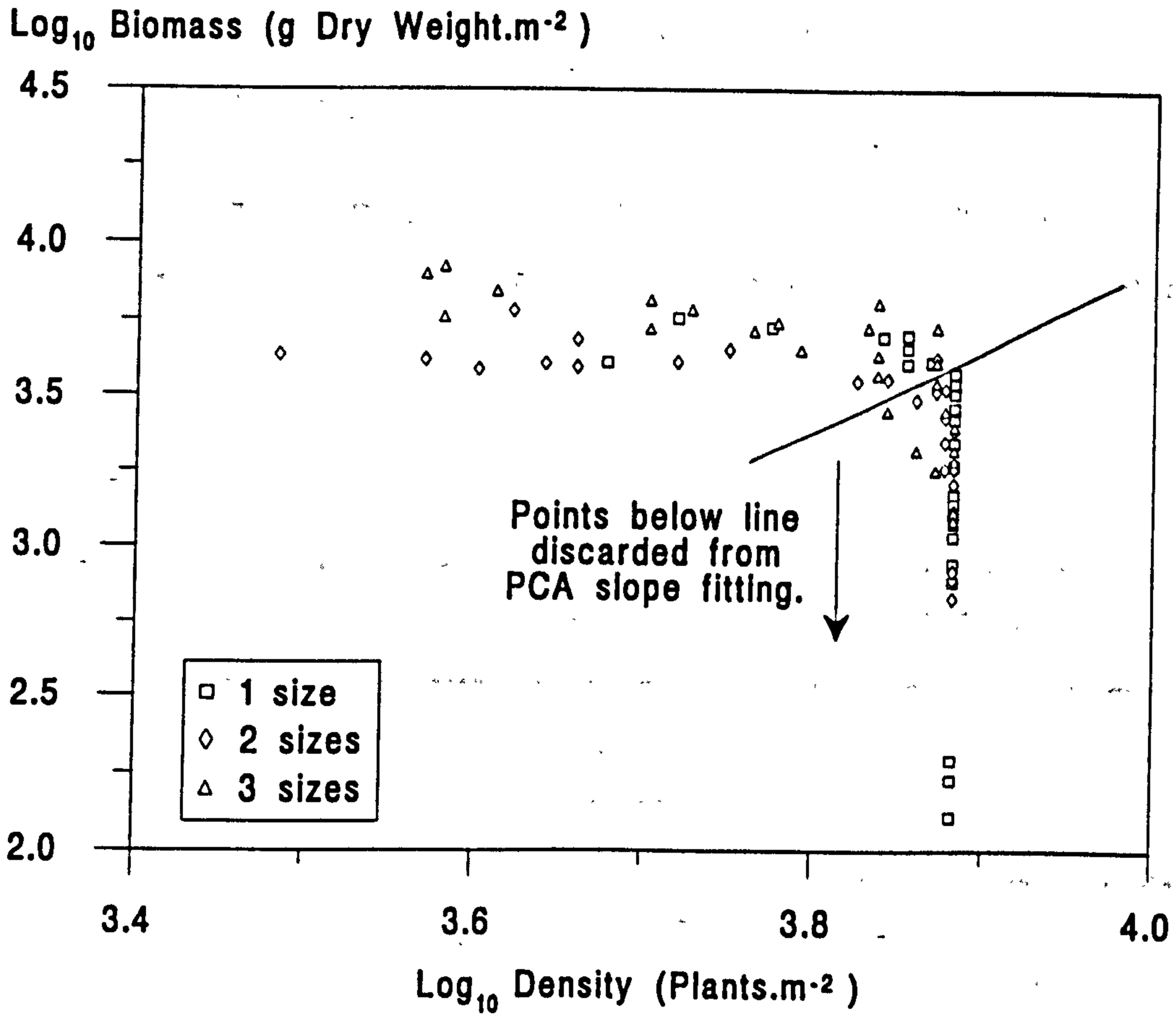
survivorship in the (small) plants in the one-size population and the medium and large sized plants in the two- and three-size population types respectively at 65-95% (Figure 8.10). The survivorship of small plants in the two- and three-size population types was much lower, and these small plants only had survivorships of 15-20% through the course of the experiment. A survivorship of 42% in the medium sized plants of the three-size population type was intermediate between larger and smaller plants of the same population type, but was lower than the medium sized plants of the two-size population (Figure 8.10).

8.3.5 Biomass density relationships

Principal component analysis revealed that the three population types conformed to the expected thinning slope of -0.5 when $\log_{10}$ biomass and $\log_{10}$ density were plotted (Figure 8.11):

$\text{Log}_{10}B = 5.88 + -0.59\text{Log}_{10}N$ Slope Confidence Limits L1 = -1.70, L2 = -0.02. Pearson Correlation -0.333 significant @$p = 0.05$, $n = 37$.

Figure 8.11 Biomass density relationships in the three population types of *Laminaria digitata*.



8.3.6 Relative growth rate

Relative growth rate decreased over time in all population types (Figure 8.12). Relative growth rate was found to be highest in the one-size population type and lowest in the three-size population type for the first 36 days of the experiment (Figure 8.12, Table 8.6). Between days 36 and 77 relative growth

rate was higher in the one-size population type than in the other two population types, though from day 77 to day 144 relative growth rates were significantly higher only in the one-size population type than the three-size population type, and the two- and three-size population types had similar relative growth rates. From day 144 until the end of the experiment all the population types had the same relative growth rates. The individually grown plants also had relative growth rates which decreased over time (Figure 8.13). Growth rates were highest in the small plants and lowest in the large plants for 57 days of the experiment, though after this time there was no difference in relative growth rates between initial plant sizes (Figure 8.13). At the start of the experiment all the relative growth rates for the individually grown plants were higher than the highest relative growth rates for the populations (Figures 8.12 and 8.13).

The relative growth rates for the single size population type were generally higher than those of any of the size fractions of the two- and three-size

Table 8.6 Analyses of Variance and Tukey tests of relative growth rate in three different populations of *Laminaria digitata*

	F value	p value	Tukey test
Relative Growth Rate			
Day 0-23	12.88	0.007	All different
Day 23-36	12.07	0.008	All different
Day 36-57	37.98	<0.001	1 size population $\neq$ 2 or 3 size populations
Day 57-77	12.35	0.007	1 size population $\neq$ 2 or 3 size populations
Day 77-108	6.19	0.035	1 size population $\neq$ 3 size populations
Day 108-144	10.84	0.010	1 size population $\neq$ 3 size populations
Day 144-169	0.00	0.998	Not Applicable
Day 169-213	0.14	0.874	Not Applicable

Figure 8.12 Mean relative growth rates in three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

