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Recruitment and Growth of Juvenile *Crassostrea virginica* (Gmelin) in Relation to Tidal Zonation

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RECRUITMENT AND GROWTH OF JUVENILE CRASSOSTREA VIRGINICA (GMELIN)

IN RELATION TO TIDAL ZONATION

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

by

G. Curtis Roegner

1989

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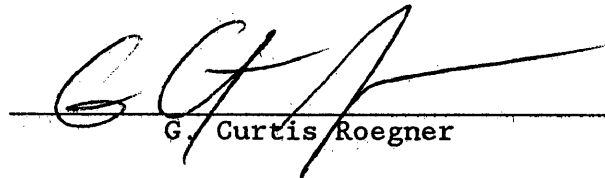
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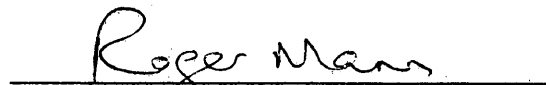
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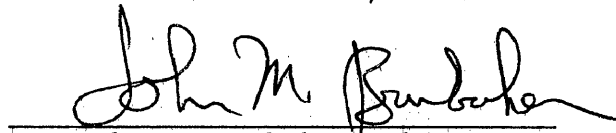
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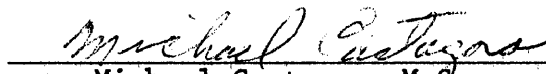
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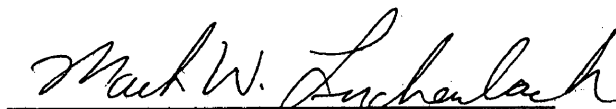
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To my parents,
for their forbearance.

"I weep for you," the Walrus said:
"I deeply sympathize."
With sobs and tears he sorted out
Those of the largest size,
Holding his pocket-handkerchief
Before his streaming eyes.

"O Oysters," said the Carpenter,
"You've had a pleasant run!
Shall we be trotting home again?"
But answer came there none-
And this was scarcely odd, because
They'd eaten every one.

-Lewis Carroll

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ABSTRACT

Pier pilings at the Virginia Institute of Marine Science, in the York River, Virginia, support a band of intertidal oysters centered around the mid-tide level. Oysters are scarce below this band. Experiments utilizing hatchery-reared oyster larvae were conducted to determine if recruitment into this zone occurred as a function of larval settlement patterns or as a result of early post-settlement mortality. Settlement and survival were measured in separate experiments. Settlement was investigated by interning larvae in PVC tubes lined with Mylar sheets. The tubes spanned the intertidal zone and the number of larvae which settled on the Mylar was evaluated as a function of tidal height. The second set of experiments measured the survival and growth of known numbers of newly settled oysters placed at various tidal heights. Ceramic plates were used as a settling substrate. Sampling was accomplished by photographing the plates at weekly intervals, thus generating a time-series of photographs for each plate. The photographic series were then processed on an image analyzer to determine proportional survival and individual sizes. Three intertidal and three subtidal levels were tested, and experiments were conducted in June, July, and September to investigate seasonal effects.

The results of the settlement experiments clearly indicate the preference for larvae to settle subtidally. Intertidal settlement was slight. The survival experiments suggest the importance of biotic and abiotic factors in determining distribution and abundances. All plates exhibited a high initial mortality during the first week of post-settlement life. This mortality was probably due primarily to metamorphic stress and was a function of larval condition; external factors were of secondary importance. The severity of the initial mortality event characterized the subsequent survival patterns. There was a clear difference in survival between the intertidal and subtidal treatments. Physical factors dominated recruitment in the intertidal zone. No survival occurred at the mid or high intertidal sites, and survival was also curtailed at the low intertidal site until aerial temperatures were moderated. In contrast, survival at the subtidal fringe and subtidal treatments tended to be more influenced by biological interactions. The mortality rates decreased greatly after the initial mortality event, but predation or disruption tended to slowly eliminate survivors. Competitive interactions were also more intense subtidally; however, the true effects of the biological factors on oyster survival are underestimated in this study due to interference caused by sampling. The growth of spat was variable, but tended to increase with age. Intertidal exposure greater than 10% significantly decreased growth rates over treatments lower on the shore: no growth reduction at the MLW level could be correlated with exposure. Overall, the best survival and growth occurred at the MLW level.

The zonation of oysters on the pier pilings thus appears to be a result of predatory exclusion from the preferred habitat. Oysters both settle in higher numbers and grow faster at subtidal sites, but they

apparently do not persist there because of predation. Recruitment into the intertidal refuge habitat is dependant on environmental conditions, especially air temperature. It is thus likely that only a limited seasonal window for successful recruitment exists at this site.

EARLY RECRUITMENT AND GROWTH OF OYSTERS

INTRODUCTION

Interest in the factors which determine the distribution and abundance of organisms has recently focused on the interplay between the settlement of pelagic larvae at a site and the processes which subsequently affect the survival of the settled organisms (Grosberg, 1982; Keough and Downes, 1982; Luckenbach, 1984; Gaines et al., 1985; Connell, 1985; Butman, 1987; Roughgarden et al., 1988; Fairweather, 1988; Osman et al., 1989). The early events of recruitment, which comprises both settlement and early post-settlement survival, is important because this period strongly influences later population parameters (Luckenbach, 1984). These recruitment processes affect the zonation of organisms found on hard substrates.

Defining settlement, metamorphosis, survival, and recruitment is necessary in order to avoid ambiguities found in the literature. Most sedentary organisms disperse reproductive propagules via a planktonic stage. The term settlement is used to describe the irreversible adherence of the planktonic larvae to the substratum, and is characterized by a permanent loss of pelagic motility. Successfully settled individuals are termed "recruits". In sedentary invertebrates, metamorphosis usually follows settlement. This is an energetically strenuous process in which the organism reorganizes its structure and physiology from the larval form to that of the juvenile, and is often associated with a high mortality rate. Post-metamorphic individuals

then commence a period of growth, and the new recruits develop from juveniles into reproducing adults. Survival of recruits during this period is influenced by a variety of biological and physical factors, and is best determined by frequent enumeration; therefore, measurements of survival are time-dependent. Recruitment is a term used to describe the establishment of individuals into the population, and encompasses both settlement and post-settlement survival. Thus, settlement refers to the arrival of propagules to a site, while post-settlement survival is a measure of the success of individuals at that site. Metamorphosis is an alteration from larval to juvenile physiology. Recruitment is a process of population dynamics.

The distribution of sedentary invertebrates along a vertical, intertidal-subtidal transect must necessarily be some function of larval settlement, with the primary factor responsible for the magnitude of settlement being the availability of larvae (Gaines et al., 1985; Roughgarden et al., 1988). Grosberg (1982) has delineated four recruitment patterns which can lead to a vertical zonation of recruits. First, larvae can settle indiscriminately within the habitat but only survive in particular areas. Second, the larvae may be cued to settle in a particular zone by recognizable environmental stimuli. Third, juveniles or adults may migrate to the adult habitat (i.e. Mytilus). Finally, zonation may reflect the nonrandom distribution of larval propagules in the water column (Grosberg, 1982). It appears that all of these patterns operate to a varied extent with different species. Post-settlement survival is then determined by the interplay of physical and biological factors which act to modify the settlement distribution. The susceptibility of an organism to these stresses is often greatest during

the early stages of recruitment: size is often a refuge from both predation and competition as well as environmental fluctuations (Paine, 1976). The distribution and abundance of individuals in a population can thus be largely determined during this period of early recruitment.

This study was performed in order to examine the roles of settlement and early post-settlement survival in defining the intertidal zonation pattern of the American oyster, Crassostrea virginica (Gmelin) in the York River, Virginia. The American oyster is known to exist intertidally over much of its southern range (Galtsoff, 1964), where it can form extensive intertidal reef systems (Galtsoff and Luce, 1930; Bahr, 1974; Bahr and Lanier, 1981). These reefs are most pronounced as components of the relatively high salinity lagoon-type estuaries associated with barrier beach systems, and are distributed from the Eastern Shore of Maryland south through the Gulf coast (Bahr and Lanier, 1981). Oysters are also known to form an intertidal component of the epifaunal communities of wharves and pilings in various areas (McDougall, 1943; Ortega, 1981; Bushek, 1988; Pers. obs.) as well as in Spartina marshes (Pers. obs.). This study was prompted by the observation of the mid-littoral zonation of oysters on the pier pilings at the Virginia Institute of Marine Science, in Gloucester Point, Virginia, USA.

Despite the regional prevalence of intertidal reefs, few researchers seem to have investigated the early recruitment and growth of intertidal oysters. Intertidal settlement has been studied by Galtsoff and Luce (1930), Mackin (1946), Chestnut and Fahy (1952), McNulty, (1953), Hidu (1968), and Hidu and Haskin (1971). These studies generally focused on natural settlement patterns (but see Lutz et al., 1970) and often sampled over time scales which did not distinguish

between settlement and post-settlement survival (Andrews, 1954; Hopkins, 1954; Keough and Downes, 1982). Determinations of the growth and survival of juvenile Crassostrea virginica in the field, especially those of new recruits, are lacking. This is surprising given that juvenile oysters suffer high, often size (age)-dependent mortality rates (Andrews, 1954; Mackin, 1959; MacKenzie, 1970, 1981) and because historical evidence indicates that intertidal reefs within both the main-stem Chesapeake Bay and its subestuarine river systems were once both extensive and productive (Moore, 1909; Marshall, 1953; DeAlteris, 1986; Haven et al., 1987). With the massive decline of oyster populations which has occurred over the last 100 years, and the concurrent interest in mariculture as a means of compensation, the determination of factors which influence settlement of larvae or reduce mortality and/or stimulate growth of juvenile oysters is of obvious interest.

Empirical evidence of Crassostrea virginica populations in the lower York River suggests that the observed distribution is indeed being controlled by some selective process(es): these oysters are found on pilings in a distinct band in the mid-littoral extending from about +25 to +60 cm relative to mean low water (MLW), and apparently are not well represented lower in the littoral or subtidally. The fact that intertidal populations do exist in Virginia environments (i.e. Seaside, Guinea Marshes, the VIMS Ferry Pier pilings) thus raises the questions of the establishment and perpetuation of oysters in these zones. The experiments reported here investigate the intertidal settlement patterns of larvae and the factors affecting the survival and growth of juveniles. The investigation was designed to address three objectives. The first objective is to determine the settlement distribution of

larval oysters under natural tidal fluctuations. The second objective is to measure recruitment and growth of known numbers of spat in relation to tidal zonation. Finally, the third objective is to evaluate these early recruitment patterns to the intertidal position of the field populations of oysters. Together these experiments illuminate some factors which influence the propagation of intertidal oyster populations in Chesapeake Bay.

Background

The intertidal zone is the portion of the shore which experiences periodic exposure to air due to tidal oscillations. The biota of the intertidal zone of hard substrates has been relatively well studied, primarily because of accessibility but also due to the interest generated by the distinct biotic zonations found on many shores. It is now known that the intertidal zone sustains a diverse and abundant biota world wide, yet the community structures found in widely separated areas and varied environmental conditions are often strikingly similar. This is because the organisms populating analogous biotic zones in differing communities have often evolved similar physiological, behavioral, and/or structural adaptations to aerial exposure (Newell, 1979). The initiation and persistence of the biotic zonations on hard substrates, especially those comprised of algae or non-motile invertebrates, has been investigated for over 100 years. Experiments conducted in the intertidal zone by many authors have proven useful for testing theories concerning ecology and population biology.

The intertidal zone has been variously defined and partitioned, primarily from studies of rocky coasts (see reviews by Stephanson and Stephanson, 1949; Southward, 1957; Lewis, 1961; Newell, 1979). The intertidal classification system of Lewis (1961), although designed for

rocky coasts in Great Britain (as opposed to estuarine environments), will be adopted here. This system developed from that of Stephanson and Stephanson (1949), who proposed an overall classification system for rocky intertidal areas after the major similarities of biotic zones between sites were realized. Prior to this, most research on intertidal zonation was local in nature, and zonal divisions were either named for the prominent local organism or community comprising each zone or by tidal measurements. Due to the great variety of zonal patterns and diversity of organisms even within a small geographic range, it was difficult to correlate zones between sites. The Stephansons' system, utilizing data from diverse locales, was based mostly on biological marker species and partially on average tidal levels, and was of great advantage because between-site comparisons could be made. This classification was modified by Lewis (1961) to exclude tidal references because it was recognized that local conditions could greatly modify the effect of tidal fluctuations. More importantly, it was seen that the biota of an area react closely to the prevalent physio-chemical gradient and are thus the best indicator of the gradient. Lewis (1961) also altered the allegiance of several groups of organisms, giving them a more marine affiliation. Recently, however, studies focusing on the physiological adaptations of intertidal organisms to aerial exposure have concentrated on computing zones as a function of percent exposure (McMahon, 1988). Such divisions are only appropriate when accurate exposures can be determined.

The intertidal classification system of Lewis (1961) is as follows. The intertidal zone, or littoral zone, is bounded shorewards by the maritime zone and seawards by the sublittoral, or subtidal zone. The maritime zone is terrestrial in affiliation and does not fall under the

guise of marine biology. The littoral zone is divided into two main sections, the upper, transitional littoral fringe, indicated by the presence of littorinid molluscs, Verucalria algae, ligiod isopods, and Myxophacea, and the main eulittoral zone which is indicated by barnacles and furoid algae. The division between the maritime zone and the littoral fringe is often imprecise, while the separation of the littoral fringe from the eulittoral zone is generally clearly marked by the conspicuous end of the barnacle zone with increasing shore height. The lower edge of the eulittoral zone is usually clearly marked by the presence of laminarid algae, which is the indicator species of the sublittoral fringe of the sublittoral zone. Within each of these major divisions, local subzones of organisms are recognized (Lewis, 1961).

The maritime, eulittoral, and subtidal zones describe a physical reality regardless of the presence or absence of any particular type organisms. The species compositions are functions of more complex factors discussed below. The type organisms are used to describe the universally recognized physio-chemical zones typical of a wide range of environments. The actual organism present in a locale may not even fulfill a similar ecological role as the type organism. The distinguishing factor concerns similar tolerances to various pressures affecting survival. For example, laminarids, the type species of the sublittoral fringe, are cold-temperate in distribution, and are replaced by ascidian-sponge communities in warm-temperate and tropical environments. All of these organisms are restricted to short periods of exposure. Similarly, the barnacle-furoid zone of protected northern eulittoral zones may lack the furoid component in warmer climes. Generic or physiologically analogous species do not exist at all locales. Conversely, some genera, such as the littorinids, appear

common to nearly all investigated areas, and fulfill a similar ecological role as well.

The causes of intertidal zonation have been widely debated. Within the limits set by the supply of larval recruits, it is now generally agreed that the upper boundary of intertidal organisms on a shore is primarily controlled by physical parameters while the lower level is mainly determined by biological factors (Connell, 1972). The structure and composition of intertidal communities are products of very complex interactions between these physical and biological processes, however, and will vary spatially and temporally in accordance to changes in the pressures affecting them. Community reactions to experimental manipulations of the prevailing environmental conditions or biological interactions of rocky intertidal zones has been relatively well studied (less so for other intertidal substrates).

The littoral zone has long been recognized as a region where marine organisms are subjected to widely varying physical stresses associated with aerial exposure. These stresses include thermal shock, desiccation, solar irradiation, decreased feeding times, reduced opportunity for respiration, and mechanical disruption (wave shock and impact damage from floating objects) (Newell, 1979). The amplitude of the tide is believed to be the primary force determining the upper limit of intertidal organisms on a shore; the upper distributions reflect zones of decreased tolerance to the prevailing affects of exposure (Lewis, 1961; Newell, 1979). These zones of lowered tolerance were initially thought to be determined solely by "critical tidal levels" (Colman, 1933), areas on the shore at which there were marked changes in the rate of aerial exposure over some time scale. For many areas, however, and especially shores without a high amplitude, strongly

inequilateral semi-diurnal tide, the critical tidal levels do not coincide with apparent faunal or floral breaks (Southward, 1957; Newell, 1964; Underwood, 1978; but see Doty, 1946). It is now realized that the effect of the tide is mitigated by many modifying factors, especially the prevailing wave regime, and the topography, aspect, and nature of the substrate (Newell, 1979), as well as some biological interactions. These mitigating factors may be temporally heterogeneous. For example, seasonal or chance events, such as periods when extremes of aerial temperature coincide with long exposures due to unusually calm conditions or low neap tides (Connell, 1961, 1970), may cause long-term fluctuations in populations.

Wave exposure is the modifying factor which probably has the greatest effect on the length of the intertidal zone and occurrence of species, and thus on the community structure (Stephanson and Stephanson, 1949; Southward, 1957; Lewis, 1961; Lubchenco and Menge, 1978). Conditions of high wave stress are extend the biological distributions shoreward. Given two locales of identical composition except for degree of wave stress, the exposed site will have a more extended littoral zone and sublittoral fringe than the sheltered site. In the latter, the littoral-sublittoral boundary will be near the extreme low water of spring tides (ELWS), while in the former the sublittoral fringe extends above ELWS due to the wetting action of the waves. Substrate considerations are also important for creating local microhabitats. The wave-mediated range extension is a main criticism of using tidal descriptors to delineate biotic zones (Lewis, 1961).

The lower limit of intertidal biotic zones and subtidal distributions cannot often be explained by physical factors alone. Instead, distributions lower on the shore appear to be closely related

to biological processes, primarily predation and interspecific competition (Menge and Sutherland, 1976; Lubchenco and Menge, 1978; Connell, 1985).

Predation strongly affects the structure of intertidal and subtidal populations. Many experimental studies, including those employing exclusion and inclusion techniques, have demonstrated that the distributions of sedentary bivalves, cirripeds, and types of algae are dependant on the presence and prevalence of their respective mobile predators or herbivores (Connell, 1970, 1972; Lubchenco and Menge, 1978; Menge, 1983; Sousa, 1984; Peterson, 1979, 1986). The prey species survive in spatial, temporal, or size "refuges" which exist outside the tolerance limits or predation ability of the predator. Spatial refuges can include high shore sites (increased aerial exposure) at which the effective time of feeding for predators may be reduced, or increased wave-beaten sites (increased wave stress) which may limit both presence and mobility of predators (Lubchenco and Menge, 1978; Menge, 1983). Size refuges occur when a prey organism reaches a size at which predation becomes ineffective (Connell, 1970; Paine, 1976), and may occur in temporally variable periods, such as when predators become locally scarce. Size-related feeding preferences, however, may reverse this trend (Connell, 1961). Many intertidal species, however, grade into the lower littoral or sublittoral levels and thus have no distinct lower boundary, although a subtidal boundary may exist (Witman, 1987). On the other hand, other species are often completely eliminated outside the refuge.

Competition also structures communities (Connell, 1972; Menge and Sutherland, 1976; Lubchenco and Menge, 1978). Space is the most limited resource on most hard substrate environments, and competitive

interactions for sites between species can be intense. Interactions between two species may result in the elimination of one through overgrowth, undercutting, crushing, or shading. To coexist in areas with high competition, organisms can survive in temporal refuges by colonizing ephemeral patches following disturbance. Such "opportunistic" species exhibit typical "r-selected" population strategies (Sousa, 1984). These interactions occur throughout the littoral and subtidal zones, but the complexity of the interactions often decreases shorewards due to the limited number of species which can tolerate the harsh physical extremes of the upper shore. Competition operates between various trophic levels, and occurs at all stages of the life cycle. Thus, an established species may prevent a competitor's propagules from colonizing a site through interference or predation (Mileikovsky, 1974; Woodin, 1976; Sutherland and Karlson, 1977; Grosberg, 1981; Keough, 1983; Luckenbach, 1987; Hunt et al., 1987; Young and Gotelli, 1988; Osman et al., 1989).

Spatial heterogeneity of populations, or patchiness, is often a distinctive feature of marine ecosystems. Patchiness within intertidal zones has been shown to be caused by disruption due to mechanical stress (Menge and Sutherland, 1976; Sousa, 1984). Such disturbances may remove dominant organisms seasonally (i.e. winter storm waves) or haphazardly (i.e. log damage). In this way, free space is created for colonization by competitively inferior species, which once established may persist for some time before being usurped by the dominant species. Patchiness may also be a result of heterogeneous larval densities (Gaines et al., 1985; Woodin, 1986; Butman, 1987; Roughgarden, et al., 1988). The evidence from temporal observations of community compositions following natural or experimental clearing events has led

to arguments for and against the occurrence of succession (Connell, 1972, 1985; Sutherland and Karlson, 1977; Lubchenco and Menge, 1978; Sousa, 1984). This issue has yet to be resolved satisfactorily.

The data available to date thus indicate the complexity of community interactions which create the distinctive biotic zones observed on hard substrates. The general consensus is that the formation and perpetuation of zonal distributions are the result of synergism between the ability of organisms to tolerate physical stresses generated predominantly by tidal oscillations, their ability to resist predation or herbivory, and their relative competitive dominance. Within the framework of "universal features" sensu Stephanson and Stephanson (1949), populations of organisms exist in a dynamic flux which is the reaction to this synergism.

MATERIALS AND METHODS

Site Specifications

All experiments were conducted in the York River, Virginia, USA, a partially-mixed estuary composing a major subsection of the Chesapeake Bay. The field site was located on the Virginia Institute of Marine Science (VIMS) Ferry Pier approximately 15 meters from shore at a depth of 0.75 meters below mean low water (MLW). All tidal heights are standardized to MLW. Experimental units faced southwest. Laboratory space equipped with a flow through water system was maintained for conditioning substrate and as a water source for settlement containers.

Structure of Piling Communities

The pilings of the VIMS Ferry Pier support a rather limited intertidal biota. The following description of the pier biota, shown in Figure 1, is general in nature and restricted to sedentary organisms occupying primary space, since the species composition varied seasonally.

Due to the small tidal amplitude and sheltered conditions typical of this site, the littoral fringe on the pilings is insignificant: littorinids and lichens are absent. The high eulittoral, beginning at +80 cm relative to MLW was occupied by the barnacle Chthamalus fragilis Darwin, which graded into the zone below. The highest individuals were often small and relegated to crevices, while both size and density increased at lower levels. The mid-eulittoral zone, at approximately +25 to +60 cm relative to MLW was dominated by a zone of Crassostrea

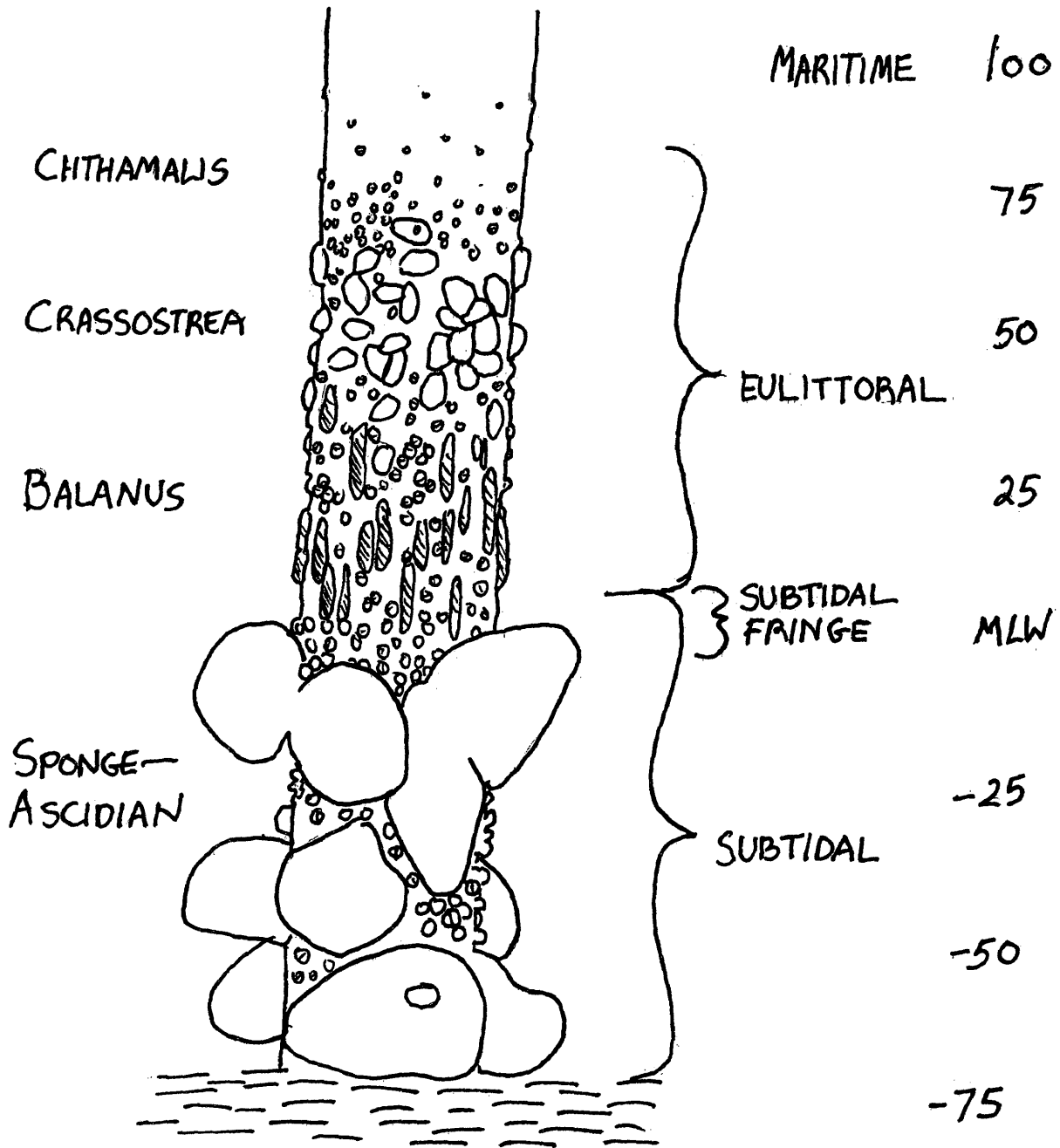
virginica. Numbers and densities of oysters varied widely between pilings, but generally the oyster distribution fell off sharply below +25 cm. Beginning within the oyster zone and extending subtidally was a zone of Balanus eburneus Gould with a seasonally abundant green algal zone (Ulva lactuca Linnaeus and Enteromorpha spp.) in the low to mid-eulittoral zone. The size and density of these barnacles also increased towards the low shore. The oyster zone was thus located between the upper and lower barnacle zones, and although barnacles of both types existed on primary (piling) and secondary space (oysters) within this zone, the oysters were able to dominate space by overgrowth. This was especially obvious when an oyster was pried from the substrate revealing the overgrown barnacles embedded in the lower valve. Mortality in the Crassostrea region was high, and oyster "boxes" and barnacle tests were common. The mussel Geukensia demissa (Dillwyn) was found throughout the intertidal zone, but was mostly confined to crevices. The density and diversity of organisms increased greatly at the sublittoral fringe, located at the MLW level, and below, where space was dominated by sponges, (predominantly the sponges Microciona prolifera (Ellis and Solander) and Halichondria bowerbanki Burton, the ascidian (Molgula manhattensis (DeKay)) and various species of hydrozoans and bryozoans, .

The eulittoral zone was thus composed of three partitions: the Chthamalis, Crassostrea, and Balanus subzones. The littoral fringe and maritime zone were depauperate, while the sublittoral fringe and subtidal zone was dominated by a mixed assemblage of sponges, ascidians, hydroids, and bryozoans.

Figure 1: Structure of the piling community.

BIOTIC ZONE

TIDAL HEIGHT (CM)



Measurement of Physical Parameters

Air and water temperatures, temperature ranges experienced in the intertidal zone, salinity, and tidal heights were recorded throughout the experimental period. Air and water temperature and conductivity readings were acquired from automated sensors located approximately 30 meters from the study site. Mean daily salinity values were computed from temperature and conductivity readings measured at six minute intervals. The daily temperature range experienced in the intertidal zone at the experimental site was measured with a minimum-maximum thermometer positioned at +35 cm relative to MLW. Hourly water heights were measured at a National Oceanographic and Atmospheric Association tide station located 100 meters from the study site, and monitored with a tide stick calibrated to the study location. All tidal heights are referenced to the mean of the low water level of the river computed over an eighteen year period from 1960 to 1978 (J. Boone, pers. com.).

At the study site, a vertically oriented wooden frame was permanently attached to the pier. The position of the frame was calibrated relative to MLW, and removeable experimental units (trellises and settlement tube racks) attached to the frame could then be secured at known tidal heights. The percentage aerial exposure experienced at any given intertidal level was computed from hourly tidal heights recorded from the tidal station. Percent exposure could be resolved to a scale of one day. Thus actual exposure/immersion curves for a given time frame could be generated, in contrast to using predicted values. This was important because atmospheric disturbances could lead to significant deviations in predicted tidal levels (D. Evans, pers. com).

Treatment of Oyster Larvae

All oyster larvae utilized in these experiments were grown to the pediveliger (competent to settle) stage at the VIMS oyster hatchery. The date of spawning, age, approximate number of larvae utilized in each experiment, and relative settling success are given in Table 1. The larvae were brought from the hatchery to the laboratory in a 500 ml beaker, where they were sieved onto a 202 μ m Nitex mesh and held to prevent premature settlement. Sieved larvae were kept moist with 5 μ m bag filtered York River water. The larvae were transferred from the mesh to allow settlement to occur.

Settlement Distribution

A microcosm system was constructed to examine larval settlement patterns relative to tidal height while limiting the influence of non-tidal factors. Hatchery-reared oyster larvae were interned within tubes in which the internal water height was in equilibrium with tidal motion. These "settlement tubes" were constructed of 5.08 cm (2 in) diameter, opaque, PVC pipe cut into 150 cm lengths. The inside of each tube was completely lined with a clean, continuous Mylar sheet scaled into 10 cm intervals. The Mylar constituted the only substrate within the tube that was available for settlement. Both ends of the tubes were sealed with 202 μ m Nitex mesh held in place with PVC ring connectors, and the ends of the Mylar strip protruded slightly from the ends of the tube thereby forming a close seal with the mesh. The mesh prevented the dispersal of the larvae or the introduction of predators. The tubes were conditioned in unfiltered flowing York River water for three days in the laboratory prior to initiation of the field experiments.

Oyster pediveligers, acquired from the VIMS oyster hatchery, were filtered onto a 202 μ m mesh sieve. Larvae were then scooped from the

sieve to the bottom Nitex mesh of the microcosm tube with a 12 ml plastic measuring spoon, and the larvae-laden meshes were sealed into the tube with the PVC ring connectors. Approximately equal numbers of larvae (about 100,000) were volumetrically transferred into each of three replicate tubes per experiment. The settlement tubes were then secured with parachute line to a wooden rack, and the rack was deployed into the York River by attaching it to the permanent wooden frame. The rack was positioned vertically so that MLW corresponded to a distance of 50 cm from the bottom of the tubes. The tubes were thus suspended approximately 25 cm above the river bottom. Tidal fluctuations resulted in a minimum of a 50% water exchange per tube within a tidal cycle, and thus basic water chemistry parameters are assumed to have been ambient with river water and nonlimiting to larval performance. This orientation resulted in a gradation of exposure heights which varied from high intertidal to subtidal (an exposure-depth gradient). The actual exposure occurring at any tidal height, which varied throughout the experiments, was later determined by examining the tidal record. Horizontal currents in the tubes were greatly reduced over natural conditions.

After a period of three to six days, depending on the observed settlement progress of a larval subset monitored in the laboratory, the rack was recovered and the tubes removed. With the PVC rings and Nitex mesh separated, the Mylar linings were gently rinsed with fresh water to remove unattached individuals, and the sheets were removed from the tubes. Each sheet was then sectioned into the premarked 10 cm intervals, and the number of settled larvae per interval counted under a dissection microscope. Since the exact number of larvae added to each

tube was not quantified, settlement per interval was evaluated as the percent of the total number of settled individuals per tube.

The experiment was repeated 4 times: the dates of initiation were 14 August, 23 August, 5 September, and 2 October, 1988 (this period encompassed part of the natural settling period of oysters in this area). The experiments were labeled Experiments S1 to S4, respectively. For each experiment, a one-way ANOVA was performed to test the null hypothesis that oyster larvae settle uniformly along the exposure-depth gradient. Proportional data was normalized with the angular transformation (Zar, 1984).

Early Post-settlement Survival

Oyster recruitment as a function of tidal height was monitored on a weekly scale from the initial numbers of settlers to a minimum post-settlement age of four weeks; settlers and recruits were clearly distinguishable. Experiments were initiated on June 3, June 16, July 8, and September 9 (Experiments R1-R4, respectively). Some experiments were continued on a monthly sampling basis thereafter.

The tidal heights investigated were +75, +50, +25, 0 (=MLW), -25 and -75 cm relative to MLW. Survival at each experimental height was computed as the mean of seven to ten replicate plates. The initial number of replicate plates per level was constant within an experiment, and depended upon the settlement success of the particular larval cohort. The number of settling larvae per plate was not controlled, and varied over an order of magnitude within an experiment. Sampling consisted of weekly photographs. Censuses were made after the completion of the experiment with a computerized image analyzer.

Unglazed ceramic plates served as a settlement substrate. They were constructed at a nearby pottery utilizing a slab roller to flatten

porcelain clay into sheets 6-7 mm thick. The sheets were then cut into rectangles of approximately 4 x 6 cm, and a hole was punched through the corner of the plates with a cork corer. This hole later served for both orientation during photography and for attachment at the field site. The plates were then allowed to dry thoroughly, after which they were bisqued (fire-hardened). The plates were not uniform as a group, the mean area of a random subset was about 25 cm². The surfaces of the plates bore a fine, cross-hatch pattern.

Before the initiation of an experiment, the settlement plates were numbered with permanent ink and conditioned in the laboratory in flowing, unfiltered York River water for three days. During conditioning the plates became water-saturated and acquired a bacterial coat. Upon receiving competent larvae, the plates were randomly sorted into one of three clear plastic settling containers filled with 2 liters of 5 um filtered York River water. About three times as many plates as necessary for a full, ten replicate-per-treatment design were used for each experiment because of nonuniform settlement distributions. Usually, the plates were shingled in orderly rows so larvae had access to both sides of the plates, but various other orientations were applied. Larvae were scooped from the sieve with a 12 ml plastic measuring spoon; approximately equal numbers of larvae were added to each container. The water in the settlement containers was not changed during the 3 to 5 day settlement period, nor were the larvae fed. Salinity was ambient with river water.

Settlement was deemed complete when the majority of larvae had ceased swimming. The plates were then removed from the containers and washed with York River water to remove unsettled individuals.

Settlement was variable both within and between containers, therefore the plates were broadly grouped into high, medium, and low density settlement and then randomly assigned to one of the six treatment levels.

For each plate, a 1 cm^2 internal scale was cut from finely ruled graph paper and labeled with the date, experiment, and treatment. This scale served both as a focusing reticule and for size determination of individual spat during data processing. Sampling was conducted by photographing each plate on a copy stand with a Olympus OM camera fitted with a 50 mm macro lens and utilizing Fujichrome 100 ASA tungsten film. A wooden frame attached to the copy stand and the convention of placing the hole in the plate in a constant position insured a reproducible orientation of the images. The camera-to-plate distance resulted in a 1:1.25 reproduction ratio which was also held constant throughout measurements. Focusing was facilitated with the internal scale as well as features on the plate.

When all the plates had been photographed (0.5-1 hours), they were attached to a rectangular wood and plastic-coated wire "trellis" at the experimental heights, which had previously been calibrated to MLW. Plastic cable ties were threaded through the hole in the plate and secured to the wire mesh. The trellis and its rows of plates were then deployed into the York River on the permanent frame. On a weekly basis for four weeks, the trellis was brought into the laboratory and the plates were removed and rephotographed. (Fouling organisms often required removal before the plates could be photographed: green algae and hydroids were especially prominent in obscuring spat.) A visual inspection of each plate was also made at this time, and dominant

fouling organisms, number of remaining spat, and evidence of predation were estimated. After the third sampling day (second week) only plates with surviving recruits were photographed. After photography, the plates were reattached to the trellis which was redeployed into the river. This process was repeated on the other sampling days a for minimum of five samples per month. The result of this procedure was a time series of photographs for each plate. The time series recorded the initial number of settlers per plate and allowed for the monitoring of individual spat throughout the experimental period.

Counting of settlers and recruits was accomplished on a computerized image analyzer. Basically, this computer network was composed of a terminal which coordinated the integration of a video camera, a high resolution (580 pixels/line) video monitor, computer memory storage, and a magnetic pad on which the images were manipulated. The basic procedure employed was as follows: the time series of photographs to be analysed was digitized and stored into computer memory in temporal order. The images were then replayed and survivors scored.

Digitization occurred under the video camera through red, green, and blue filters. The initial photograph, termed SD1 (=sample day 1) or age 1 (post-settlement age), was digitized and the corners of the plate were outlined with wax pencil on an acetate sheet taped to the monitor screen. The outline was used to ensure that the successive images were digitized and filed in an overlapping fashion. The SD1 image was then enhanced with a "linear stretch" function by which the light contrast and the various color planes could be adjusted to the operator's discretion. Once the computer-generated image was deemed satisfactory, the image was stored in computer memory, and the process repeated for the remaining images in the time series. The images were then recalled

in sequence, resulting in a display resembling a time-lapse movie. The speed of the movie could be controlled. Censuses of the individual spat were then made for each sample day. Tracings of the spat onto the acetate sheet were sometimes necessary to track individuals on plates with high density settlements or when fouling organisms obfuscated the image. In addition to the high-precision scoring of settlers and recruits, the time-lapse function also allowed the monitoring of the settlement and subsequent recruitment of other fouling organisms, most notably barnacles. Inter- and intraspecific competitive interactions were noted where applicable.

Survival on each replicate plate was measured for each sampled day, and was determined by dividing the number of recruits for each age by the number of settlers. Statistical tests were then performed on the angularly transformed data. A three-way analysis of variance (ANOVA) was first performed on the mean proportional survival by experiment, treatment level, and sampled day (age) in order to evaluate interaction terms. A two-way ANOVA was then performed with experiment held constant, thus testing for level-sample day interactions. Finally, one-way ANOVA tests were performed with both experiment and age held constant, and a Student-Newman-Keuls test (SNK) was performed when significant differences were determined. These analyses tested the hypothesis of no difference between the mean survival of the treatment levels within an experiment. In a similar fashion, seasonal differences between levels were investigated by running one-way ANOVA tests with level and sampled day held constant. Instantaneous percent mortality rates, expressed as mean daily percent mortality per time interval (mean

percent mortality day^{-1} interval $^{-1}$), were computed from the percent survival data for all experiments.