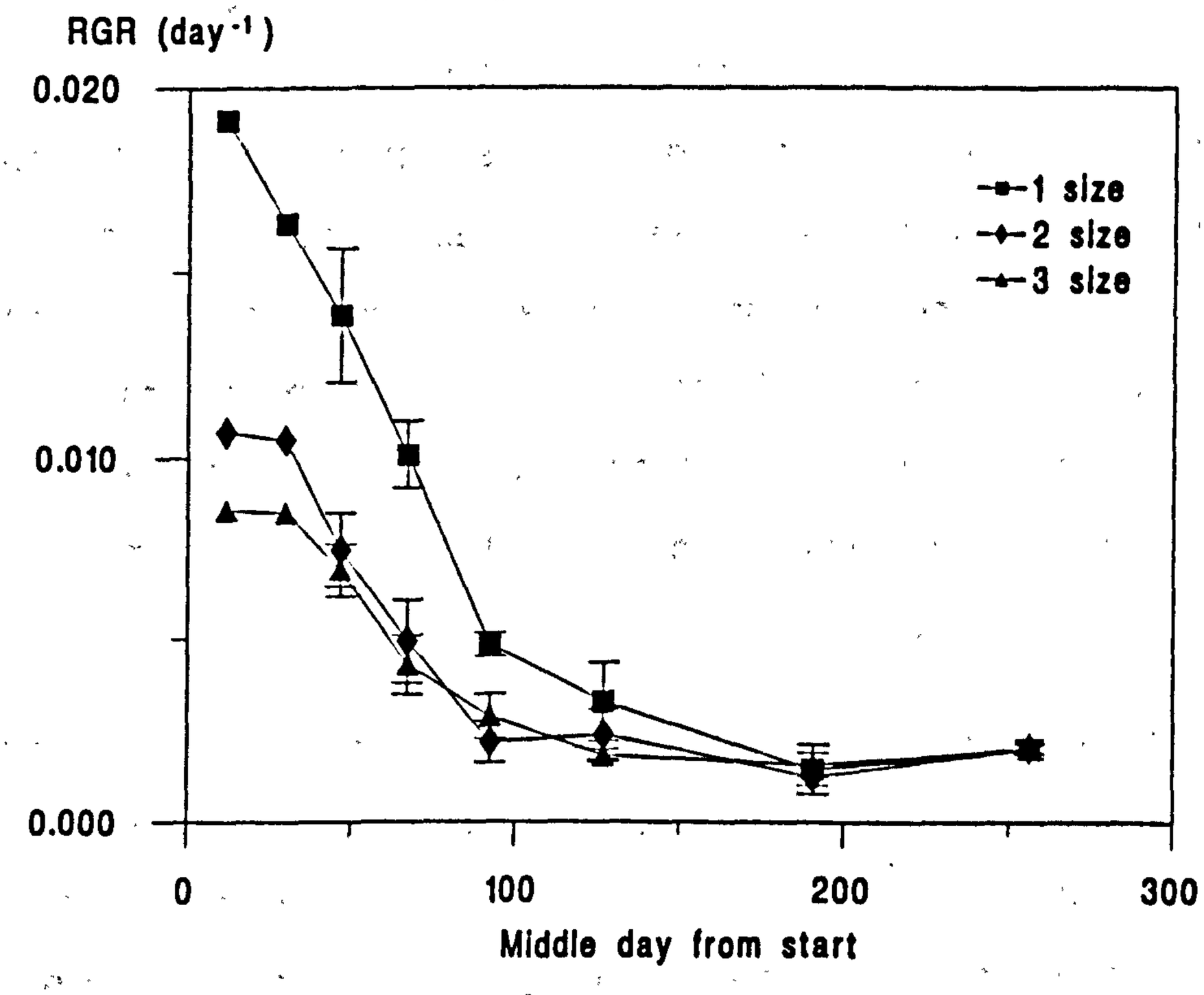
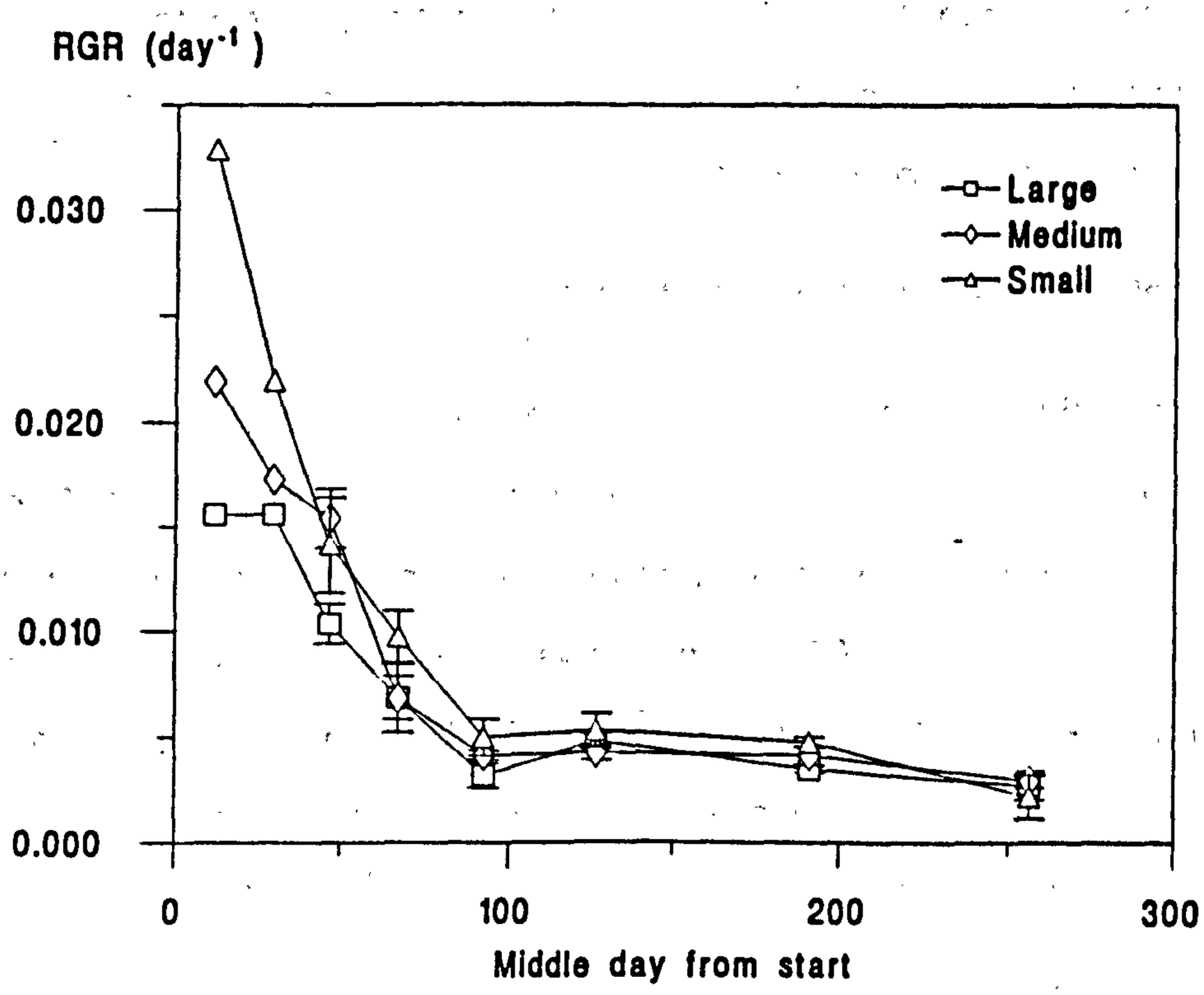


Figure 8.13 Relative growth rates of individually grown plants of *Laminaria digitata* over time (bars = ± 1.S.E.).



population types (Figure 8.14). The medium sized plants in the two-size population type had higher relative growth rates than the small sized plants, though relative growth rates became similar later on (Figure 8.14*b*). The relative growth rates of the small plants in the two-size population were lower than those for (small) plants in the single size population type, and similar to relative growth rates exhibited by the small and medium sized plants in the three-size population type (Figure 8.14). In the three-size population type large plants had the highest relative growth rates and the small and medium sized plants the lowest, though relative growth rates for small and medium sized plants were similar (Figure 8.14*c*).

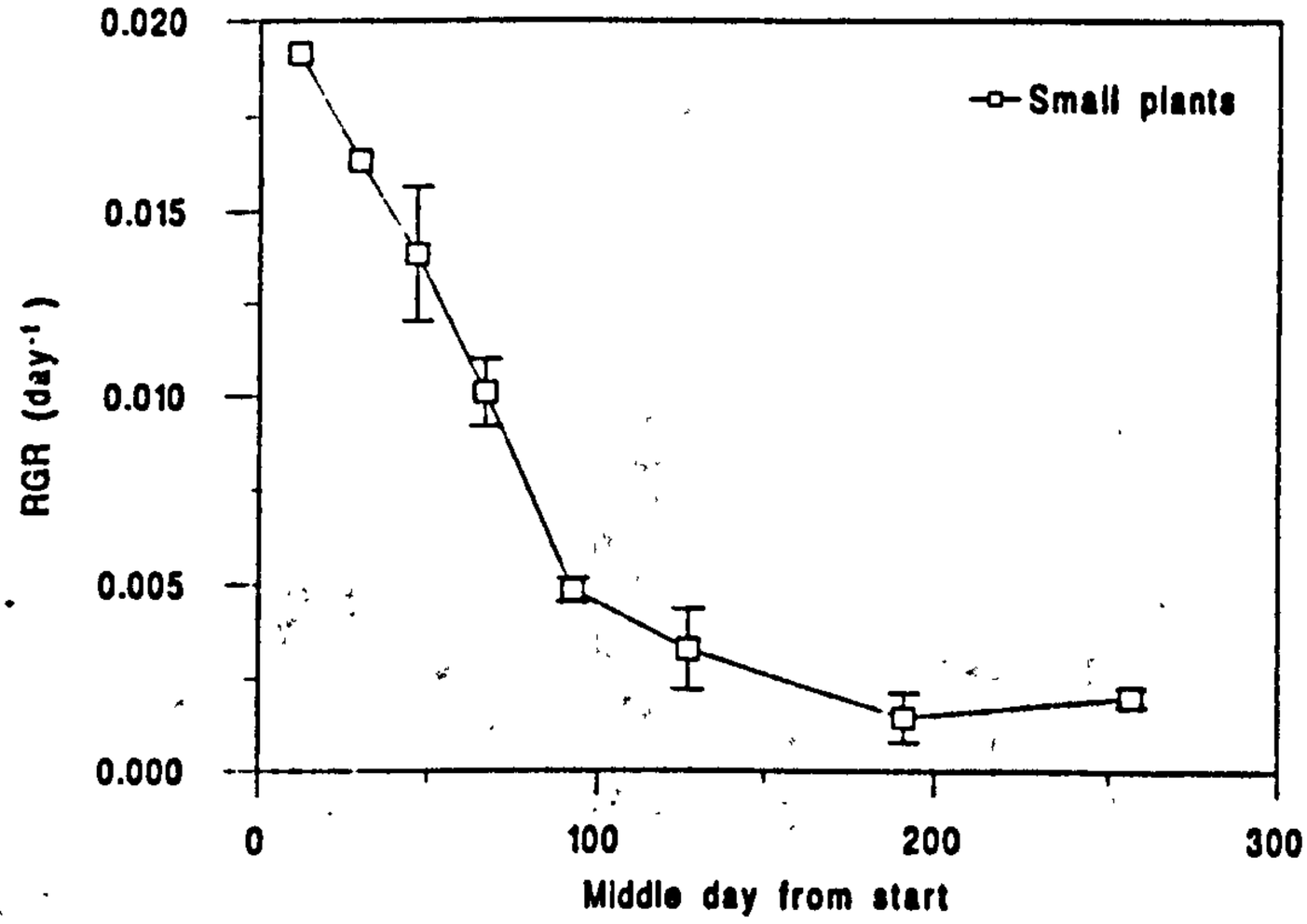
Over all times relative growth rate was inversely related to initial plant size in plants grown individually (Figure 8.15*a*) and to the population complexity (Figure 8.15*b*). Comparing the three population types, generally three levels of relative growth rate were found. The highest level of growth occurred in the one-size population type (Figure 8.15*c*). An intermediate level of growth occurred in the medium and large size plants of the two- and three-size population types respectively. A low level of growth occurred in the small plants of the two-size population type and the small and medium sized plants of the three-size population type (Figure 8.15*c*).