Size

The size of individual spat, expressed as area (cm^2), was determined at each date sampled. Due to logistics, only the settlers which survived the first week (SD2) were measured on SD1. Size measurements were accomplished on the image analyzer with a "blotch" function which determined the number of pixels within an operator-defined area. (A pixel is the smallest unit of light intensity and color value resolvable by the video monitor.)

The procedure was to first measure the number of pixels composing the 1 cm^2 internal scale. This was done by "blotching" the corners of the scale and allowing the computer to connect the corners. The mean of three scale measurements was used in computing spat sizes. Next, the number of pixels composing each of the spat on the image was determined by carefully tracing the outline of the spat with the cursor. The results of these tracings, expressed as numbers of pixels, were stored in a raw data file. These data were then fed into a PASCAL program (K. Kiley, 1988) which first determined the mean number of pixels cm^{-2} (from the scaling measurements), and then multiplied the reciprocal of that ratio by the number of pixels/spat to give area of each spat. These results were presented in a data file which could be modified for statistical analysis or graphical display. In most cases, the growth of individual spat was determined; however, plates with high density settlements sometimes precluded the accurate tracking of individuals through time. In these cases, size measurements were made without attempting to identify individuals over time. The statistical procedure

was similar to that described for survival, and called for a one-way ANOVA analysis of mean size plate⁻¹ sample day⁻¹ level within experiments to test the hypothesis of no difference in size between levels. Experiments were also compared within levels to evaluate the seasonal effect. SNK tests were performed where appropriate. The mean instantaneous growth rates over each weekly interval (cm² day⁻¹ interval⁻¹) was also determined for the four experiments.

Table 1: Settlement characteristics.

<u>Experiment</u>	<u>N Larvae</u>	<u>Date Spawned</u>	<u>Age</u>	<u>Set Interval</u>	<u>Time</u>	<u>T°C</u>	<u>Set Density</u>
S1	300,000	?		Aug 14-16	2d		
S2	300,000	Aug 2	21d	Aug 23-27	4d		
S3	300,000	Aug 16	20d	Sep 5-10	5d		
S4	200,000	Sep 17	15d	Oct 2- 8	6d		

R1	200,000	May 18	17d	Jun 3- 7	4d	20	Low
R2	300,000	May 31	14d	Jun 14-16	2d	27	Low
R3	250,000	?		Jul 5- 8	3d	24	High
R4	100,000	Aug 16	20d	Sep 5- 9	4d	22	High

RESULTS

Temperature Data

The minimum and maximum temperatures experienced at the +35 cm level for the experimental period June 1 to November 10 are shown in Figure 2. In the intertidal zone, the maximum temperatures generally correspond to periods of aerial exposure while the minimum values occurred during inundation until mid-September, when the reverse is true. Maximum temperatures rose rapidly during the early summer and consistently reached peaks in excess of 35°C until early September, after which temperatures remained below 30°C and steadily declined. Minimum temperatures generally shadowed maximum temperatures and reached a high of 25°C in mid summer. Periods of intense rainfall usually depressed temperatures significantly. Daily temperature ranges commonly exceeded 10°C and reached a high of 21°C on June 15. At this same time, the temperature ranged 28°C in three days.

The mean daily, mean daily maximum, and mean daily minimum air and water temperatures recorded from the automated sensors are shown in Figures 3 and 4, respectively. These curves agree with the intertidal results, but are dampened because they are mean values.

Salinity

The mean daily salinity values (ppt) for the experimental period are shown by Figure 5. The mean salinity exhibited a rapid increase

from a low of about 16 o/oo on June 1 until mid July, after which it remained between 21 and 24 o/oo for most of the remaining study period. A sharp peak to above 25 o/oo was measured near the end of October, and dips of over 2 o/oo can be correlated with heavy rainfall. The salinity thus remained between 16 and 25 o/oo during the study period.

Tidal Heights

Water levels recorded at the VIMS Oyster Pier for the experimental period are presented in Figures 6-10. All heights have been converted to the metric scale and calibrated to MLW. Figure 6 depicts the tidal amplitudes for the entire sampling period, while Figures 7-10 display the range over the thirty day interval which composed the primary sampling period of each of the four recruitment experiments.

The tides at Gloucester Point are semi-diurnal with inequilateral high waters, but the tidal amplitude rarely exceeds 1 m. However, atmospheric disturbances are capable of rapidly raising or depressing the sea surface. This can lead to deviations in the predicted astronomical tides amounting to more than 60 cm (pers. obs.). These deviations resulted in unpredictable periods of prolonged exposure or increased inundation; often both occurred as water piled on shore by wind stress rapidly oscillated away after the storm. Such coupled deviations can be observed between June 3-13 during Experiment R1 and a smaller disturbance at the end of Experiment R4 (Figures 6 and 9).

In general, although tidal amplitudes were similar throughout the sampling period, water levels were higher after mid-August. Thus the lower littoral zone was more frequently immersed later in the summer and during the fall.

Aerial Exposure

The percent aerial exposure by tidal height experienced during the

thirty days of each of the recruitment experiments are compared together in Figure 11. On a shorter scale, the percent aerial exposure at each treatment level is computed over the weekly sampling periods for the four experiments in Table 2. The exposure data for the settlement experiments are presented elsewhere (Tables 3 and 4).

The exposure curves (Figure 11) indicate substantial differences in the average exposure time experienced by the treatment levels zones during the four recruitment experiments. The greatest differences were in the low littoral zone between Experiments R3 and R4, where a 20% longer exposure was suffered by Experiment R3. This difference was only about 10% in the upper littoral. Experiments R1 and R2 were more similar and intermediate to the latter two.

These results are corroborated by Table 2, where weekly variations in percent exposure can be compared. Over these periods, the -25 cm and -75 cm level treatments were wholly subtidal for all experiments. Exposure at the MLW level ranged from subtidal to an exposure of nearly 10%; the +25 cm level was exposed between 16.7 and 47.4%; the +50 level was between 42.7 and 75.0%; and the +75 cm level ranged from 73.4 to 99.0% exposed.

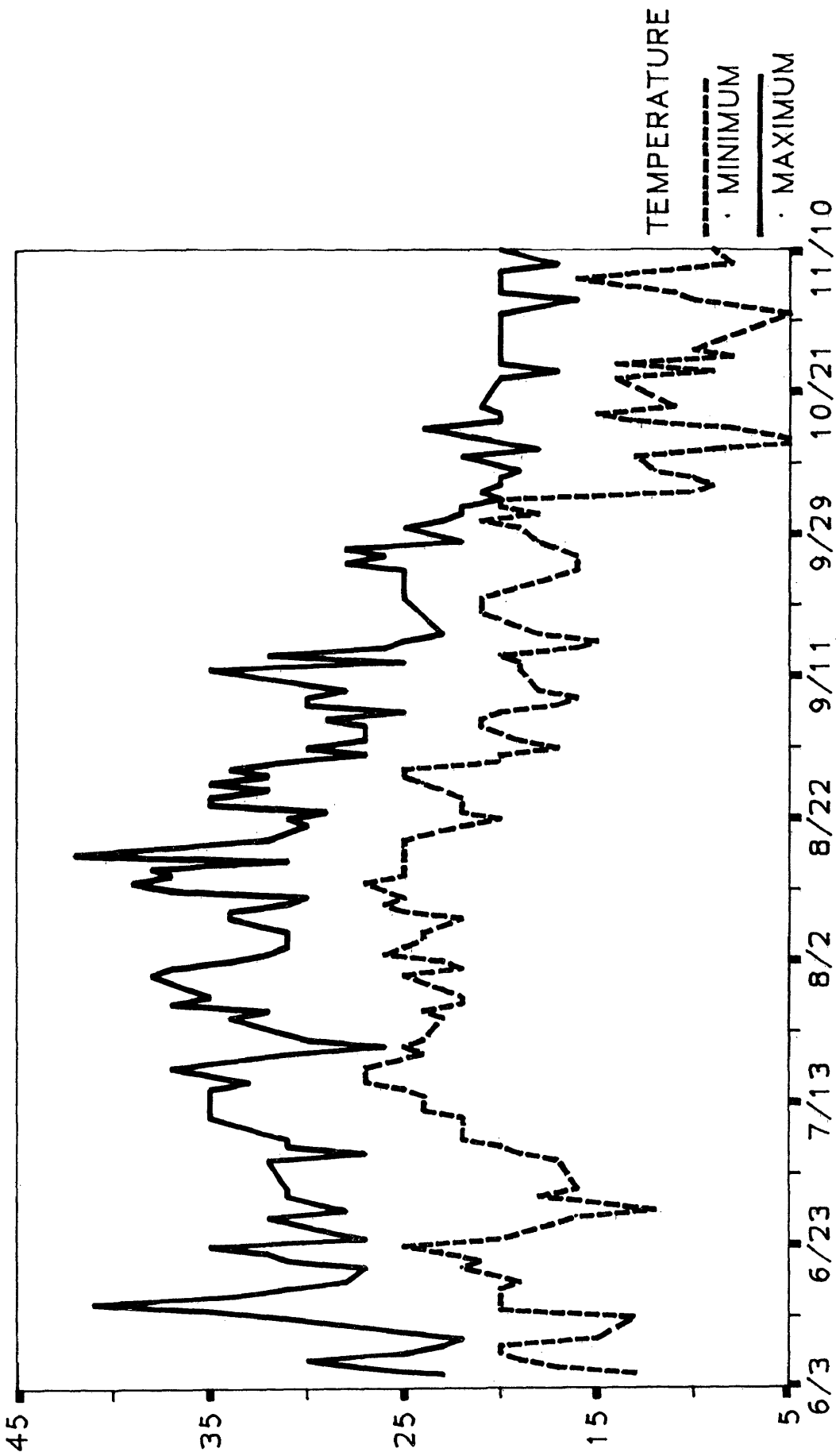
Summary of physical data

In summary, mean air temperatures peaked near the end of August, and declined with great variation thereafter. The maximum mean air temperature was 35°C. Mean water temperatures increased until mid-August before declining. Daily minimum and maximum ranges of water temperatures were not great. The intertidal temperatures recorded with the min-max thermometer exhibit slightly higher maximum temperatures than the mean maximum air values, and similar minimum temperatures to

the mean minimum water values. The salinity was minimal and increasing during June and the first half of July, and stabilized at about 25 o/oo thereafter, with declines associated with rainfall. Average exposure levels varied throughout weekly sampling periods. Generally, the exposures were highest in July, least in September, and intermediate in June.

The experiments were thus conducted under differing environmental conditions. Experiments R1 and R2 experienced increasing salinity, moderate to high temperatures, and intermediate exposures. Experiment R3 was subjected to high, stable salinity, high temperatures, and long exposures. Experiment R4 also had high salinity but was coupled with decreasing temperatures and low exposures.

Figure 2: Temperature ranges (degrees Celsius) recorded in the intertidal zone at +35 cm relative to MLW from 4 June to 11 November, 1988.



TEMPERATURE (DEGREES C)

DATE

Figure 3: Mean daily, mean daily maximum, and mean daily minimum water temperatures (degrees Celsius) recorded from automated sensors on the VIMS Ferry Pier from 1 June to 10 November, 1988.

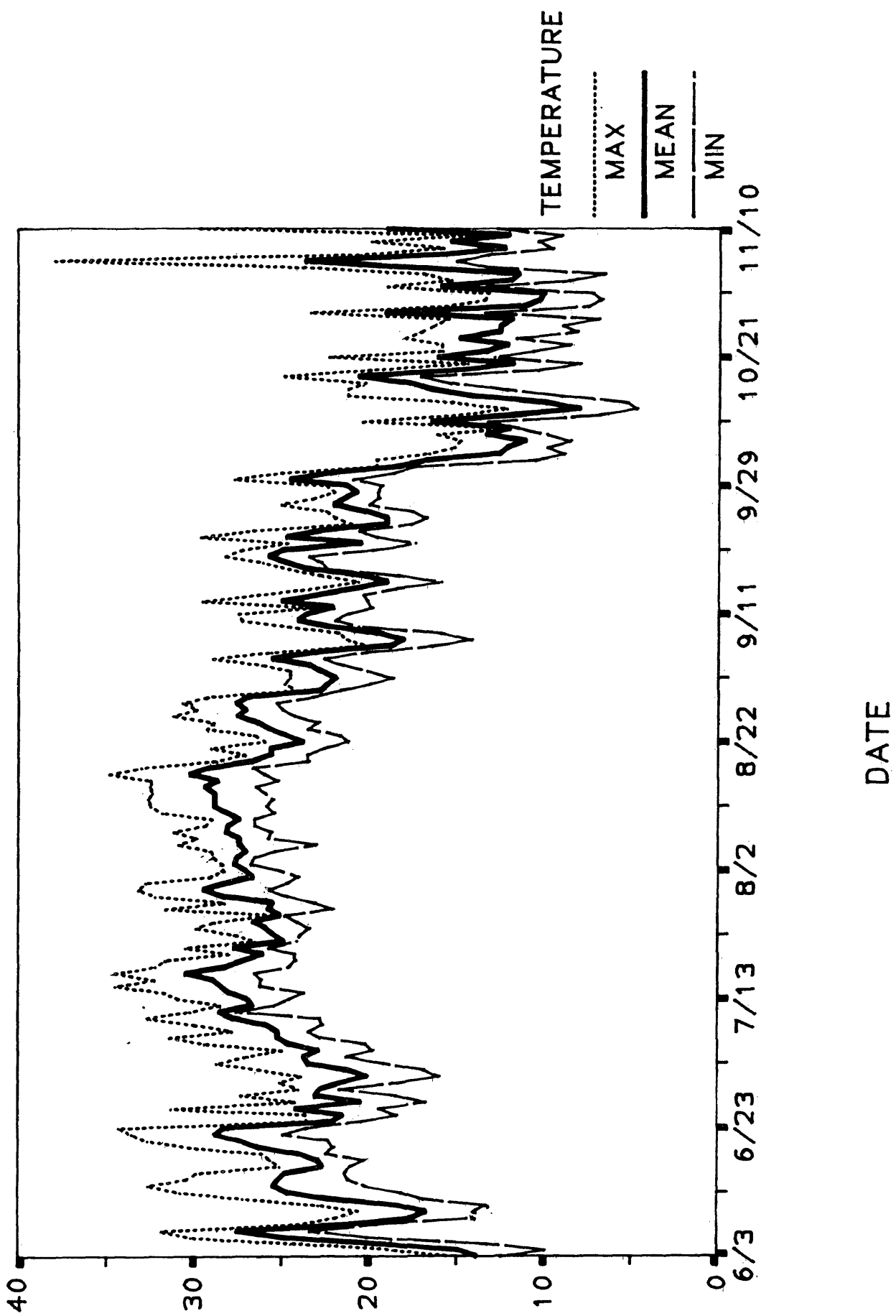
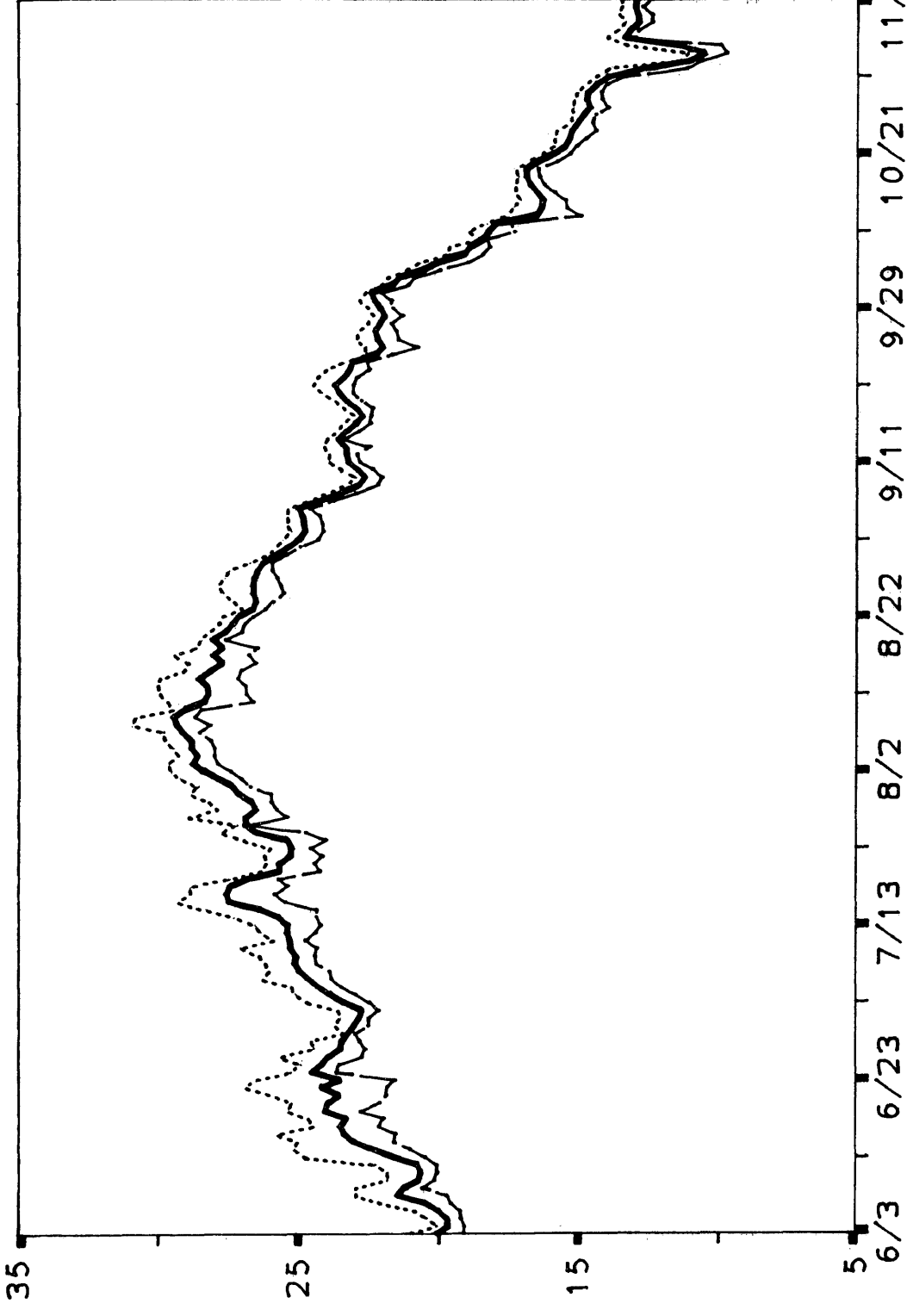


Figure 4: Mean daily, mean daily maximum, and mean daily minimum air temperatures (degrees Celsius) recorded from automated sensors on the VIMS Ferry Pier from 1 June to 10 November, 1988.



MEAN DAILY TEMPERATURE (°C)

TEMPERATURE
..... MAX
———— MEAN
- - - - MIN

DATE

Figure 5: Mean daily salinity (parts per thousand) recorded from automated sensors on the VIMS Ferry Pier from 1 June to 10 November, 1988.