8.3.7 Relative growth rate and plant size

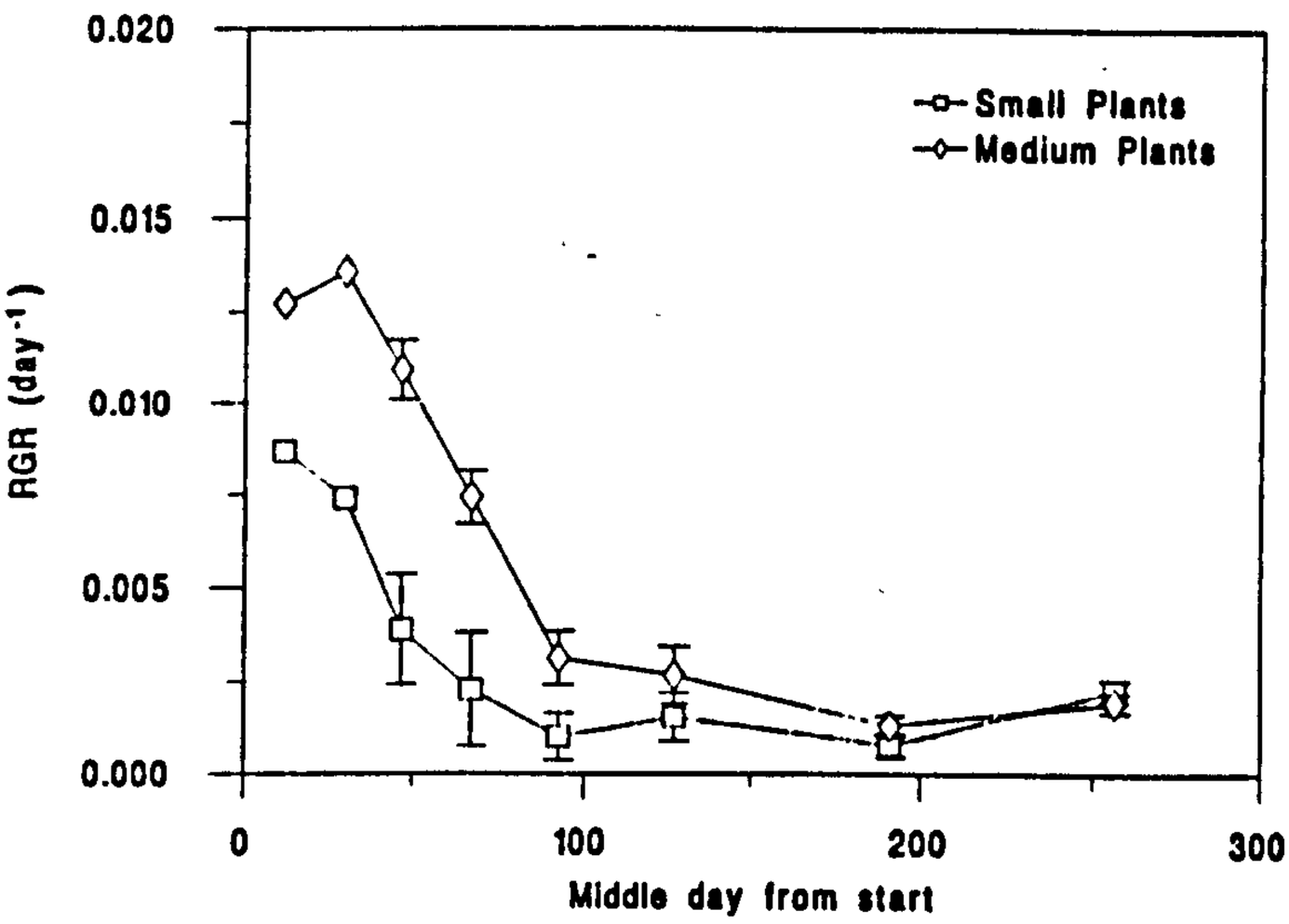
Understandably, there was no relationship between overall relative growth rate and initial plant size in the single size population (Pearson's $r = 0.116$, $n = 96$, $p = 0.5$), although there was a positive correlation for the two- (Pearson's $r = 0.476$, $n = 239$, $p = 0.001$), and three- (Pearson's $r = 0.478$, $n = 236$, $p = 0.001$) size population types (Figure 8.16). There was a negative relationship between initial plant size and relative growth rate for plants grown individually (Pearson's $r = -0.823$, $n = 18$, $p = 0.001$, Figure 8.16).

Figure 8.14 Mean relative growth rate of different sized parts of three population types of *Laminaria digitata* over time (bars = ± 1.S.E.).

a) One sized (all small) population



b) Two sized (small and medium) population



c) Three sized (small, medium and large) population

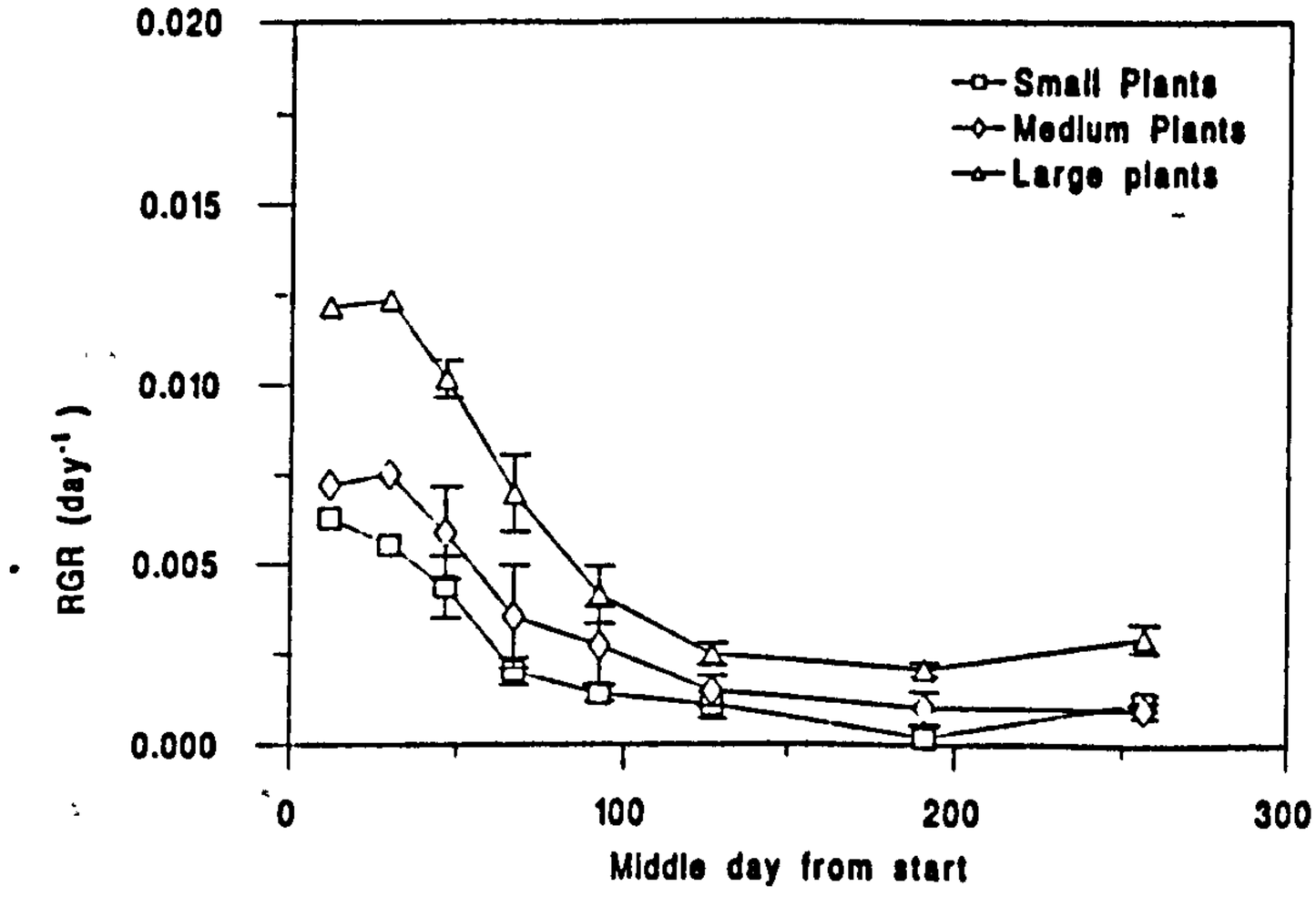


Figure 8.15 Mean relative growth rate of different sized parts of three population types and individually grown plants of *Laminaria digitata* over all times (bars = ± 1.S.E.).