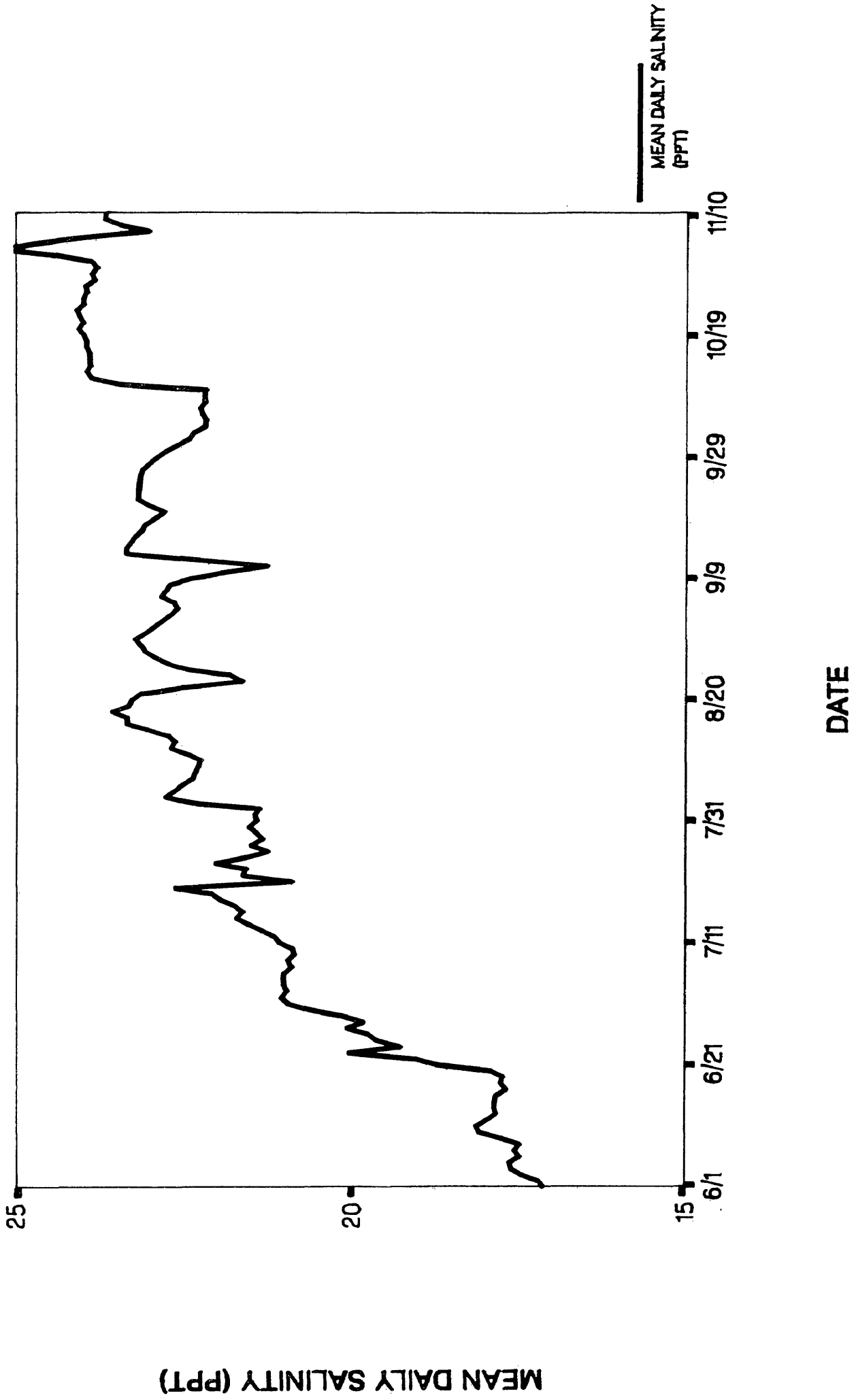
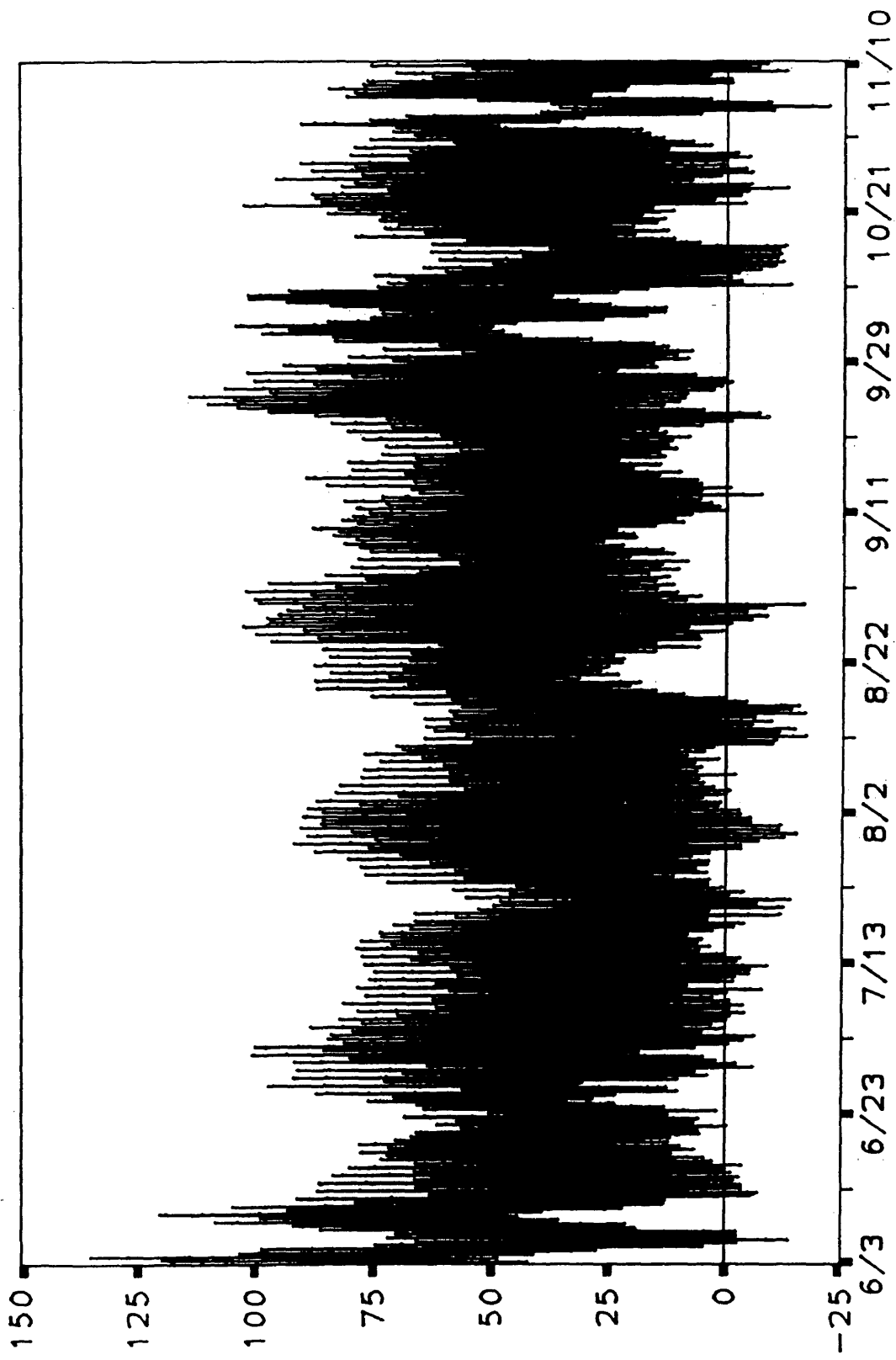


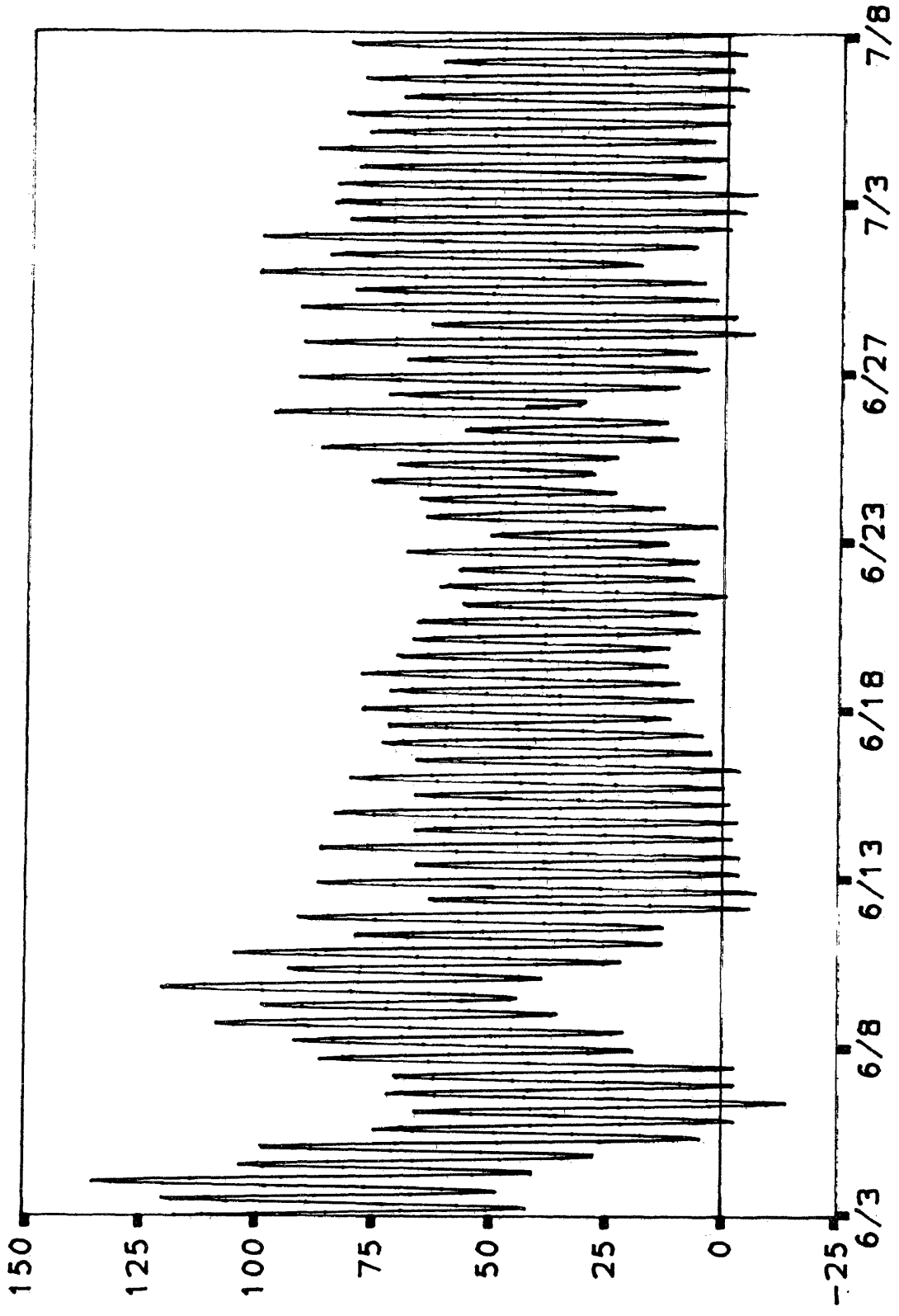
Figure 6: Hourly tidal heights (centimeters relative to mean low water) measured at an automated tidal station on the VIMS Oyster Pier during the experimental period 1 June to 10 November, 1988.



WATER LEVEL (CENTIMETERS)

DATE

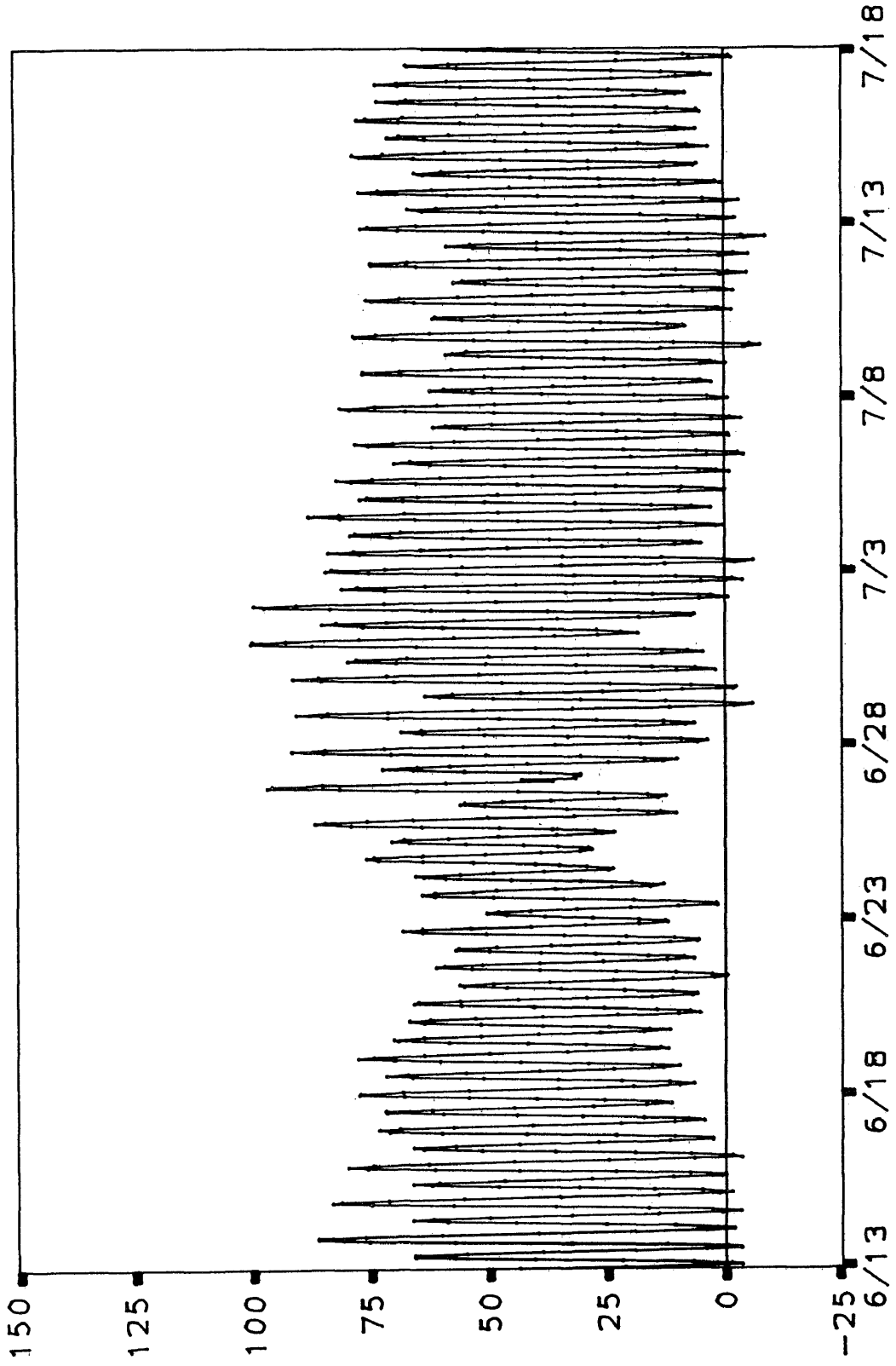
Figure 7: Hourly tidal heights (centimeters relative to mean low water) measured at an automated tidal station on the VIMS Oyster Pier during the experimental period 1 June to 10 July, 1988. Experiment R1.



WATER LEVEL (CENTIMETERS)

DATE

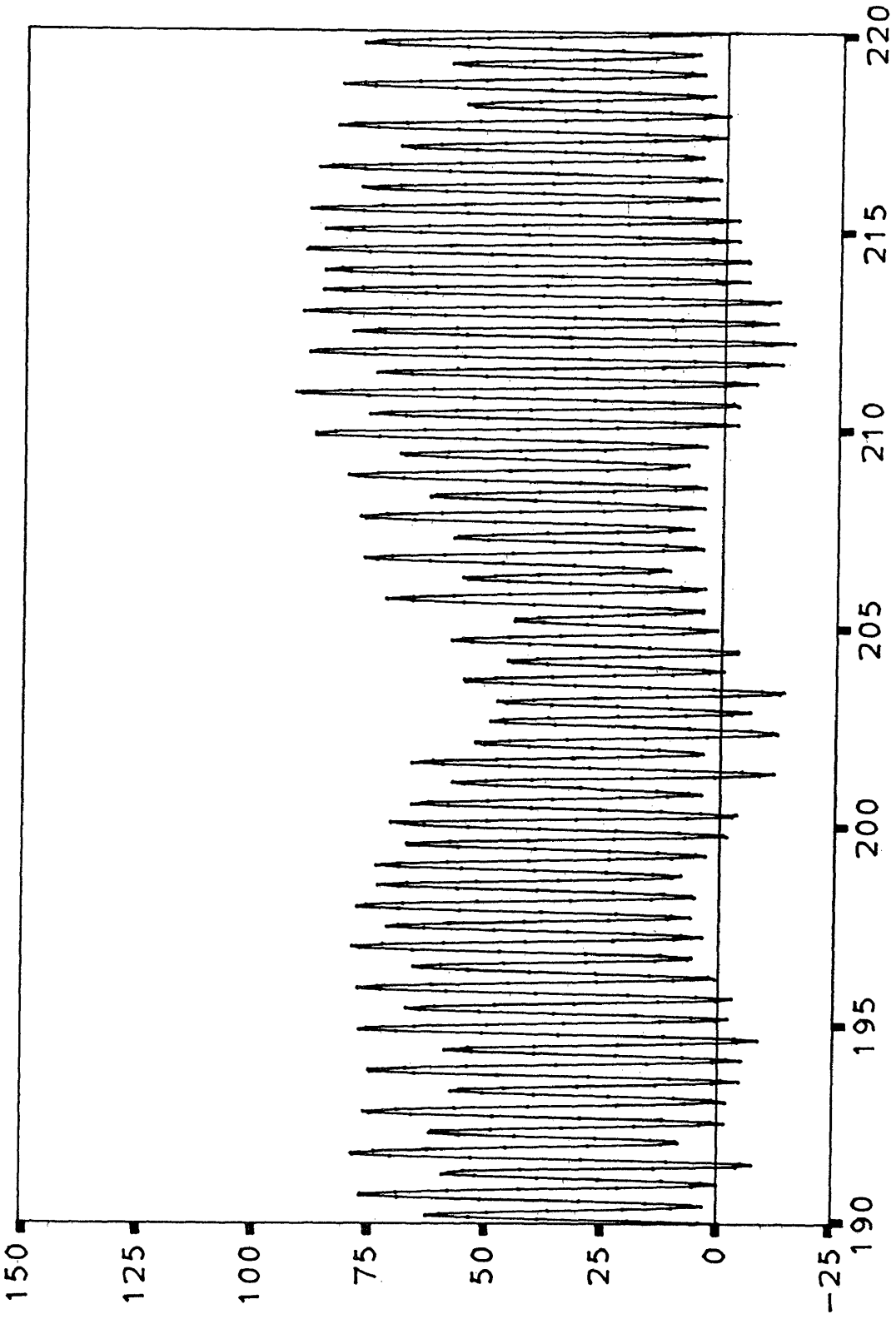
Figure 8: Hourly tidal heights (centimeters relative to mean low water) measured at an automated tidal station on the VIMS Oyster Pier during the experimental period 13 June to 18 July, 1988. Experiment R2.



WATER LEVEL (CENTIMETERS)

DATE

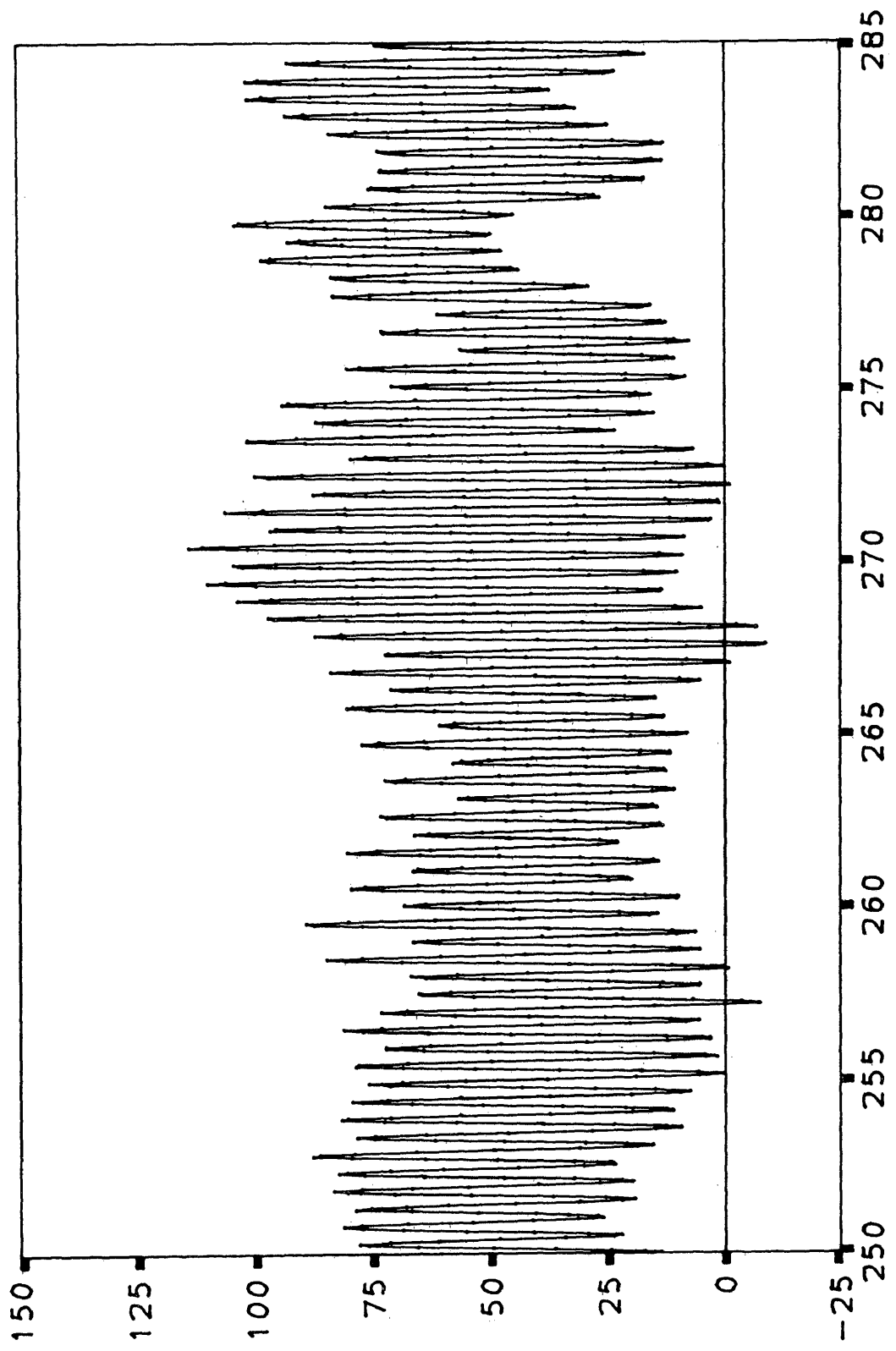
Figure 9: Hourly tidal heights (centimeters relative to mean low water) measured at an automated tidal station on the VIMS Oyster Pier during the experimental period 8 July to 7 August, 1988. Experiment R3.



WATER LEVEL (CENTIMETERS)

DATE

Figure 10: Hourly tidal heights (centimeters relative to mean low water) measured at an automated tidal station on the VIMS Oyster Pier during the experimental period 6 September to 11 October, 1988. Experiment R4.



WATER LEVEL (CENTIMETERS)

DATE

Table 2: Percent aerial exposure by tidal level

		TIME INTERVAL					
EXP	TH	6/7 -6/14	6/14 -6/21	6/21 -6/30	6/30 -7/7	7/7 -7/16	7/16 -8/13
1	+75	73.4	94.8	89.6	80.7	92.5	91.5
	+50	46.3	64.0	59.2	57.8	62.5	66.7
	+25	24.5	38.5	27.9	36.5	39.6	42.0
	0	4.7	2.1	1.7	3.7	5.8	8.5
	-75	0.0	0.0	0.0	0.0	0.0	0.0

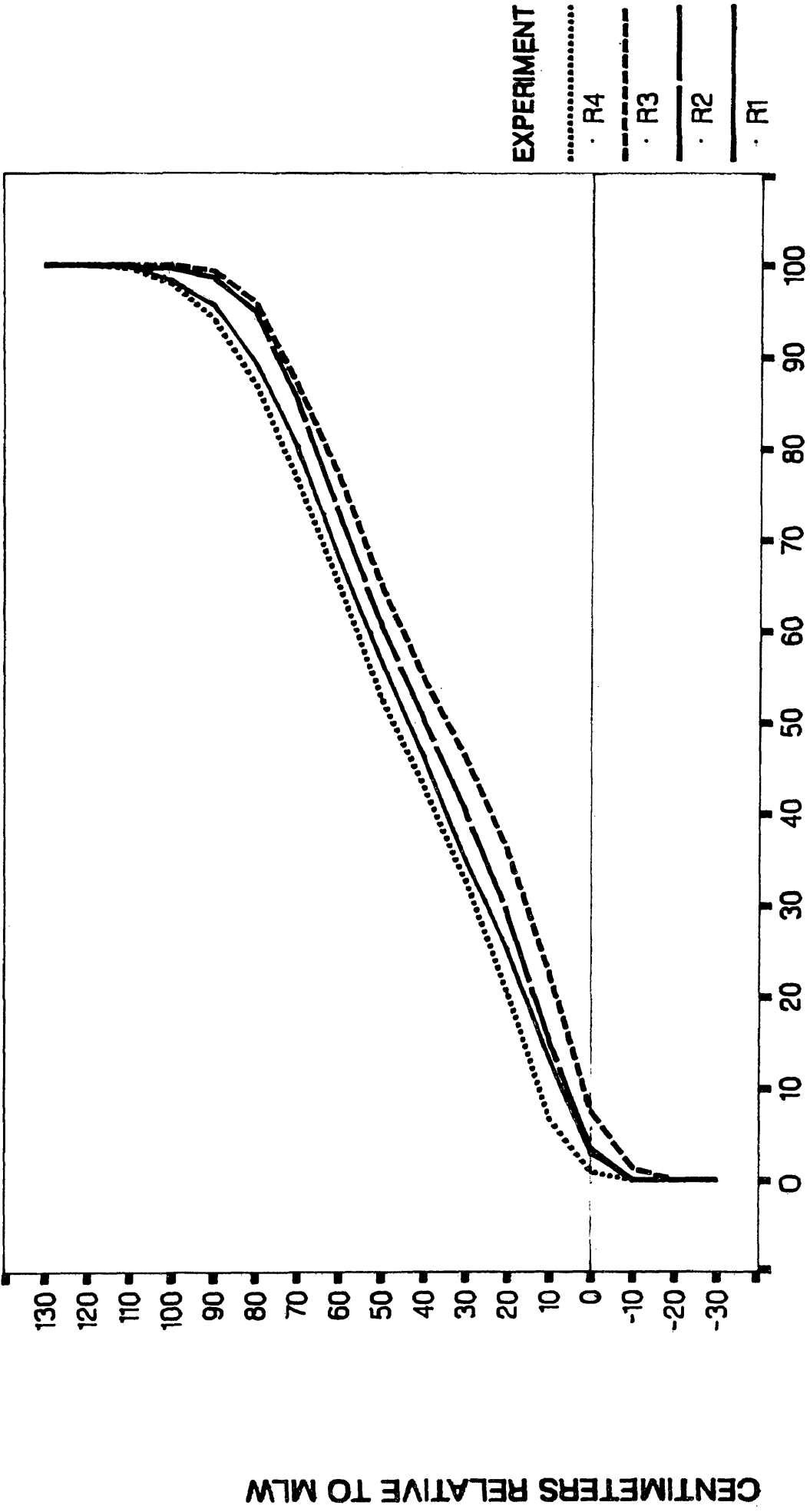
		TIME INTERVAL				
EXP	TH	6/16 -6/23	6/23 -6/30	6/30 -7/7	7/7 -7/16	7/16 -8/13
2	+75	85.6	91.9	80.7	92.5	91.5
	+50	56.1	60.3	57.8	62.5	66.7
	+25	29.2	30.8	36.5	39.6	42.0
	0	2.6	1.7	3.7	5.8	8.5
	-75	0.0	0.0	0.0	0.0	0.0

		TIME INTERVAL				
EXP	TH	7/8 -7/15	7/15 -7/22	7/22 -7/29	7/29 -8/5	8/5 -9/5
3	+75	92.2	99.0	89.1	80.8	86.2
	+50	63.0	75.0	65.1	58.9	59.5
	+25	40.1	47.4	38.0	41.2	32.3
	0	6.8	9.4	5.2	9.9	6.3
	-25	0.0	0.0	0.0	0.0	0.0
	-75	0.0	0.0	0.0	0.0	0.0

		TIME INTERVAL				
EXP	TH	9/9 -9/16	9/16 -9/23	9/23 -9/30	9/30 -10/7	10/7 -11/7
4	+75					
	+50	59.4	60.2	50.0	42.7	59.6
	+25	32.8	30.7	29.7	16.7	31.9
	0	1.0	1.0	2.1	0.0	7.3
	-25	0.0	0.0	0.0	0.0	0.0
	-75	0.0	0.0	0.0	0.0	0.0

EXP: Experiment; TH: Tidal Height (cm relative to MLW)

Figure 11: Percentage aerial exposure by vertical height (centimeters relative to MLW) for Experiments R1 to R4. Each percentage exposure was calculated over a 28 to 31 day period.



PERCENT AERIAL EXPOSURE

EXPERIMENT

- R4
- R3
- R2
- R1

CENTIMETERS RELATIVE TO MLW

Settlement

The oyster larvae exhibited a strong preference for the bottom interval as a settlement site (Tables 3-6, Figures 12-16). Between 72 and 96% of the mean settlement occurred at the -50 cm interval, and most of that actually occurred within the bottom 5 centimeters of the tube. Larvae settled within this zone in extremely dense aggregations. Overall, settlement tended to increase with depth, and intertidal settlement was slight. Mean settlement in the intertidal zone ranged from 8 to only 0.5% of the total mean settlement per experiment. With the exception of Experiment S1, the intertidal settlement which occurred was mainly confined to aerial exposure heights lower than 30%. The presence of oysters that settled in areas of 100% emersion (Experiment S1) is an artifact which resulted from larvae stranding during the positioning of the tubes. All one-way ANOVA tests resulted in highly significant F ratios (Table 8). The hypothesis that oyster larvae settle uniformly along the tidal-depth gradient is thus rejected.

Several observations recorded during the data collection are of interest. First, growth, obvious as a "flattening out", or spreading of the posterior margin of the shell, was noted occasionally, but the majority of individuals did not appear to have completed metamorphosis. Indeed, "eye spots", characteristic of the immediate presettlement larval form, were still visible in many settled individuals. This observation indicates that, over the time scales utilized, the recorded distribution of oysters probably reflects actual settlement patterns and not the effects of post-settlement mortality, which can rapidly alter initial distributions. The presence of metamorphosing individuals with a growing margin was mainly confined to the subtidal zone. There also was a strong tendency for larvae to settle with the posterior margin of

the shell pointing downward and the umbone region oriented up. It is uncertain if this orientation, which occurred at all heights, is indicative of some tube-related effect (i.e. water flow into the tube was from the bottom).

Table 3: Settlement distribution.

Experiment S1

		REP: 1		2		3	
TH	%E	NS	PS	NS	PS	NS	PS
90	100.00	0	.00	7	.24	0	.00
80	100.00	0	.00	5	.17	0	.00
70	96.88	1	.04	1	.03	0	.00
60	90.63	0	.00	0	.00	0	.00
50	75.00	5	.18	4	.13	0	.00
40	62.50	14	.51	11	.37	6	.30
30	54.17	18	.65	27	.91	11	.55
20	42.17	26	.94	35	1.18	15	.75
10	32.25	36	1.30	59	1.98	17	.85
0	19.79	61	2.20	63	2.12	19	.96
-10	7.29	74	2.67	58	1.95	22	1.11
-20	0.0	56	2.02	77	2.59	55	2.77
-30	0.0	75	2.71	67	2.25	44	2.21
-40	0.0	151	5.46	162	5.44	100	5.03
-50	0.0	~2250	81.32	~2400	80.65	~1700	85.47
Sum		~2767		~2976		~1989	

Experiment S2.

		REP: 1		2		3	
LEV	%E	NS	PS	NS	PS	NS	PS
90	90.63	6	5.08	0	.00	0	.00
80	79.17	0	.00	0	.00	1	.39
70	71.88	0	.00	0	.00	0	.00
60	60.42	3	2.54	0	.00	1	.39
50	53.13	0	.00	0	.00	0	.00
40	40.63	0	.00	0	.00	0	.00
30	33.33	1	.85	4	.53	2	.78
20	19.79	2	1.69	23	3.03	0	.00
10	7.29	7	5.93	9	1.18	1	.39
0	0.0	4	3.39	35	4.61	19	7.36
-10	0.0	8	6.78	21	2.76	5	1.94
-20	0.0	0	.00	19	2.50	11	4.26
-30	0.0	2	1.69	45	5.92	11	4.26
-40	0.0	6	5.08	40	5.26	14	5.43
-50	0.0	79	61.95	554	72.89	193	74.81
		118		750		258	

REP: Replicate tube; TH: Tidal Height (cm relative to MLW); %E: Percent aerial exposure; NS: Number of settled larvae; PS: Percent of total settlement per tube.

Table 4: Settlement distribution, cont.

Experiment S3.

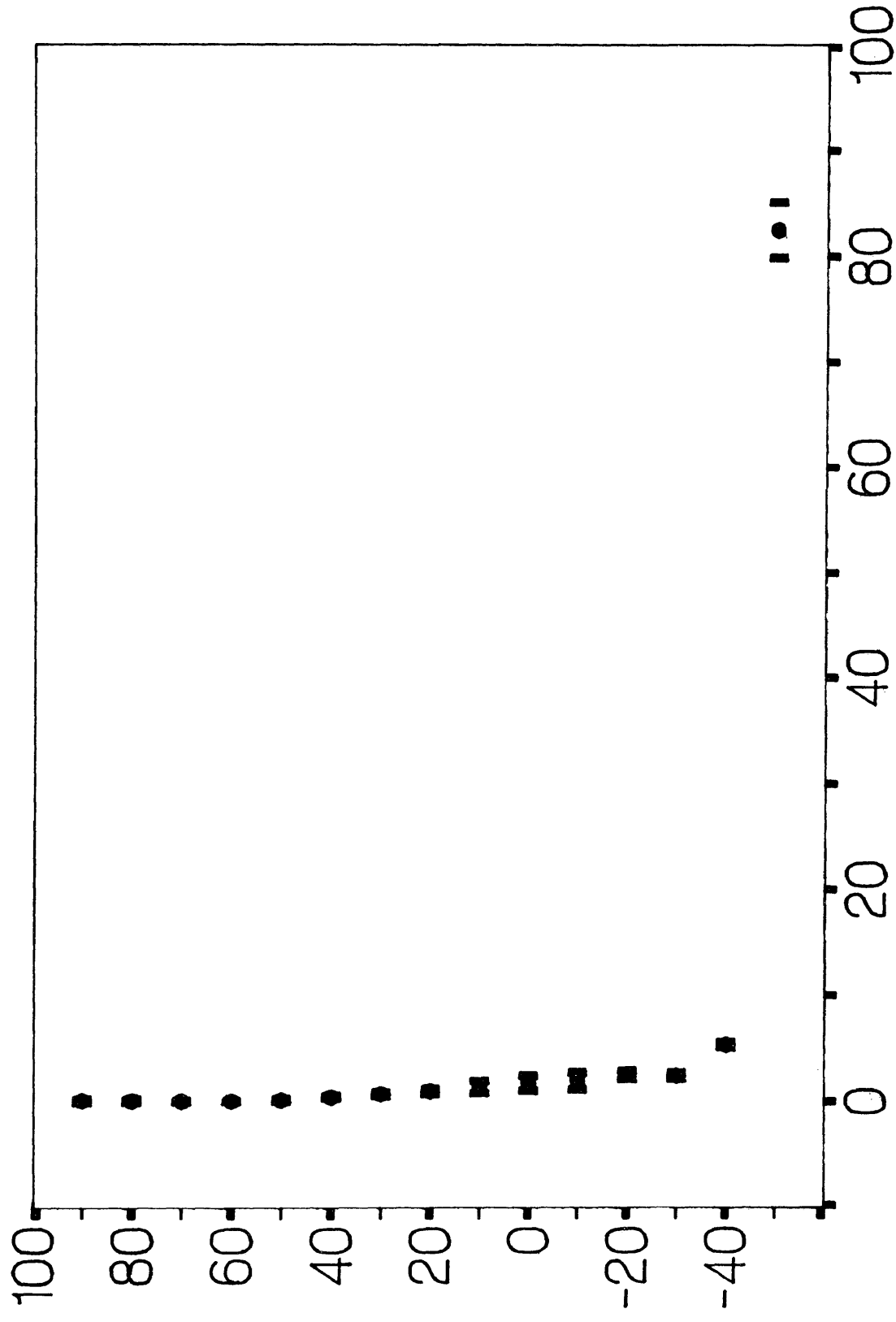
		REP: 1		2		3	
TH	%E	NS	PS	NS	PS	NS	PS
90	100.00	0	.00	0	.00	0	.00
80	91.67	0	.00	0	.00	0	.00
70	75.00	0	.00	0	.00	0	.00
60	61.11	0	.00	0	.00	0	.00
50	50.00	0	.00	0	.00	0	.00
40	40.28	0	.00	0	.00	0	.00
30	27.08	2	.11	1	.05	0	.00
20	10.42	5	.28	1	.05	2	.15
10	0.69	36	1.98	32	1.72	16	1.17
0	0.0	23	1.27	54	2.90	11	.80
-10	0.0	31	1.71	71	3.82	25	1.83
-20	0.0	47	2.59	64	3.44	13	.95
-30	0.0	53	2.92	60	3.22	39	2.85
-40	0.0	120	6.60	78	4.19	35	2.56
-50	0.0	~1500	82.26	~1000	73.48	1227	89.69
		~1817		~1361		1368	

Experiment S4.