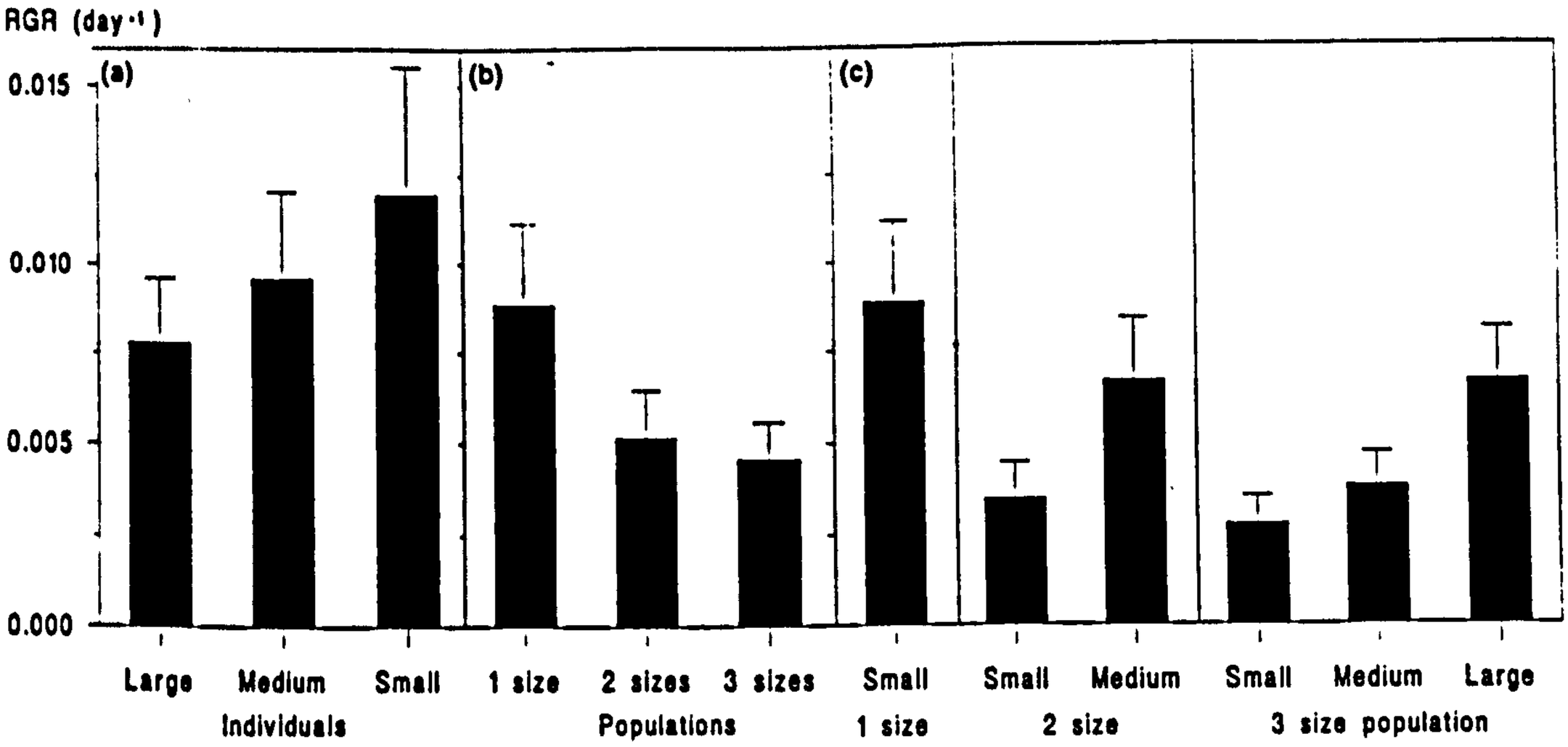
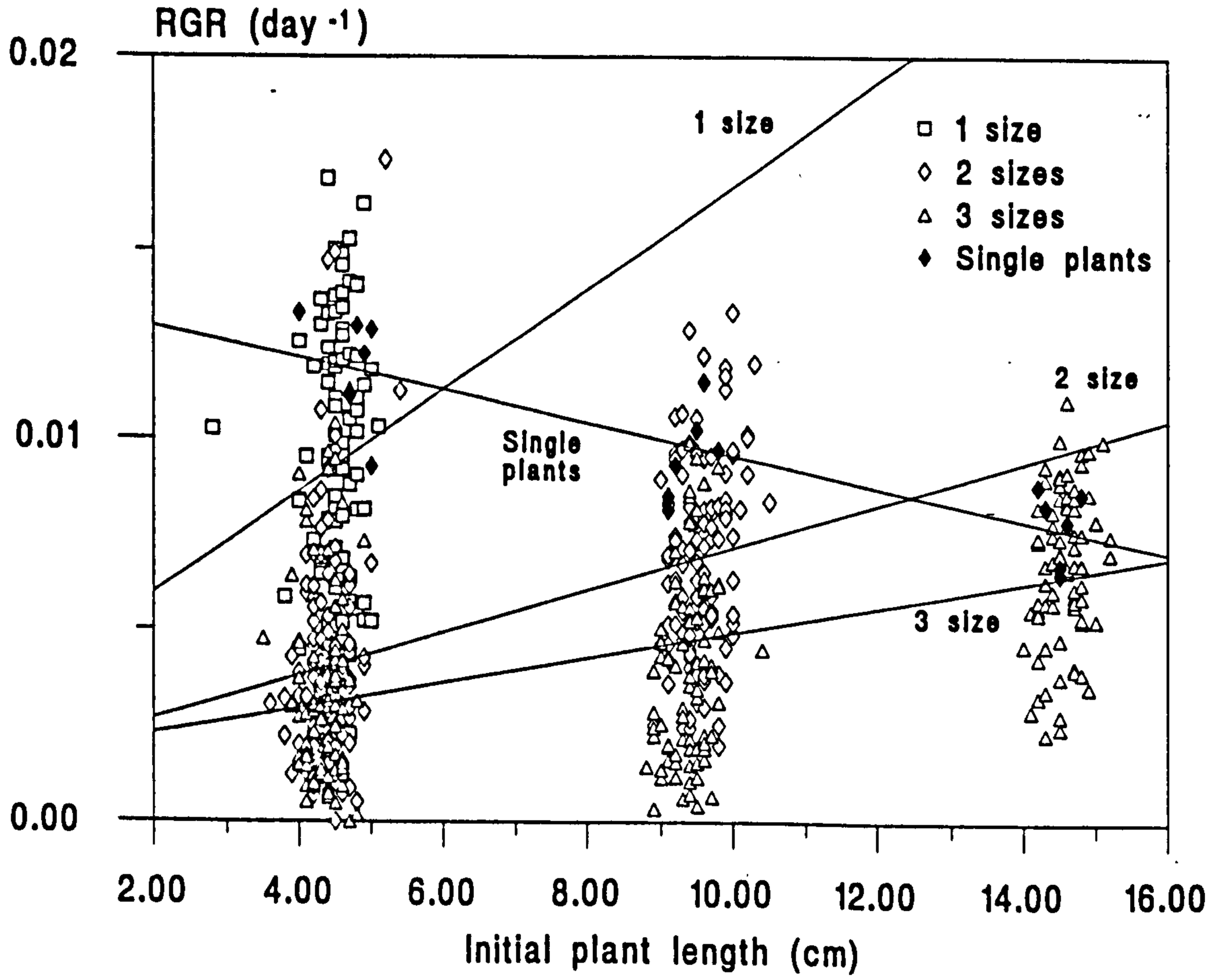


Figure 8.16 Relative growth rate and initial plant length relationship in *Laminaria digitata* grown with different population structures.