		REP: 1		2		3	
LEV	%E	NS	PS	NS	PS	NS	PS
90	92.26	0	.00	0	.00	0	.00
80	83.33	0	.00	0	.00	0	.00
70	68.45	0	.00	0	.00	0	.00
60	55.95	0	.00	0	.00	0	.00
50	38.69	0	.00	0	.00	0	.00
40	27.38	0	.00	0	.00	2	.06
30	17.26	0	.00	0	.00	0	.00
20	8.93	0	.00	1	.06	2	.06
10	0.60	28	1.33	2	.12	1	.03
0	0.0	8	.38	5	.30	7	.21
-10	0.0	9	.43	6	.36	9	.27
-20	0.0	8	.38	18	1.07	39	1.15
-30	0.0	24	1.14	13	.77	32	.95
-40	0.0	26	1.24	8	.48	50	1.48
-50	0.0	~2000	95.10	1626	96.84	3239	95.80
		~2103		1679		3381	

REP: Replicate tube; TH: Tidal Height (cm relative to MLW); %E: Percent aerial exposure; NS: Number of settled larvae; PS: Percent of total settlement per tube.

Figure 12: Mean percent settlement by tidal height
(centimeters relative to MLW). Experiment S1.



MEAN PERCENT SETTLEMENT (SD)

LEVEL (CM RELATIVE TO MLW)

Figure 13: Mean percent settlement by tidal height
(centimeters relative to MLW). Experiment S2.

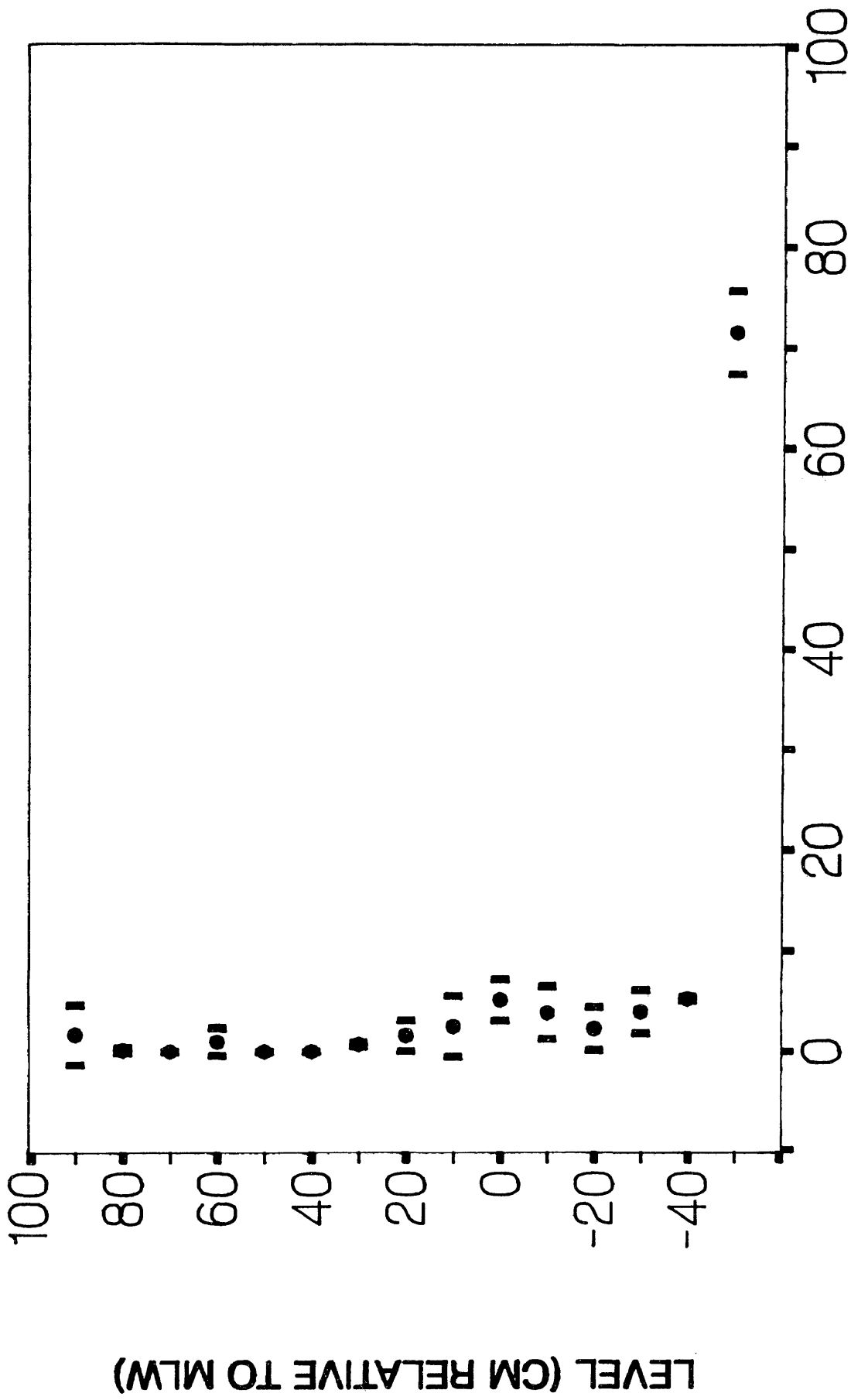
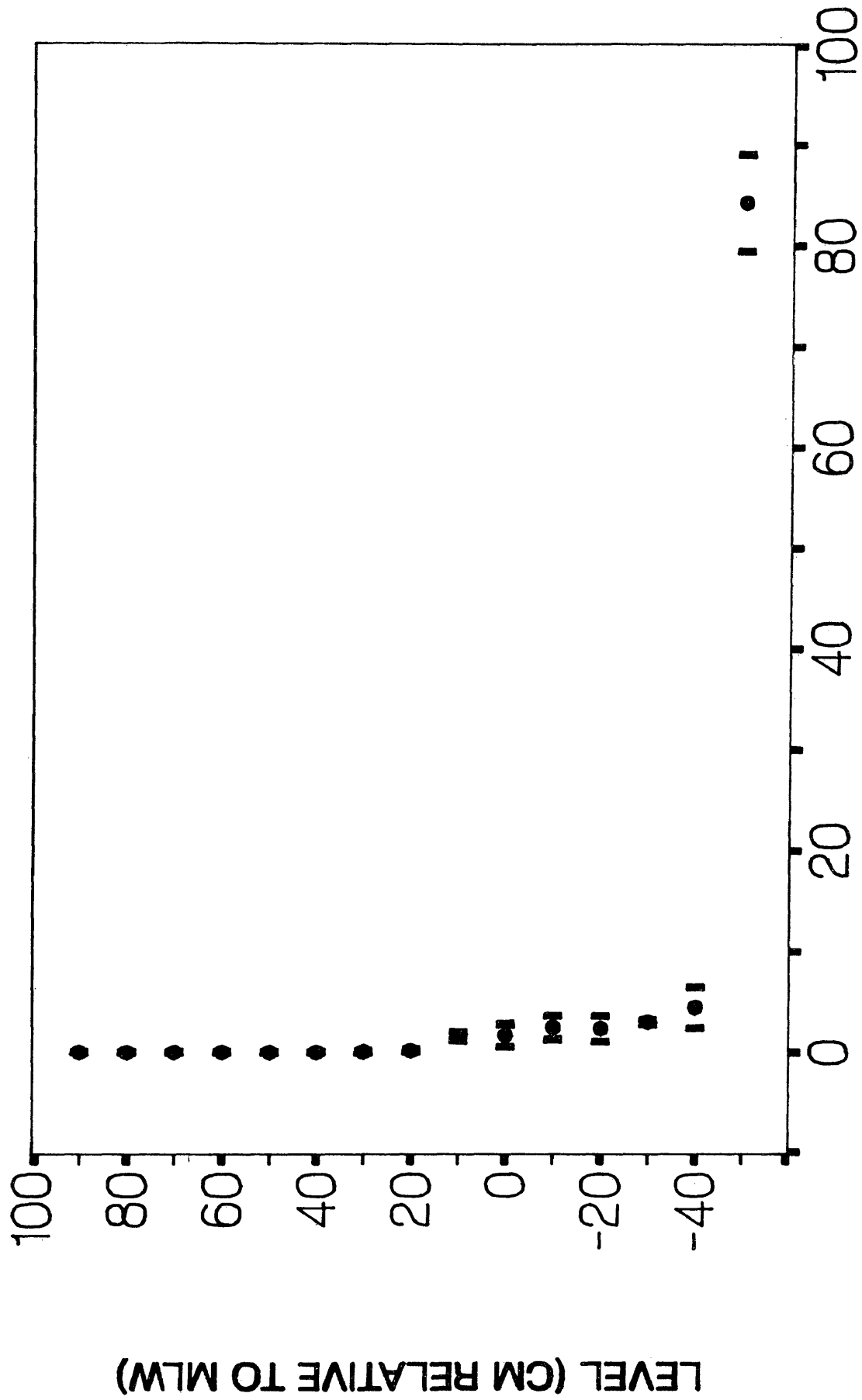


Figure 14: Mean percent settlement by tidal height
(centimeters relative to MLW). Experiment S3.



MEAN PERCENT SETTLEMENT (SD)

Figure 15: Mean percent settlement by tidal height
(centimeters relative to MLW). Experiment S4.

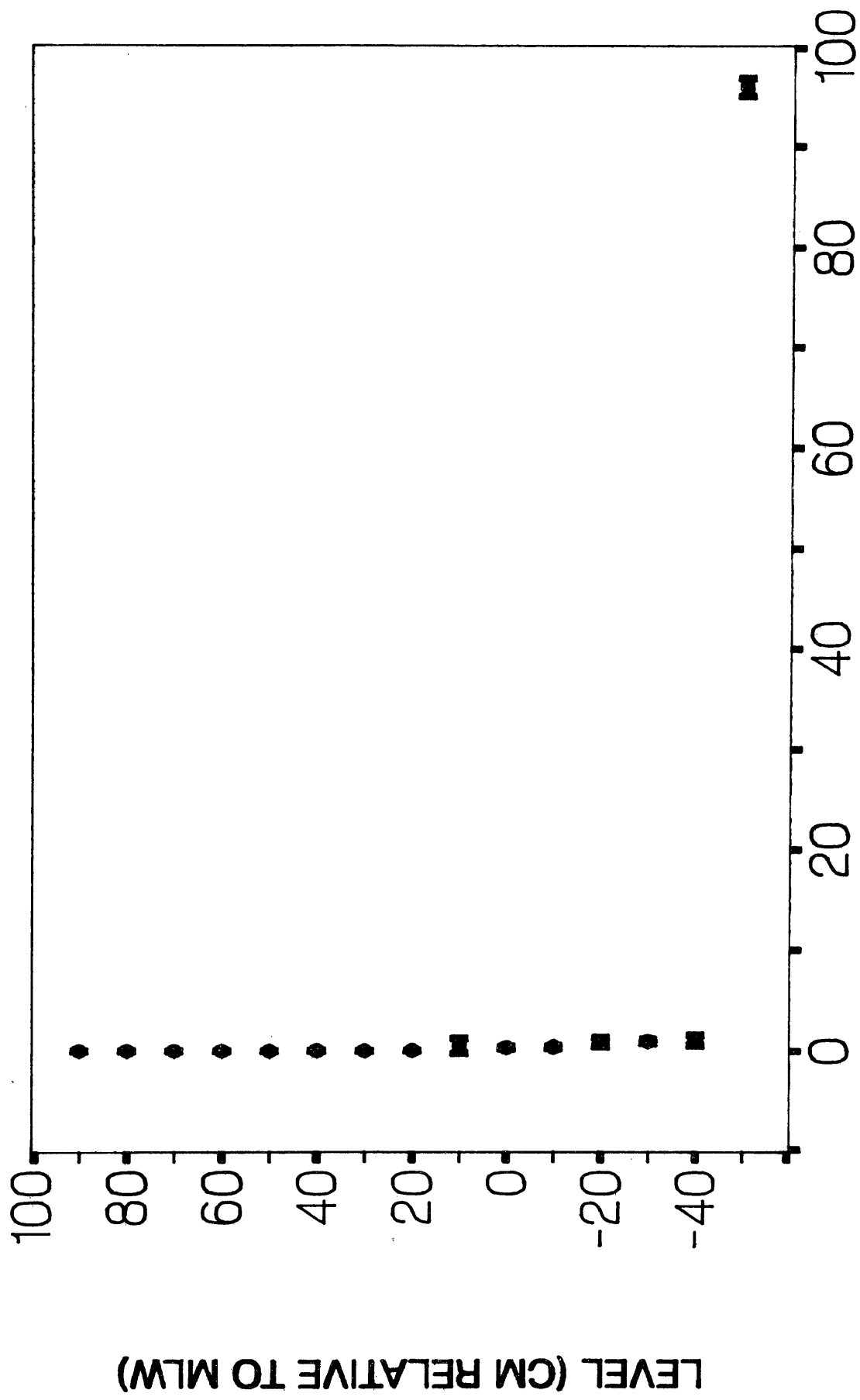


Table 5: Summary Statistics for settlement distribution.

Experiment S1

TH	MPS	SD	95% CONF. INTER.	
90	.08	.14	-.26	.42
80	.06	.10	-.18	.30
70	.02	.02	-.03	.07
60	.00	.00	.00	.00
50	.11	.09	-.13	.34
40	.39	.10	.13	.65
30	.70	.18	.25	1.16
20	.96	.21	.43	1.48
10	1.38	.57	-.03	2.79
0	1.76	.70	.03	3.49
-10	1.91	.78	-.04	3.86
-20	2.46	.39	1.50	3.42
-30	2.39	.28	1.70	3.08
-40	5.31	.24	4.70	5.92
-50	82.48	2.61	75.98	88.97

Experiment S2

TH	MPS	SD	95% CONF. INTER.	
90	1.69	2.93	-5.60	8.99
80	.13	.22	-.43	.69
70	.00	.00	.00	.00
60	.98	1.37	-2.43	4.38
50	.00	.00	.00	.00
40	.00	.00	.00	.00
30	.72	.17	.30	1.13
20	1.57	1.52	-2.19	5.34
10	2.50	3.00	-4.95	9.95
0	5.12	2.04	.06	10.18
-10	3.83	2.59	-2.61	10.26
-20	2.25	2.14	-3.07	7.58
-30	3.96	2.13	-1.33	9.25
-40	5.25	.17	4.83	5.68
-50	71.55	4.10	61.37	81.73

TH: Tidal Height (cm relative to MLW); MPS: Mean percent set;
SD: Standard deviation; 95% CONF. INTER: 95% confidence interval.

Table 6: Summary Statistics for settlement tubes, cont.

Experiment S3

TH	MPS	SD	95% CONF. INTER.	
90	.00	.00	.00	.00
80	.00	.00	.00	.00
70	.00	.00	.00	.00
60	.00	.00	.00	.00
50	.00	.00	.00	.00
40	.00	.00	.00	.00
30	.05	.06	-.08	.19
20	.16	.11	-.12	.43
10	1.62	.41	.59	2.65
0	1.66	1.10	-1.08	4.40
-10	2.45	1.18	-.49	5.39
-20	2.33	1.26	-.82	5.47
-30	3.00	.20	2.50	3.49
-40	4.45	2.04	-.60	9.51
-50	84.28	4.79	72.39	96.17

Experiment S4

TH	MPS	SD	95% CONF. INTER.	
90	.00	.00	.00	.00
80	.00	.00	.00	.00
70	.00	.00	.00	.00
60	.00	.00	.00	.00
50	.00	.00	.00	.00
40	.02	.03	-.07	.10
30	.00	.00	.00	.00
20	.04	.03	-.05	.12
10	.49	.73	-1.31	2.30
0	.30	.09	.08	.51
-10	.35	.08	.15	.55
-20	.87	.42	-.17	1.92
-30	.95	.18	.50	1.41
-40	1.06	.52	-.24	2.36
-50	95.91	.88	93.74	98.10

TH: Tidal Height (cm relative to MLW); MPS: Mean percent set;
SD: Standard deviation; 95% CONF. INTER: 95% confidence interval.

Table 7: Settlement statistics: Two-way ANOVA

Transformed Proportional Settlement by Tidal Height,
Experiment

SOURCE	SS	DF	MS	F	P
WITHIN	201.24	120	1.68		
CONSTANT	7982.46	1	7982.46	4759.94	.000
TH	76268.35	14	5447.74	3248.49	.000
EXP	.03	3	.01	>0.01	.999
TH BY EXP	1028.89	42	24.50	14.61	.000

TH: Tidal Height (cm relative to MLW); EXP: Experiment; DF: Degrees of freedom; SS: Sums of squares; MS: Mean square; F: F ratio; P: F probability.

Table 8: Settlement statistics: One-way ANOVA

Transformed Proportional Settlement by Tidal Height

EXPERIMENT S1

SOURCE:	DF	SS	MS	F	P
BETWEEN	14	3.28	0.23	578.1	0.0000
WITHIN	30	0.01	<0.001		
TOTAL	44	3.30			

EXPERIMENT S2

SOURCE:	DF	SS	MS	F	P
BETWEEN	14	2.56	0.18	41.5	0.0000
WITHIN	30	0.13	0.004		
TOTAL	44	2.69			

EXPERIMENT S3

SOURCE	DF	SS	MS	F	P
BETWEEN	14	3.61	0.58	293.0	0.0000
WITHIN	30	0.03	<0.001		
TOTAL	44	3.64			

EXPERIMENT S4

SOURCE	DF	SS	MS	F	P
BETWEEN	14	5.04	0.36	1020.0	0.0000
WITHIN	30	0.01	<0.001		
TOTAL	44	5.05			

DF: Degrees of freedom; SS: Sums of squares; MS: Mean square;
F: F ratio; P: F probability.

Post-settlement Survival

The overall larval settlement on the ceramic plates was non-uniform and patchy, with heavy gregariousness occurring on some plates while neighboring plates were not colonized. The density of spat per plate was very variable: thus the number of individuals composing a treatment was not controlled, and three times as many plates were usually needed to ensure a complete experimental design. Even so, Experiments R1 and R2 did not have sufficient plates with more than 15 spat plate⁻¹ to fulfill the six treatment, ten replicate matrix. For these experiments, the -25 cm level was removed from consideration and only seven replicates per treatment were employed.

The percent survival from the initial number of settlers, measured over 7-9 day periods, is summarized for Experiments R1-R4 in Tables 9-12, respectively. Figures 16-19 depict mean percent survival by time for each experiment. (In the following text, tables, and figures, all references to the age of spat refer to age since settlement: age 1 is set at the initial day of photosampling. Age is thus post-settlement age, not actual biological age.)

A three-way ANOVA was performed, testing transformed proportional settlement by date sampled, tidal level, and experiment (Table 13). All main effects are highly significant, as is the experiment x tidal level interaction term. A two-factor ANOVA performed for each experiment (transformed proportional settlement by date sampled and tidal level), presented in Table 14, indicates highly significant F ratios for all main factors, but nonsignificant values for all tidal level x sample day interaction terms except in Experiment R3, which was significant. One-way ANOVAs (transformed proportional settlement by tidal level) were

then performed at each sample date for each experiment (Table 15), and an SNK analysis performed where appropriate to distinguish significantly different groups (Figure 20). The relatively high standard deviations, which were proportional to the mean, indicate the rather high degree of variation within some of the samples. These high values, and the 95% confidence intervals which extended below zero, are characteristic of treatments in which extensive mortalities resulted in local extinctions of spat on many replicate plates (Experiments R2 and R3).

Treatments at the +75 and +50 cm levels were not included in the statistical analyses or graphics because no survival past the first sample date occurred during any experiment; however, it is important note the failure of recruitment at these levels.

The specific findings for each experiment will be individually addressed before the trends are summarized.

In Experiment R1, all oysters placed at the +75 and +50 cm levels died within the first week. Among the remaining treatments, highly significant differences in survival between exposure levels were found at all dates. Initial survival was greatest at the MLW level, and was significantly different from the +25 and -75 cm levels. Thereafter, the +25 cm level, which had the lowest initial survival, exhibited complete mortality and statistically remained different from the other two levels. The MLW level continued to have significantly higher survival until the recruits were 31 days old, at which time no statistical differences were detected. This was due to the relatively high standard deviations between plates: the MLW level had nearly twice the mean percent survival of the subtidal treatment.

At 31 days post-settlement age, the percent survival at the MLW level had decreased from an initial value of nearly 35% to 12%, while

survival at the -75 cm level declined from 15% to 7%; the rank order of the percent survival values was conserved throughout each sample period. All levels exhibited high initial mortalities with a subsequent flattening of the survival-time curve indicating a decrease in the mortality rate. This rate was very low for the -75 cm level: survival after 14 days was good. The oysters at the MLW level exhibited a steeper mortality curve, although it also tended to flatten out with time.

In Experiment R2, initiated eleven days after Experiment R1, significant differences in recruitment were found between levels during the first month (four samples), when the MLW level had greater survival than the mid-littoral or subtidal treatments. No differences were found after 59 days of growth, when there was very low survival and high standard deviations. Initial percent survival was universally low. Again, all spat at the high and mid littoral sites were killed within the first week, while the spat at the +25 cm level were exterminated after 14 days. Oysters at the -75 cm level were reduced to less than 1% of the initial numbers of settlers by 21 days post-settlement life, and only one plate harbored survivors at this time. The +25 and -75 cm levels never exhibited significant differences (and after the second sample day were not significantly different from zero). The MLW level oysters experienced a continuous decline of individuals from 13.6% to 3.1%. There were wide confidence intervals in this experiment due to 100% mortality which occurred on many plates by the first sample period (recruitment failure). The ranking of treatment level was consistent over time and followed the pattern of Experiment R1.

Tidal levels tested during Experiment R3 included the -25 cm level, but survival was measured for only four weeks. Significant differences

between levels were found at all sampled dates, but the SNK analysis indicates the existence of a complex of subgroups (the recruitment patterns are indistinct). Once again, many plates suffered early recruitment failures, and no survival occurred at the high or mid littoral sites.

The initial survival ranged from medium for the low littoral and sublittoral fringe levels to low for the subtidal levels, with only the +25 cm level being statistically different from the -75 cm level (the high and low survival values, respectively). After 14 days, only the intertidal and sublittoral fringe treatments were different from each other, and this pattern persisted throughout the experiment. The MLW treatment alone maintained significantly greater survival than zero. Complete mortality again occurred at +25 cm by age 21, and by age 30 the -25 cm level had less than 1% survival.

The ranking of the percent survival by sampled date was not consistent over time: level +25, with the highest initial survival, was soon reduced to zero, and the -25 cm level and -75 cm level exchanged rankings through the experimental period. The mortality slopes were generally low after the first week and followed the pattern described above except the +25 cm level. Spat at this level were probably dead (see Growth section below), but were still attached to the plate.

Experiment R4 exhibited an inconsistent pattern. With the exception of the upper two intertidal sites, the initial survival was high at all levels, with no significant differences between levels. After 14 days, the -75 cm level had become significantly different from the other three groups and had about half the mean percent survival. By age 21, only the +25 cm and -75 cm levels were significantly different, with the intertidal level having the greater survival. At the fifth

sampled date, the -75 cm level exhibited significantly lower survival than the +25 and MLW levels. After 60 days, the +25 level had significantly greater survival than the other three levels. Thus, in contrast to the previous experiments, spat at the +25 cm level during this period not only survived but showed the highest recruitment measured. Additionally, survival at the MLW level was not as high as that at the -25 cm level. The rank order was not consistent over time, with the -25 cm and MLW levels exchanging positions. The percent survival at the +25 cm level decreased from 35.8% to 13.3% in four weeks; the MLW level declined from 26.9% to 7.7%, the -25 cm level from 26.4% to 11%, and the -75 cm level, with an initial recruitment of 22.8%, ended with 5.2% of the initial spat surviving.

Table 9: Post-settlement Survival: Summary Statistics

Experiment R1

TH	AGE	MPS	SD	N	95% Conf. Interval	
+25	1	100.00	0.00	7	100.00	100.00
	8	9.93	12.10	7	-1.25	21.12
	15	0.49	1.30	7	-0.71	1.70
	24	0.00	0.00	7	0.00	0.00
	31	0.00	0.00	7	0.00	0.00
	40	0.00	0.00	7	0.00	0.00

0	1	100.00	0.00	7	100.00	100.00
	8	34.84	11.07	6	23.23	46.46
	15	20.38	9.38	7	11.70	29.06
	24	14.87	7.72	7	7.73	22.02
	31	12.30	9.04	7	3.94	20.66
	40	10.48	6.98	7	4.03	16.94

-75	1	100.00	0.00	7	100.00	100.00
	8	14.62	10.12	7	5.24	24.00
	15	8.04	5.62	7	2.84	13.24
	24	7.41	5.53	7	2.29	12.53
	31	6.78	5.75	7	1.46	12.09
	40	6.78	5.75	7	1.46	12.09

TH: Tidal Height (CM Relative to Mean Low Water); AGE: Age (Days) after Settlement; MPS: Mean Percent Survival; SD: Standard Deviation; N: Number of Replicate Plates; 95% Conf. Interval: 95 Percent Confidence Interval.

Table 10: Post-settlement Survival: Summary Statistics
Experiment R2

TH	AGE	MPS	SD	N	95% Conf. Interval	
+25	1	100.00	0.00	7	100.00	100.00
	8	1.02	1.89	7	-0.73	2.77
	15	0.00	0.00	7	0.00	0.00
	24	0.00	0.00	7	0.00	0.00
	31	0.00	0.00	7	0.00	0.00
	59	0.00	0.00	7	0.00	0.00

0	1	100.00	0.00	7	100.00	100.00
	8	13.57	12.50	7	2.01	25.14
	15	7.54	8.19	7	-0.03	15.12
	24	4.50	4.70	7	0.16	8.84
	31	3.19	4.26	6	-1.28	7.66
	59	2.07	3.88	7	-1.52	5.66

-75	1	100.00	0.00	7	100.00	100.00
	8	5.58	7.17	6	-1.94	13.11
	15	1.43	3.04	7	-1.38	4.24
	24	0.58	1.54	7	-0.84	2.00
	31	0.34	0.91	7	-0.50	1.18
	59	0.05	0.14	7	-0.08	0.18

TH: Tidal Height (CM Relative to Mean Low Water); AGE: Age (Days) after Settlement; MPS: Mean Percent Survival; SD: Standard Deviation; N: Number of Replicate Plates; 95% Conf. Interval: 95 Percent Confidence Interval.

Table 11: Post-settlement Survival: Summary Statistics

Experiment R3

TH	AGE	MPS	SD	N	95% Conf. Interval	
+25	1	100.00	0.00	10	100.00	100.00
	8	20.54	11.12	10	12.58	28.50
	15	0.23	0.72	10	-0.29	0.74
	22	0.00	0.00	10	0.00	0.00
	29	0.00	0.00	10	0.00	0.00

0	1	100.00	0.00	10	100.00	100.00
	8	16.54	14.10	10	6.46	26.63
	15	8.49	9.05	10	2.02	14.96
	22	5.71	6.77	10	0.87	10.56
	29	4.33	5.25	10	0.58	8.09

-25	1	100.00	0.00	9	100.00	100.00
	8	8.78	12.41	8	-1.59	19.16
	15	3.02	5.07	8	-1.22	7.26
	22	2.03	2.80	8	-0.31	4.37
	29	0.87	1.20	7	-0.25	1.98

-75	1	100.00	0.00	10	100.00	100.00
	8	6.62	9.17	10	0.06	13.18
	15	3.75	5.46	10	-0.16	7.66
	22	2.25	3.11	10	0.03	4.47
	29	1.47	2.16	10	-0.08	3.01
69	0.53	0.76	10	-0.01	1.08	

TH: Tidal Height (CM Relative to Mean Low Water); AGE: Age (Days) after Settlement; MPS: Mean Percent Survival; SD: Standard Deviation; N: Number of Replicate Plates; 95% Conf. Interval: 95 Percent Confidence Interval.

Table 12: Post-settlement Survival: Summary Statistics

Experiment R4

TH	AGE	MPS	SD	N	95% Conf. Interval	
+25	1	100.00	0.00	10	100.00	100.00
	8	35.82	17.64	10	23.20	48.44
	15	19.21	9.91	10	12.12	26.29
	22	16.62	9.17	10	10.06	23.17
	29	13.27	7.65	10	7.79	18.74
	60	11.48	7.86	10	5.86	17.10

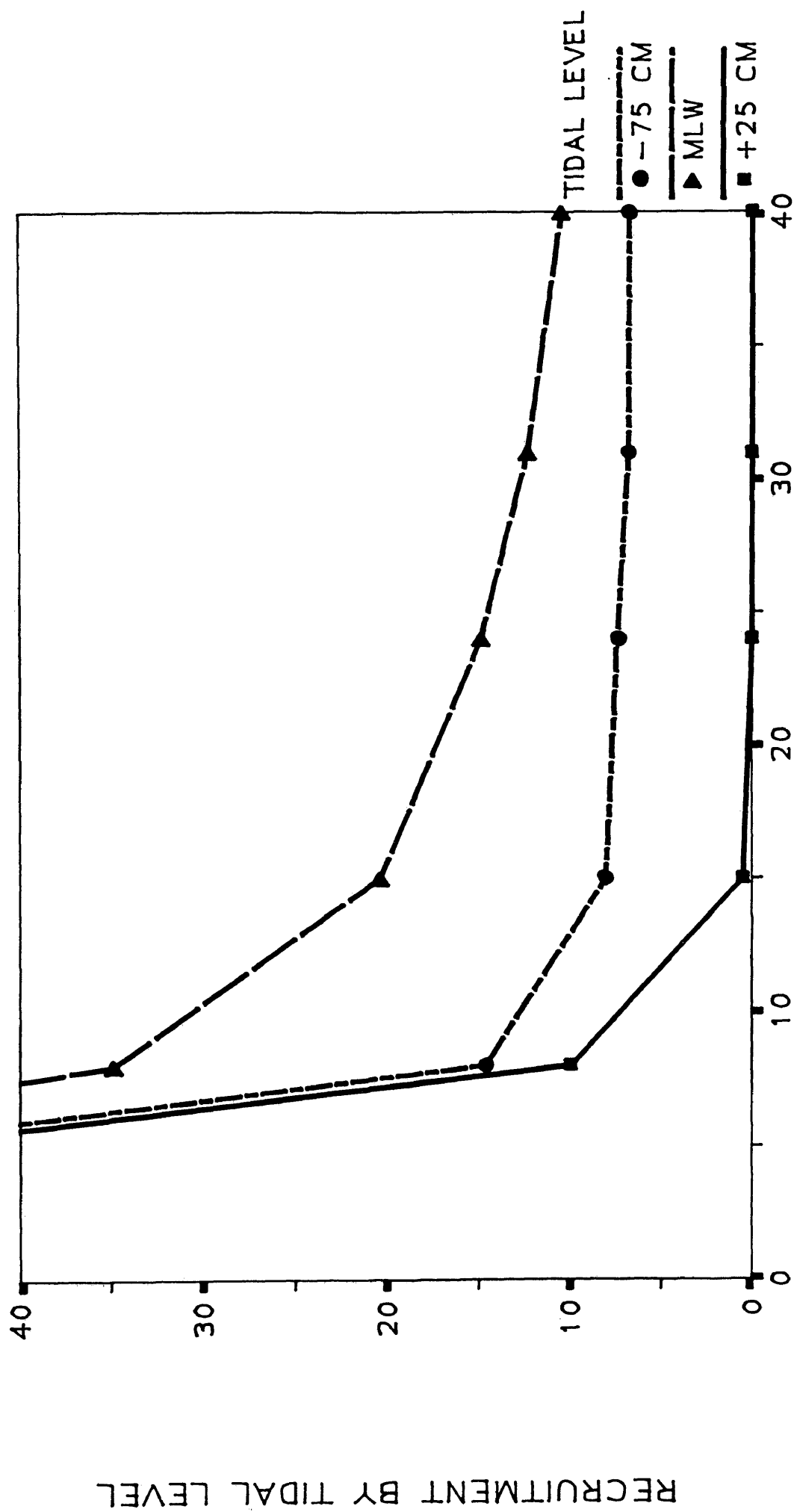
0	1	100.00	0.00	10	100.00	100.00
	8	26.94	8.91	10	20.57	33.31
	15	16.27	6.75	10	11.44	21.10
	22	11.19	6.77	10	6.34	16.03
	29	7.73	4.70	10	4.36	11.09
	60	6.54	4.48	10	3.33	9.74

-25	1	100.00	0.00	9	100.00	100.00
	8	26.37	14.08	8	14.59	38.14
	15	15.63	5.55	8	10.99	20.28
	22	13.52	3.93	7	9.89	17.16
	29	10.97	4.53	8	7.18	14.75
	60	7.85	5.11	9	3.92	11.78

-75	1	100.00	0.00	10	100.00	100.00
	8	22.79	8.65	10	16.60	28.98
	15	8.69	6.63	10	3.95	13.43
	22	6.65	5.52	9	2.40	10.89
	29	5.17	5.55	9	0.90	9.43
	60	4.55	5.16	10	0.86	8.24

TH: Tidal Height (CM Relative to Mean Low Water); AGE: Age (Days) after Settlement; MPS: Mean Percent Survival; SD: Standard Deviation; N: Number of Replicate Plates; 95% Conf. Interval: 95 Percent Confidence Interval.

Figure 16: Mean percent survival by post-settlement age.
Experiment R1. Tidal levels +25, MLW, and -75
are shown.



AGE (DAYS SINCE SETTLEMENT)

RECRUITMENT BY TIDAL LEVEL

Figure 17: Mean percent survival by post-settlement age.
Experiment R2. Tidal levels +25, MLW, and -75
are shown.