8.4 Discussion

8.4.1 The influence of initial population structure on relative growth rates

Relative growth rates were far higher in individually grown plants than in any of the populations. This was obviously due to intraspecific competition acting within the populations. Large individually grown plants had lower relative growth rates than small individually grown plants, which is an inherent attribute in *Laminaria digitata* as well as most other plants growing under optimum conditions. However, in the two- and three-size populations relative growth rates were lowest in the small size plants and highest in the largest plants. Under intraspecific competition the largest plants severely limit the relative growth rates of smaller plants. It is interesting to note that in the three-size population type, the relative growth rates of small and medium sized plants were similar, which would suggest that large plants had a far greater effect on small plants than medium sized plants did in this population type. However, medium sized plants (the largest) had an equally profound effect on relative growth rates of small plants in the two-size populations as large plants did on medium and small sized plants in the three-size populations. Assuming competition for light is limiting growth, this result may be partially explained by the fact that a linear increase in plant size is associated by a squared increase in plant area, and it is this area which cuts down light. Also, as we have seen from the individually grown plants, medium sized plants have inherently lower relative growth rates than small plants anyway.

8.4.2 Light limitation

Certain characteristics of the populations suggested that growth in these populations was light limited. A positively skewed size distribution developed in all the populations, and the differing relationships between initial length and relative growth rate in the populations and individual plants confirmed that dominance and suppression was occurring. This is usually the result of light limitation (Schmitt *et al.*, 1986; 1987). Furthermore, the rates of change of many

population parameters (*eg* relative growth rates, size variability, standing crop, maximum frond length) shifted at approximately day 100. Day 100 equates to July 1st 1992, just ten days after the longest day of the year.

8.4.3 Mortality

None of the singly grown plants died during the experiment, though in all the populations some plants died. Density dependent mortality was thus an important feature of these populations. Mortality was size dependent in the populations. For instance, in the three-size population type, by the end of the experiment only 18 % of the small plants remained, while 87 % of the large plants were still alive. However, mortality rates of small and medium sized plants in the three-sized population were not similar as relative growth rates had been in the same population type, but rather mortality was inversely proportional to the size group.

8.4.4 Biomass-density processes

While self-thinning progressed in accordance with the -0.5 self-thinning rule, no difference was detected between the one-, two- or three-sized populations with respect to self-thinning trajectories. The only differences were temporal, in that the one-sized populations had not travelled as far along the thinning line (to the left) as had the two- and three-sized populations by the end of the experiment. These results are totally in accordance with those of Westoby and Howell (1986) who found that population structure was not important in thinning in one- and two-size radish populations, and concluded that this made the rule all the more generally applicable.

8.4.5 The struggle for similarity

The creation of these variable sized populations could be considered analogous to multiple cohort populations which should theoretically often be found in nature. However, at least in the marine phycological literature, distinct cohorts or multimodal populations are not often reported despite a sound

theoretical basis for them (see General introduction). The reason for this may be partly explained by the fact that populations are dynamic assemblages of plants. When asymmetric competition for light takes place, dominance and suppression results in systematic variations in relative growth rate and mortality. The result of the interaction of relative growth rate and mortality is to standardise a population structure. By the end of this experiment the three populations could not be distinguished from one another statistically in terms of Gini coefficient, coefficient of variation or skewness. Though this experiment used simple mixtures of plant sizes, the mechanisms of size dependent relative growth rate and mortality may apply to any ranges and proportions of different sized plants. My results suggest that given enough time populations with different structures may converge to the positive skewness which seems to be the norm in seaweeds.

Chapter 9 The spatial dynamics of a seaweed population

9.1 Introduction

As self-thinning due to intraspecific competition occurs in an even-aged, monospecific plant stand, the spatial pattern of plants may be expected to come more regular over time (Antonovics and Levin, 1980). Indeed, a regular rather than random or clumped spatial pattern should be interpreted as strong evidence of intraspecific competition (Pielou, 1962; Greig-Smith, 1964). Kenkel (1988) reviewed studies of this kind.

Numerous statistical methods have been developed for the description of spatial pattern in biological systems (*eg* Diggle, 1983; Upton and Fingleton, 1985). Some spatial statistical analyses have been carried out on self-thinning plant populations (see Kenkel, 1988 for a review), and models have been developed to describe such processes (*eg* Leps and Kindlmann, 1987). No such studies have been carried out on seaweed populations.

Kenkel (1988) suggested that investigations of spatial change in self-thinning populations should use "a long-lived, non-clonal species that forms even-aged, pure stands, and whose seeds are randomly dispersed at high initial density over a relatively homogeneous substrate". *Himanthalia elongata*, at the 'button' stage, makes a suitable candidate, fulfilling all the above criteria except longevity, which after all is relative. Environmental homogeneity at centimetre scales may be far greater on a flatish rock on the shore than soil, as nutrients and water are not localised in the sea. *H. elongata* buttons can be photographically 'sampled', and are relatively simple and standard in form, which are useful attributes for the study of spatial dynamics.

The aims of this chapter are twofold. Firstly, I will investigate the spatial distribution of propagules very soon after settlement, by experimental settle-

ment on an artificial substratum. Secondly, I will describe the spatial changes that occur in well developed populations of *H. elongata* buttons on the shore.

9.2 Materials and Methods

9.2.1 Material and mapping

a) Settlement

Suspensions of *Himanthalia elongata* gametes were made using methods identical to those used for *Fucus vesiculosus* in Chapter 6. An epoxy plate of 15 x 15cm was manufactured using similar methods as for the settlement discs in Chapter 1 for *Fucus serratus*. Six settlement plates was placed in a plastic aquarium tank and covered with filtered sea-water to a depth of 30 cm. The gamete suspensions were mixed and dribbled onto the surface of the water as in Chapter 6. The tank and plates were left undisturbed for 24 hours before the plates was removed. Random areas (avoiding edges) were viewed under a stereo-microscope and the distribution of zygotes was mapped with the aid of a *camera lucida*. This could be done under low power with accuracy because *H. elongata* zygotes are very large (visible with the naked eye).

b) The development of natural populations

The same photographs were used as in Chapter 3 for the non-destructive sampling of *H. elongata* populations. However, an extra population not used in Chapter 3 because it contained an unfeasibly large number of plants was also used for the most detailed examination of spatial pattern using refined nearest neighbour analysis (see below). At the start of the study (27th April) a 10 x 10 cm area was randomly located within the population (avoiding the edges) and mapped using acetate sheets. There were 262 plants. A map was also made of the plants remaining on 23rd October, as well as a map of the plants which had died during the study. 77 plants remained and 185 had died.

Maps were digitised as individual points and saved as IBMPC ASCII text files as coordinates. All six settlement maps were analysed by the Clark-Evans method, while one was randomly chosen for refined nearest neighbour analysis (see below).

9.2.2 Statistical analysis

Two nearest neighbour methods were used to analyse the spatial patterns of the populations.

9.2.2.1 Modified Clark-Evans statistic

Clark and Evans (1954) nearest neighbour statistic has been modified by Donnelly (1978) to take account of edge effects, and this modification was used to describe the populations. The rationale of total nearest neighbour analysis is outlined in Donnelly (1978), and the calculated value (*CE*) is compared to the normal distribution, with randomness rejected in favour of clumping or regularity. The calculations necessary are:

$$T=\sum_{i=1}^{n} \min_{j\neq 1} d(u_i,u_j)$$ Equation 9.1

Where T is the sum of all nearest neighbour distances, and $d(u_i,u_j)$ is the distance between u_i and u_j, then $E(T)$ the expected T and var T the variance:

$$E(T) = \tfrac{1}{2}\sqrt{(nA)} + \left(0.05137+\frac{0.041}{\sqrt{n}}\right)L.$$ Equation 9.2

$$\mathrm{var}T = 0.0703\,A + 0.037\,L\sqrt{(A/n)}$$ Equation 9.3

where A is area of study and L is the perimeter

CE, the modified Clark-Evans statistic is calculated:

$$CE = \frac{T - E(T)}{\sqrt{(\mathrm{var}\ T)}}$$ Equation 9.4

and *CE* is compared to the normal distribution.

9.2.2.2 Refined nearest neighbour analysis

Refined nearest neighbour analysis was used in order to gain a more detailed insight into the spatial pattern at different scales. The method compares the expected cumulative distribution function to the observed one, and must take into account edge effects, as some plants near the boundary may have a theoretical nearest neighbour outside the boundary which is not considered (Upton and Fingleton, 1984 cover the methods). The expected cumulative distribution function for nearest neighbour distances is:

$$G(w) = 1 - \exp\left(-\rho\pi w^2\right) \qquad \text{Equation 9.5}$$

Where n individuals are randomly distributed in area A, $\rho = n/A$ and w is the nearest neighbour distance (Kenkel, 1988). $G(w)$ is compared with $G(\hat{w})$, the empirical cumulative distribution function corrected for edge effects (see Upton and Fingleton, 1985:80, but beware misprint top page 81: G(v) should be calculated from Equ.1.48). Comparison of empirical and expected is by $G(\hat{w}) - G(w)$, which are the x-axis values. Positive values of $G(\hat{w}) - G(w)$ signify clumping while negative values signify regularity, and $G(\hat{w}) - G(w)$ is usually plotted over a range of spatial scales. Significance of departures from randomness are evaluated using Monte Carlo simulation (Kenkel, 1988). Ninety nine random populations consisting of the same number of plants as the original data are generated, and distribution functions calculated for each one. Maximum and minimum values are taken as the confidence envelopes, outside which values differ significantly from the Poisson (or random) spatial distribution expectation.

9.2.2.3 Random mortality hypothesis

Kenkel (1988) suggested that the random mortality hypothesis (*ie* that mortality is a random event) be quantified by randomly selecting from the original

(starting) coordinate data set a subset with n = number of surviving plants at the end of the study. The cumulative distribution for this and $m = 98$ other randomisations are calculated, and used to define upper and lower random mortality confidence envelopes. The same proceedure is used for n = number of plants dying during the study (Kenkel, 1988).

9.3 Results

9.3.1 Settlement

a) Modified Clark-Evans statistic

Four of the six plates which had artificially settled propagules all exhibited a significantly clumped spatial pattern, while the other one exhibited a random one (Tables 9.1 and 9.2). The mean nearest neighbour distance was 0.35 mm.

b) Refined nearest neighbour analysis

The distribution of settled propagules was clumped (Figure 9.1*a*, Table 9.2) on a scale of between 0.25 and 0.6 mm. There is also some tendency towards regularity at distances between 1.2 and 1.7 mm, and at about 0.2mm (Figure 9.2).

9.3.2 Mature natural populations

a) Modified Clark-Evans statistic

At the start of photographic sampling all three populations were closely packed, and the distribution of plants in all the populations was highly regular (Table 9.2, 9.3). As time went on, the degree of regularity decreased in all the populations, though all were still highly regular at the end of monitoring (Table 9.3).

In order to see which population parameters were most likely to have influenced spatial pattern, the three populations not analysed by the refined nearest

Table 9.1 Modified Clark-Evans Statistics for settled propagues of *Himanthalia elongata*

Replicate	**CE statistic**	*p*	*n*	**Interpretation**
1	-4.69	< 0.001	133	Clumped
2	-1.96	0.05	152	Clumped
3	-1.51	0.136	165	Random
4	-2.21	< 0.05	144	Clumped
5	-5.15	< 0.001	117	Clumped

Figure 9.1 Distribution maps of randomly selected areas of (a) settled and (b) natural populations of *Himanthalia elongata* plants

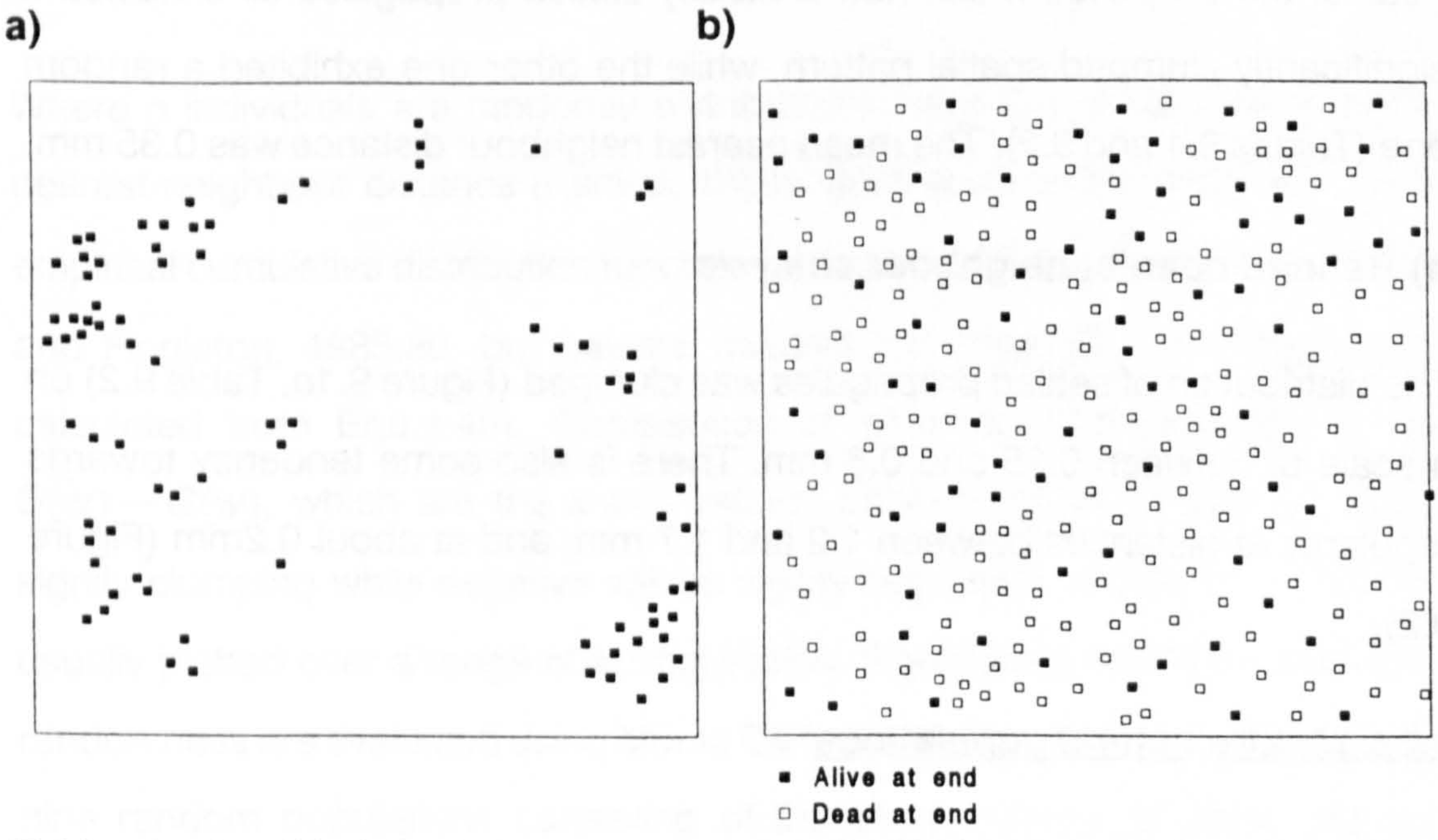
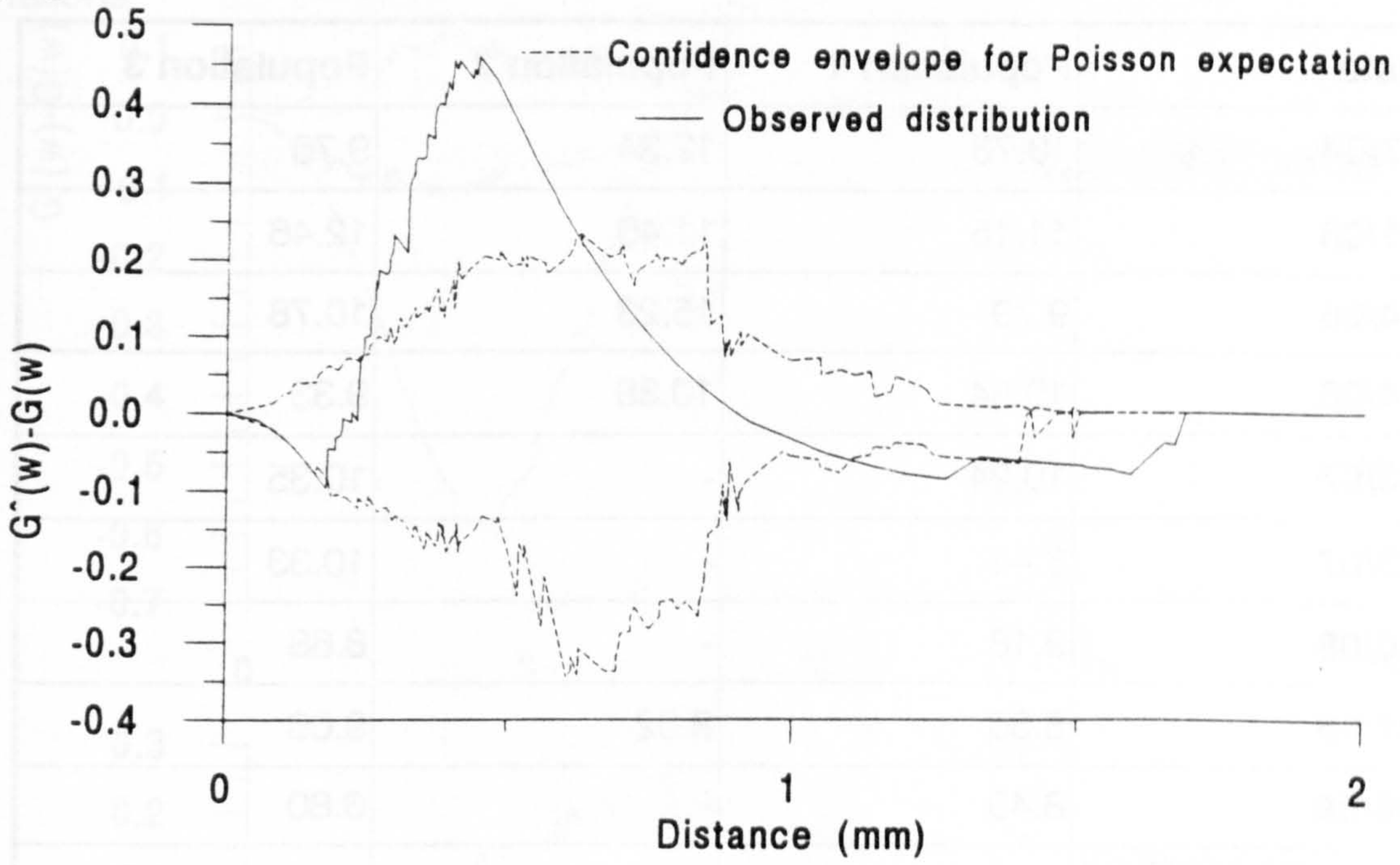


Table 9.2 Modified Clark-Evans statistics for settled and natural *Himanthalia elongata* populations also examined in more detail by refined nearest neighbour analysis

Population	*CE* **statistic**	*p*	*n*	**Interpretation**
Settled	-5.12	< 0.001	82	Clumped
Natural population				
Beginning	18.06	< 0.001	262	Regular
Alive at end	5.21	< 0.001	77	Regular
Dead at end	9.26	< 0.001	185	Regular

Figure 9.2 Cumulative distribution function of nearest neighbour distances $\{[\hat{G}(w) - G(w)]$ versus $w\}$ for recently settled *Himanthalia elongata* propagules



neighbour method (below), were considered in more detail. The population parameters mean button diameter, time, coefficient of variation, skewness, density, biomass and population number (*ie* difference between populations) were stepwise regressed on *CE* value and mean nearest neighbour distance. The two best predictors of the *CE* statistic were time and biomass (72 % and together 79 % respectively of the variation explained, $n = 30$, $p < 0.001$). Mean nearest neighbour distance for the pooled populations was best predicted by mean button diameter (88 % of variation explained), then biomass (together 95 %) and then time (all together 98 %, $n = 30$, $p < 0.001$).

b) Refined nearest neighbour analysis

The cumulative distribution function of plants at the start of monitoring indicated a highly regular pattern on a scale from 2 to 7 mm, with maximum regularity at 4-4.5 mm (Figure 9.3a). 150 days later, only 77 of the original 262 plants remained, so 71% of the plants had died (Table 9.2, Figure 9.1*b*).

The cumulative distribution of the remaining plants indicated a highly significant regularity in the range 2-7.5 mm for departure from the Poisson envelope

Table 9.3 Change in modified Clark-Evans statistics for three natural populations of *Himanthalia elongata* over time

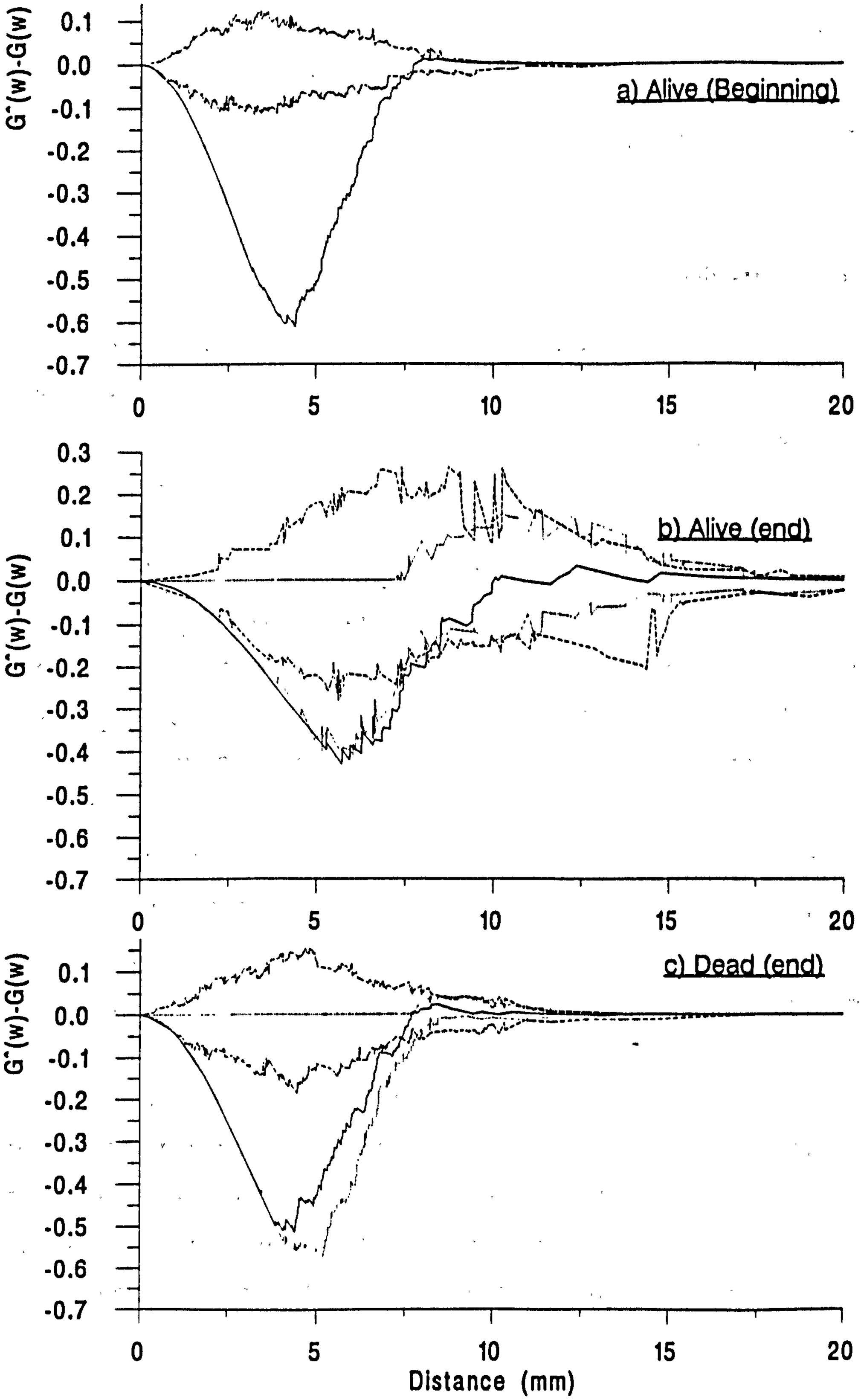
Date	Population 1	Population 2	Population 3
27/04	10.73	12.34	9.70
11/05	11.15	11.40	12.46
14/06	9.79	15.23	10.78
24/06	10.84	10.38	9.33
13/07	10.24	-	10.35
23/07	8.44	-	10.33
10/08	9.18	-	8.68
21/08	8.36	8.02	9.06
06/09	8.49	-	6.80
23/09	7.99	-	6.89
20/10	7.64	-	6.64
01/11	7.37	7.00	5.35

$p < 0.001$ for all populations at all times, indicating that all had a significantly regular spatial pattern.

(Figure 9.3*b*). Rather less clear is the relationship between the random mortality envelope and observed distribution, which follows the minimum boundary, sometimes inside and sometimes outside from 0 to 8 mm. The most safe interpretation of this relationship is that the distribution of live plants at the end of the study did not depart from that predicted by random mortality. The minimum boundary of the random mortality confidence envelope and the observed distribution had very similar shapes (Figure 9.3*b*). The deviation from the Poisson expectation in the plants alive at the end of the study was not as great as the deviation at the beginning (Figures 9.3*a* and *b*).

The distribution of plants dead by the end of the study was also highly regular compared to the confidence envelope for the Poisson expectation (Figure

Figure 9.3 Cumulative distribution function of nearest neighbour distances $\{[\hat{G}(w) - G(w)]$ versus $w\}$ for naturally occuring *Himanthalia elongata* populations



9.3c). The random mortality model did not indicate any departure from random mortality in the dead plants. The scale over which the observed distribution of dead plants exhibited a regular spatial pattern was almost identical to the observed distribution of plants exhibiting a regular spatial pattern at the beginning of monitoring (Figures 9.3a and c).

9.4 Discussion

While numerous studies of patch dynamics and community structure have been undertaken to examine spatial pattern at large scales (*eg* see reviews by Schiel and Foster, 1986; Santelices, 1990a), few studies have considered the within-stand, spatial distribution of marine macroalgae.

Dayton (1973) reported clumping within stands of *Postelsia palmaeformis* at centimetre scales, as did Rice (1987) for *Xiphophora gladiata*. Gunnill (1980a) reported clumping at similar scales in *Pelvetia fastigiata*, as did Panayotidis *et al*. (1981) for the seagrass *Posidonia oceanica*. Generally, authors have employed nearest neighbour or inter-plant distances as estimates of density (Drew, 1974), as analogous to density (Chapman and Goudey, 1982) or as a factor affecting the physical or biological attributes of plants (Santelices and Ojeda, 1984*b* and *c*; Santelices, 1990a) rather than as measures of spatial pattern. However, Dean *et al*. (1989) used the Clark-Evans index to investigate spatial pattern in recruiting stands of *Macrocystis pyrifera*. They concluded that while stands were spatially uniform, recruitment was clumped and differential mortality in clumps of recruits restored the random spatial distribution. Panayotidis *et al*. (1981) and Rice (1987) used quadrat count methods rather than points to describe their clumped populations with an index of dispersion. Far more attention has been given to the spatial pattern of sessile animals (*eg* Knight-Jones and Moyse, 1961; Underwood, 1976) than marine plants.

Post settlement clumping was found in my study of artificially settled *Himanthalia elongata* propagules despite every effort to make the substratum and propagule supply homogeneous. In nature, high spatial heterogeneity, especially at the scale of propagules, is the norm (Amsler *et al.*, 1992). Recently settled propagules should not be regularly spaced in such a context (Fowler, 1986; Kenkel, 1988). It is probable that propagules of seaweeds are highly clumped in nature. Certainly this seems to be the case with *Fucus serratus* propagules which have naturally settled onto artificial substrata (personal observation). However, larger naturally grown *H. elongata* plants were found to be highly regularly spaced in this study. Regular spacing is evidence of intraspecific competition in monospecific stands (Kenkel, 1988). It seems likely that self-thinning was well under way at the start of this study of mature plants, as the stand was already highly regular. The *H. elongata* population studied here conformed to the random mortality hypothesis, though the plants dying during the course of self-thinning were also highly regular in distribution, unlike the clumping found by Kenkel (1988) in jack pine, and infered from Dean *et al.*'s (1989) study of *M. pyrifera*. The high regularity of dead plants in my study simply reflected the regularity already present. However, the decrease in the spatial regularity of surviving plants was somewhat puzzling, as Kenkel (1988) found an increase in regularity over time. Possibly, if a population is highly ordered and mortality is imposed on a random basis, the only potential outcome may be a decrease in spatial ordering.

In summary, it appears that intraspecific competition is responsible for high spatial regularity in *H. elongata* buttons in packed populations.

General discussion

Seaweeds have received less attention than their terrestrial counterparts with respect to studies of single species population dynamics (Chapman, 1986*b*). Population studies have traditionally been carried out on large subtidal kelps (*eg* Santelices, 1990*a*). Often 'population' studies have been more concerned with yield or standing crop than plant interactions (*eg* Gunnill, 1980*b*). However, the ecology of intertidal canopy forming brown algae is relatively well known (*eg* Schonbeck and Norton, 1978, 1980*a* and *b*). Unfortunately the population dynamics of such species have not generally been addressed in detail in the past. Recently though, matrix modelling has been used to describe the population dynamics of *Ascophyllum nodosum* and *Fucus distichus* with considerable success, and the blank spaces are gradually being filled (Aberg, 1990*a-d*; Ang, 1991; Ang and De Wreede, 1992). Furthermore the role of density in seaweed populations is being addressed (Reed, 1990*a* and *b*; Reed *et al.*; 1991; Ang and De Wreede, 1992). In many ways monospecific seaweed stands are governed by processes similar to those influencing stands of terrestrial plants.

The assumption of an initial normal distribution of propagule sizes seems to hold true for *Fucus serratus* (Chapter 3). This is an important starting point as the distribution of sizes has been shown to have a profound effect on the subsequent growth of constituent plants if intraspecific competition is taking place (Ross and Harper, 1972; Weiner and Thomas, 1986). Both dominance and suppression (Schmitt *et al.*, 1986, 1987) and inherent variance in exponential growth rates (Hutchings and Budd, 1981*b*; Turner and Rabinowitz, 1983) between plants in the absence of competition may be responsible increased size variability after propagule settlement. For this reason, a positively skewed or highly variable population should not be interpreted as evidence of intraspecific competition.

On the shore successive waves of propagules may settle and recruit into an area. This will depend partly on 'supply side' heterogeneity. Settlement and

recruitment events have been well studied in seaweeds (see reviews of Hoffman, 1987; Santelices, 1990*b*; Amsler *et al*., 1992; Fletcher and Callow, 1992; Norton, 1992*a*; Vadas *et al*, 1992). The consequence of multiple recruitment events in the absence of other factors is a multimodal population structure. If large number of propagules join a population then size variability may increase and a positive skewness become more evident. While multimodal population structures are likely, there is little evidence for their existence in the marine literature. Most population studies of marine macroalgae have been carried out on visible plants. There is evidence from my work (Chapter 8) to suggest that under intraspecific competition initially multimodal population structures are lost through dominance and suppression and size selective mortality of small plants. The suggestion is that any multimodal populations of germlings become unimodal by the time they become visible. Having said this, my studies revealed no multimodal population structure in microscopic *Fucus serratus* populations at any time.

There is some evidence both for and against intraspecific competition between microscopic plants in seaweed populations, and even negative competition has been found (see General Introduction). In my laboratory culture studies intraspecific competition took place in both *Fucus serratus* and *Fucus vesiculosus*. Nutrient competition was implicated as limiting growth. However, in the wild, water movement has a substantial affect on nutrient supply, and it is probable that light rather than nutrient supply more often limits growth. Certainly in my populations of larger plants competition for light was implied.

'Seed' banks were found in natural populations of *Fucus vesiculosus*. Ang (1991) and Ang and De Wreede (1992) presented substantial evidence of seed banks in *Fucus distichus* and my findings support the current view that 'seed' banks may be important in certain species of marine algae (Hoffman and Santelices, 1991). Whether a species exhibits a seed bank is dependent partly on the ability of propagules to survive. I found no evidence of a seed bank in populations of *Himanthalia elongata*. It seems that larger plants so effectively

cut out light in this species that underlings cannot survive. *Himanthalia elongata* also showed an essentially normal distribution, and a decrease in plant size variability over time, which is further evidence of strong size dependent mortality selecting small plants. Seed banks may be important sources of genetic novelty in plants, or may reduce variations in population size by buffering plant losses (Levin, 1990).

My work corroborates the suggestion that dominance and suppression occurs in seaweed stands undergoing intraspecific competition (Dean *et al.*, 1989; Reed, 1990*a*), just as the majority of studies of land plants have demonstrated. While the consequence of dominance and suppression is increased plant size variability, size specific mortality may mask such an effect. In fact, some authors have found plant size variability to be maximal at the onset of self-thinning (eg Mohler *et al.*, 1978), or to decrease during self-thinning (Kohyama and Fujita, 1981; Weiner and Thomas, 1986). Most seaweed populations probably exhibit Deevey (1947) Type III survivorship curves, and while other types have been reported, they are probably false because observations have been carried out over too short a time. Type III survivorship indicates extensive early mortality.

Ultimately the result of growth and mortality is the self-thinning trajectory. I found that many of my stands of both naturally occurring and artificially created algal populations presented thinning trajectories not significantly different from those predicted by 'the' self-thinning rule. I feel that density-biomass relationship data are most useful as a part of a suite of methods which, when presented in conjunction, can allow the ecologist to describe competitive processes in plant monocultures (*eg* West *et al.*, 1989*a*).

Self-thinning may be dependent on plant form. I found two discrete slopes with similar gradients and different *y* intercepts for 'button' and 'thong' stage populations of *Himanthalia elongata*. The button to thong transition represents a substantial change of form in this species. Self-thinning intercepts have been related to plant geometry (Weller, 1987*b*, 1989).

Other evidence of intraspecific competition has come from investigations of the spatial dynamics of *Himanthalia elongata*. Highly regular patterns were found, indicative of strong competition, though mortality was random.

While numerous examples of the effects of intraspecific competition on both artificial and natural seaweeds have been presented here, the factors which limit growth are the least well understood. I feel that competition for light is most important on the shore and subtidally. Only future experiments in which light and nutrients, the two most likely candidates, are manipulated in the field will indicate which factor limits seaweed growth in the wild. Future experiments should use an approach which unifies measurements of populations in terms of their temporal and spatial dynamics, and takes advantage of the models recently developed by terrestrial plant ecologists (*eg* Bonan, 1988).

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Appendix 1

To make F/2 seawater media

Guillards enrichment
1.5ml H_2O
2.5g $NaH_2PO_4H_2O$
37.5g $NaNO_3$
2.5g Fe Sequestrene

0.5ml of each of the following trace metal solutions
$CuSO_45H_2O$ 0.98g/100ml
$ZnSO_47H_2O$ 2.2g/100ml
$CoCl_26H_2O$ 1.0g/100ml
$MnCl_24H_2O$ 18.0g/100ml
$NaMoO_42H_2O$ 0.63g/100ml

2.5ml Biotin 0.1mg/ml
0.25ml $VitB_{12}$ 1.0mg/ml
50mg Thiamine

Make up to 1750ml and store frozen in 250ml aliquots

Stand for 24 hours at room temperature prior to use

USE 3.5 ml/l OF THE ABOVE ENRICHMENT TO MAKE F/2 MEDIUM