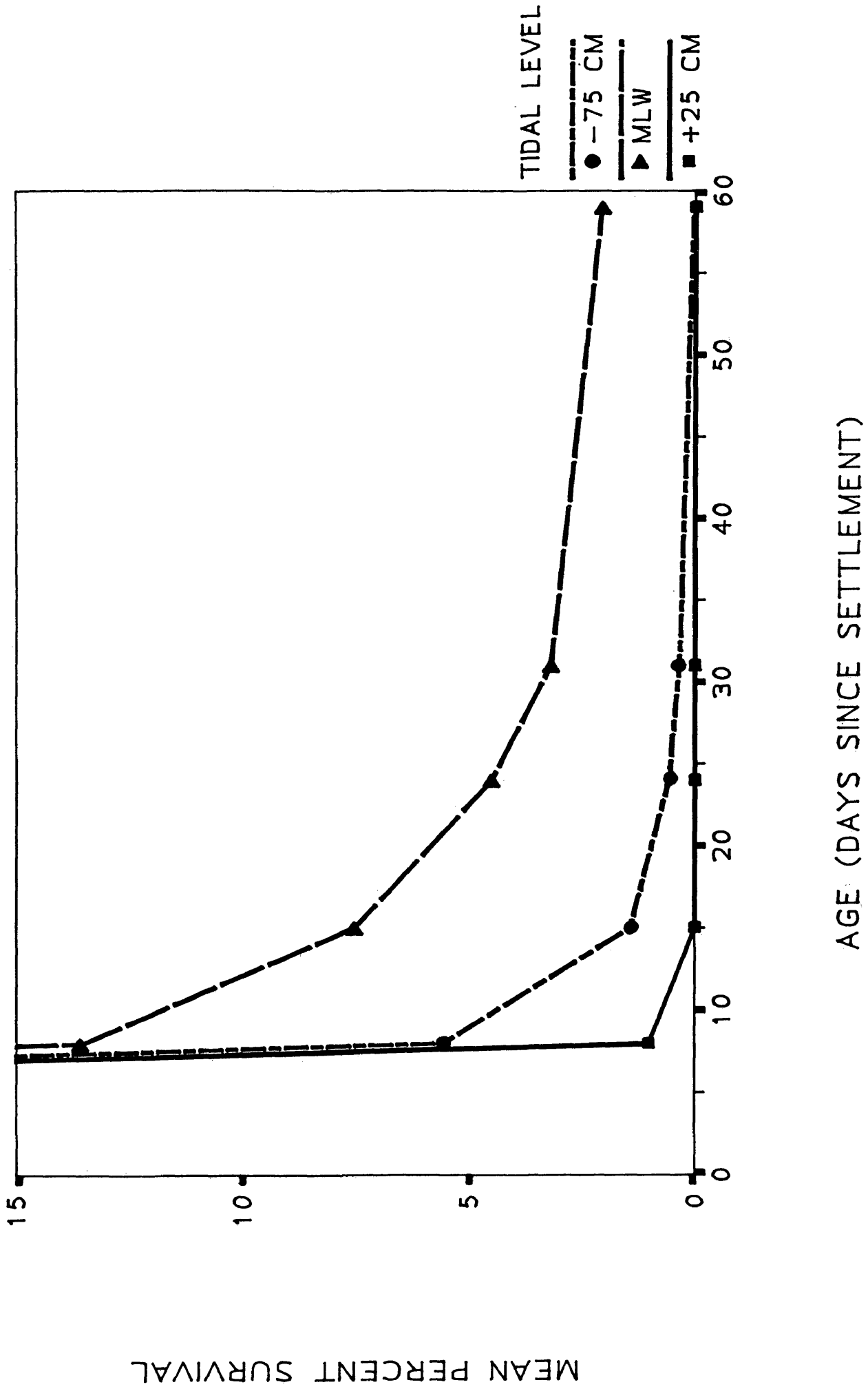
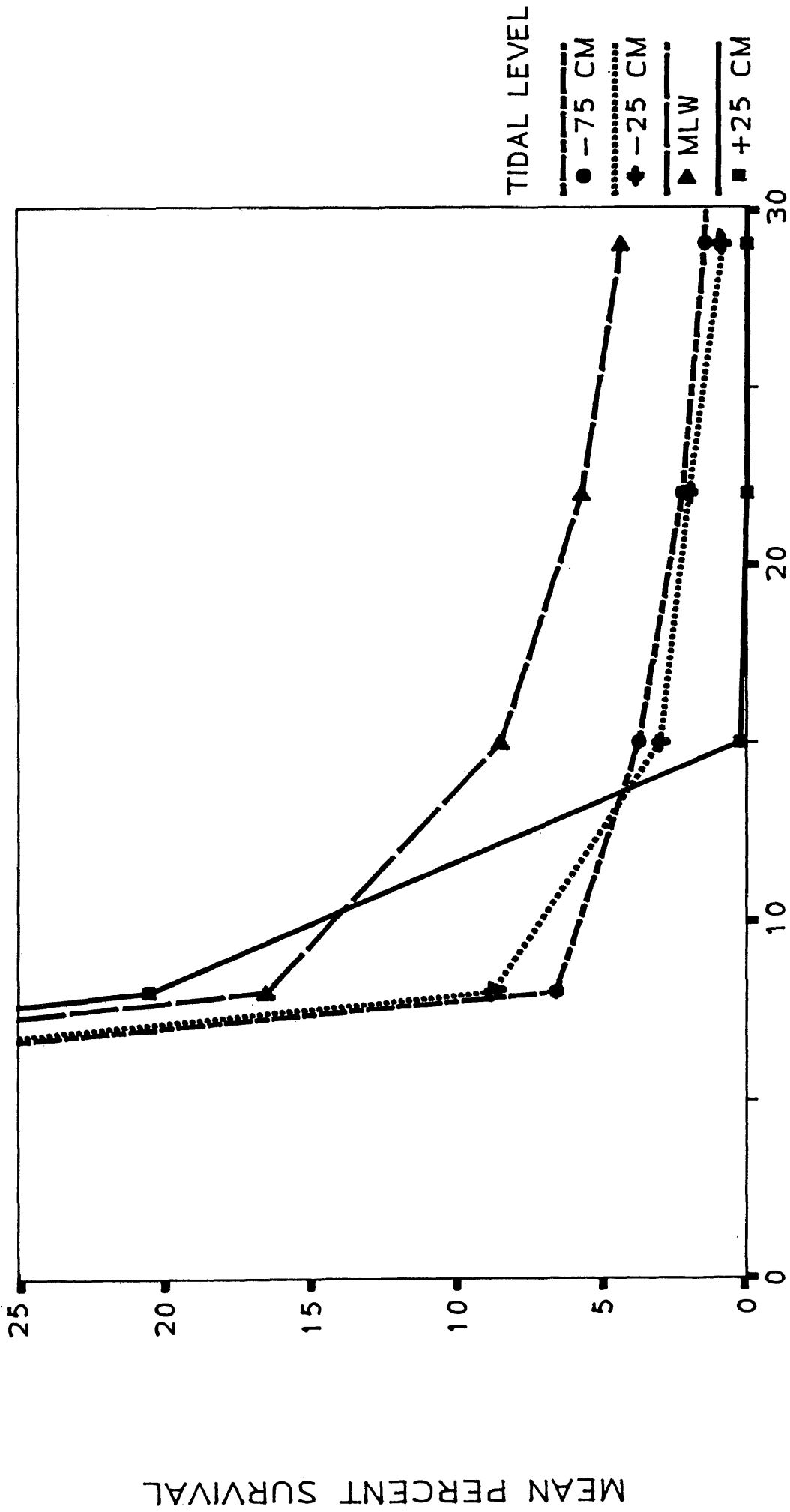
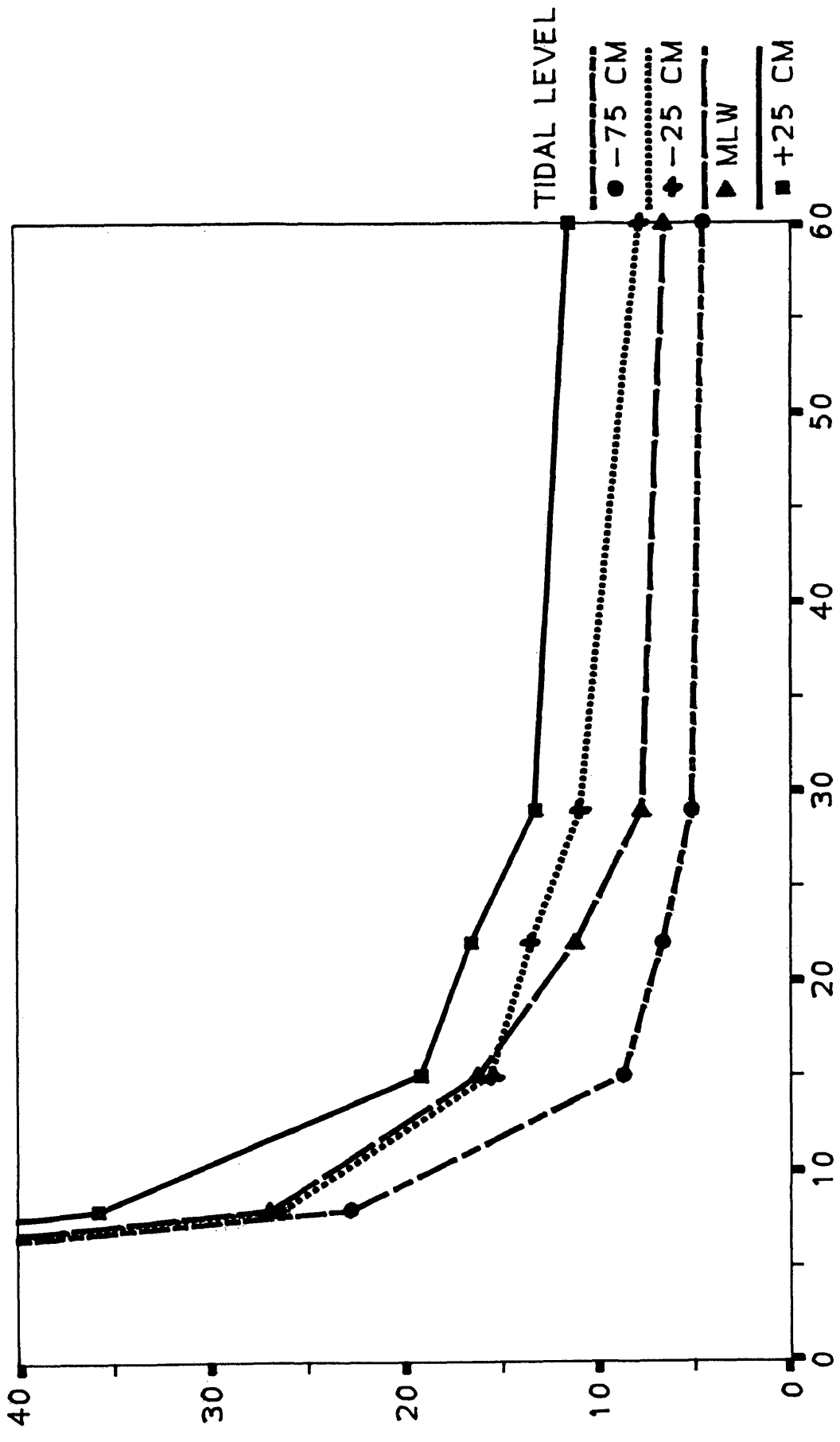


Figure 18: Mean percent survival by post-settlement age.
Experiment R3. Tidal levels +25, MLW, -25, and
-75 are shown.



AGE (DAYS SINCE SETTLEMENT)

Figure 19: Mean percent survival by post-settlement age.
Experiment R4. Tidal levels +25, MLW, -25, and
-75 are shown.



MEAN PERCENT SURVIVAL

AGE (DAYS SINCE SETTLEMENT)

Table 13: POST-SETTLEMENT SURVIVAL: THREE-WAY ANOVA
 Transformed Proportional Survival by Experiment, Tidal
 Height, Age

SOURCE	DF	F	P	SIG
Within	409			
Constant	1	618.01	0.000	***
EXP	3	108.55	0.000	***
TH	3	33.24	0.000	***
SD	3	25.41	0.000	***
EXP x TH	7	16.65	0.000	***
EXP x SD	9	1.17	0.311	NS
TH x SD	9	1.32	0.223	NS
EXP x TH x SD	21	1.37	0.126	NS

DF: Degrees of freedom; F: F Ratio; P: Probability value; SIG: Significance of P (***: $P < 0.001$; **: $0.001 < P < 0.010$; *: $0.010 < P < 0.050$; NS: Not significant); SD: Sample day; EXP: Experiment; TH: Tidal height.

TABLE 14: POST-SETTLEMENT SURVIVAL: TWO-WAY ANOVA
Transformed Proportional Survival by Tidal Height, Age

EXPERIMENT R1, TPS x TH(1,3), SD(2,5)

SOURCE	DF	F	P	SIG
Within	71			
Constant	1	332.76	0.000	***
TH	2	59.20	0.000	***
SD	3	11.06	0.000	***
TH x SD	6	0.67	0.669	NS

EXPERIMENT R2, TPS x TH(1,3), SD(2,5)

SOURCE	DF	F	P	SIG
Within	70			
Constant	1	45.15	0.000	***
TH	2	15.85	0.000	***
SD	3	4.01	0.011	**
TH x SD	6	0.42	0.866	NS

EXPERIMENT R3, TPS x TH(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	135			
Constant	1	147.19	0.000	***
TH	3	6.29	0.000	***
SD	3	18.12	0.000	***
TH x SD	9	3.25	0.000	***

EXPERIMENT R4, TPS x TH(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	133			
Constant	1	1370.31	0.000	***
TH	2	12.50	0.000	***
SD	3	31.50	0.000	***
TH x SD	9	0.42	0.924	NS

TPS: Transformed proportional survival; DF: Degrees of freedom; F: F Ratio; P: Probability value; Sig: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant); SD: Sample day; EXP: Experiment; TH: Tidal height.

TABLE 15: POST-SETTLEMENT SURVIVAL STATISTICS: ONE-WAY ANOVA
Transformed Proportional Survival by Tidal Height

EXPERIMENT R1: TPS x TH(1,3)

SD	N	F	P	SIG
2	20	6.73	0.007	**
3	21	26.91	0.000	***
4	21	28.34	0.000	***
5	21	18.38	0.000	***
6	21	18.45	0.000	***

EXPERIMENT R2: TPS x TH(1,3)

SD	N	F	P	SIG
2	20	3.49	0.054	NS
3	21	5.88	0.011	*
4	21	5.13	0.017	*
5	20	3.78	0.045	*
6	21	2.86	0.083	NS

EXPERIMENT R3: TPS x TH(1,4)

SD	N	F	P	SIG
2	38	3.89	0.017	*
3	38	3.74	0.020	*
4	38	4.36	0.011	*
5	37	4.83	0.007	**

EXPERIMENT R4: TPS x TH(1,4)

SD	N	F	P	SIG
2	38	1.88	0.152	NS
3	38	4.25	0.012	*
4	36	3.77	0.020	*
5	36	4.34	0.011	*
6	39	3.27	0.032	*

TPS: Transformed proportional survival; DF: Degrees of freedom; F: F Ratio; P: Probability value; Sig: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant); SD: Sample day; EXP: Experiment; TH: Tidal height.

Figure 20: Post-settlement survival by tidal height and age. Results of Student-Newman-Keuls test for the determination of significantly different proportional survival values between tidal levels for each date sampled. The significantly different groups are denoted by different stiple patterns. EXP: Experiment; MPS: Mean Percent Survival; SIG: Significance of ANOVA test.

Seasonal survival patterns

Statistical analyses were conducted to elucidate any similarities between levels across experiments; however, the results of this investigation must be tempered with the realization that factors such as genetic constitution, the composition of the fouling community, and density of settlers were not controlled in the experiments and thus their effects are unknown.

A comparison of the mean percent survival curves for each level (+25 to -75 cm) are given in Figures 21-24. Table 16 presents the results of two-way ANOVA test (transformed percent survival x experiment, sampled date) performed for each level, and all factors and interaction terms are significant. Table 17 gives the results of the one-way ANOVA for each sampled date, and Figure 25 the results of the SNK analyses.

The results of these comparisons reveal a more consistent pattern (with some indistinct SNK results). Survival at the +25 cm level occurred only in Experiment R4: all other spat placed at this treatment died within 14 days, and probably within the first week. At the MLW and -75 cm levels, percent survival during Experiments R1 and R4 were never significantly different, and both had a higher survival than Experiments R2 and R3, although the significance of these comparisons varied. At the -25 cm level, Experiments R3 and R4 were significantly different at each sampled date, with Experiment R4 having the higher survival (survival at this level was not measured in Experiments R1 or R2).

Figure 21: Seasonal percent survival by post-settlement age.
+25 cm level. Experiments R1 to R4 are shown.

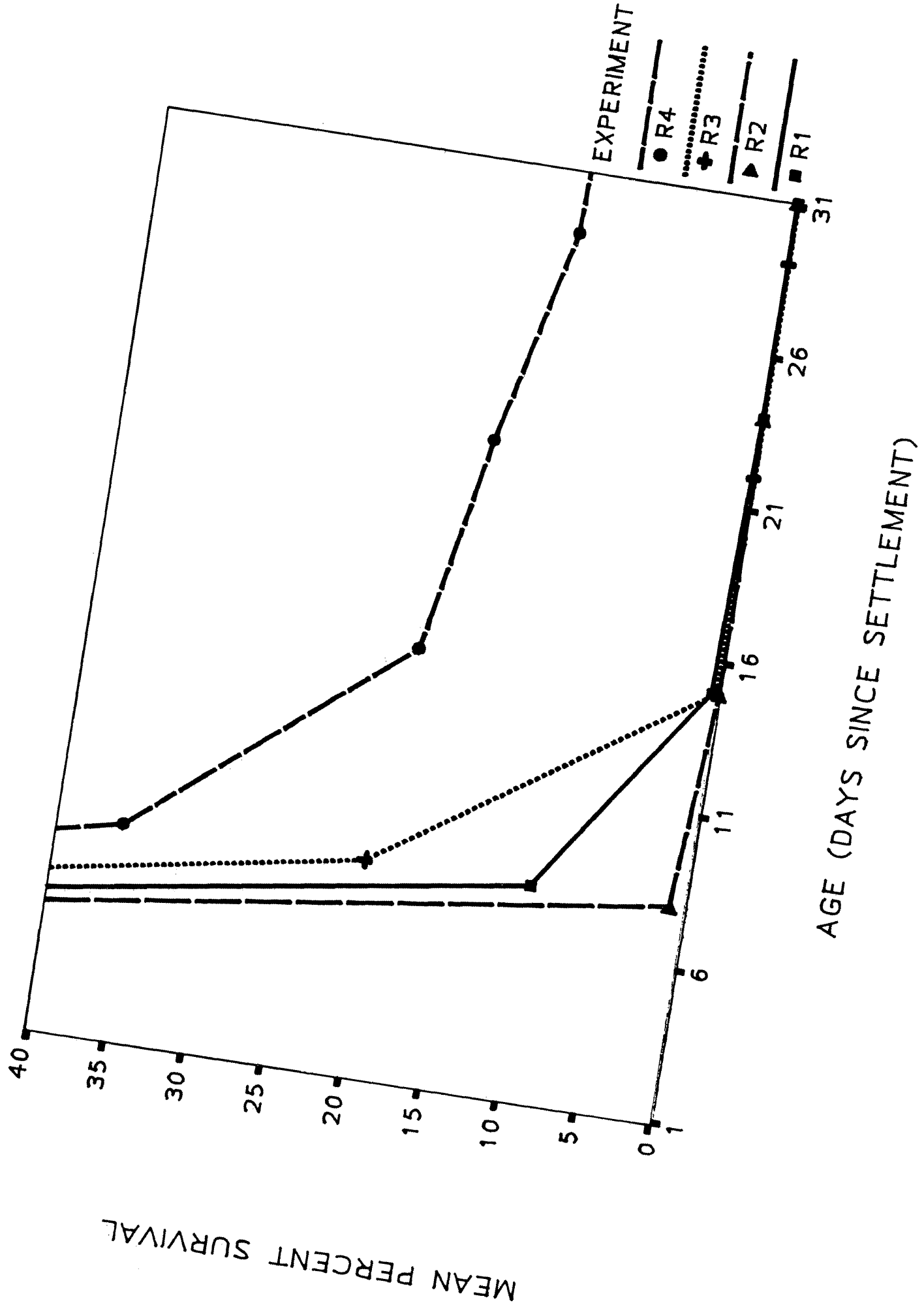
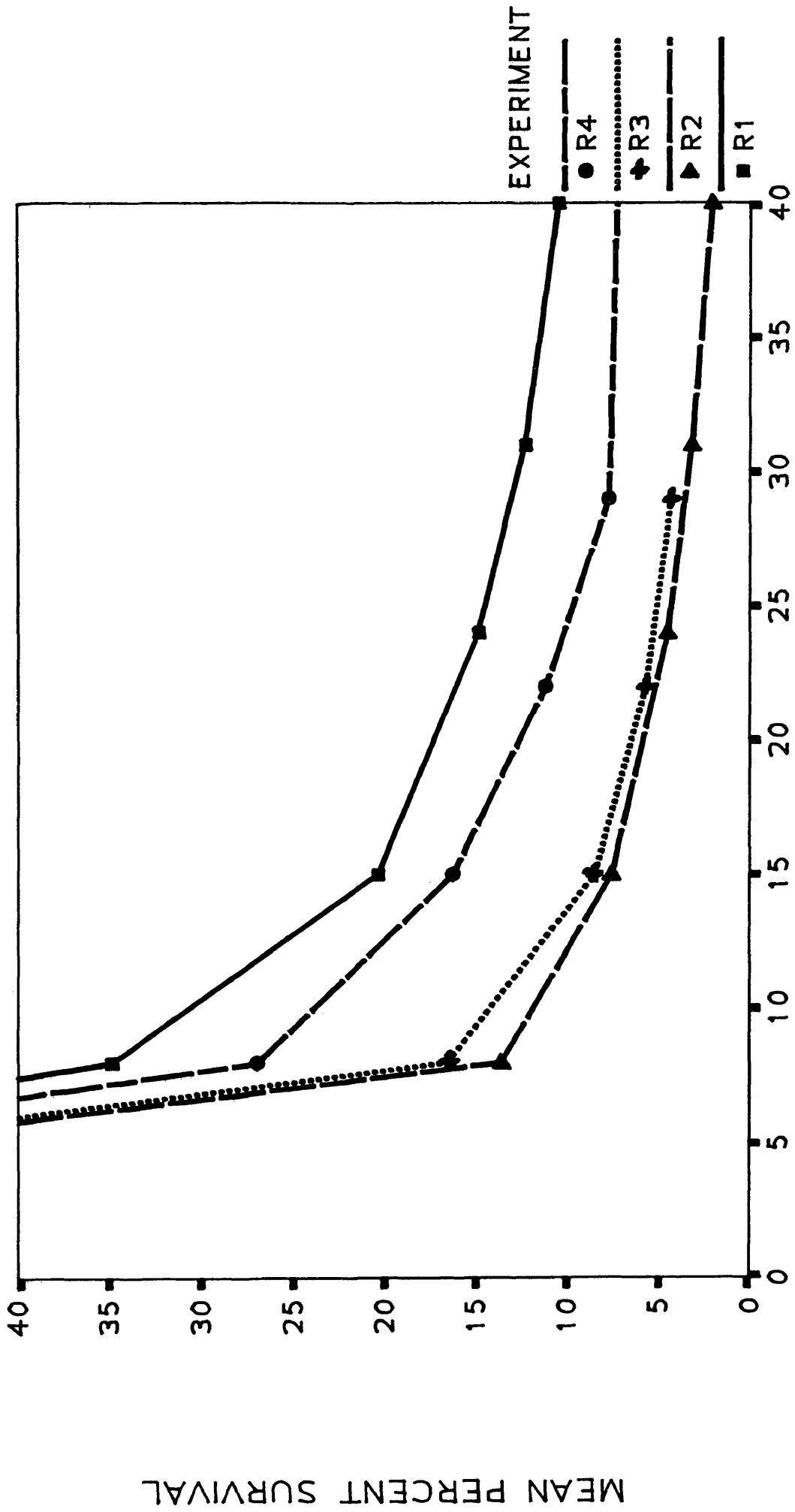


Figure 22: Seasonal percent survival by post-settlement age.
MLW cm level. Experiments R1 to R4 are shown.



AGE (DAYS SINCE SETTLEMENT)

Figure 23: Seasonal percent survival by post-settlement age.
-25 cm level. Experiments R3 and R4 are shown.

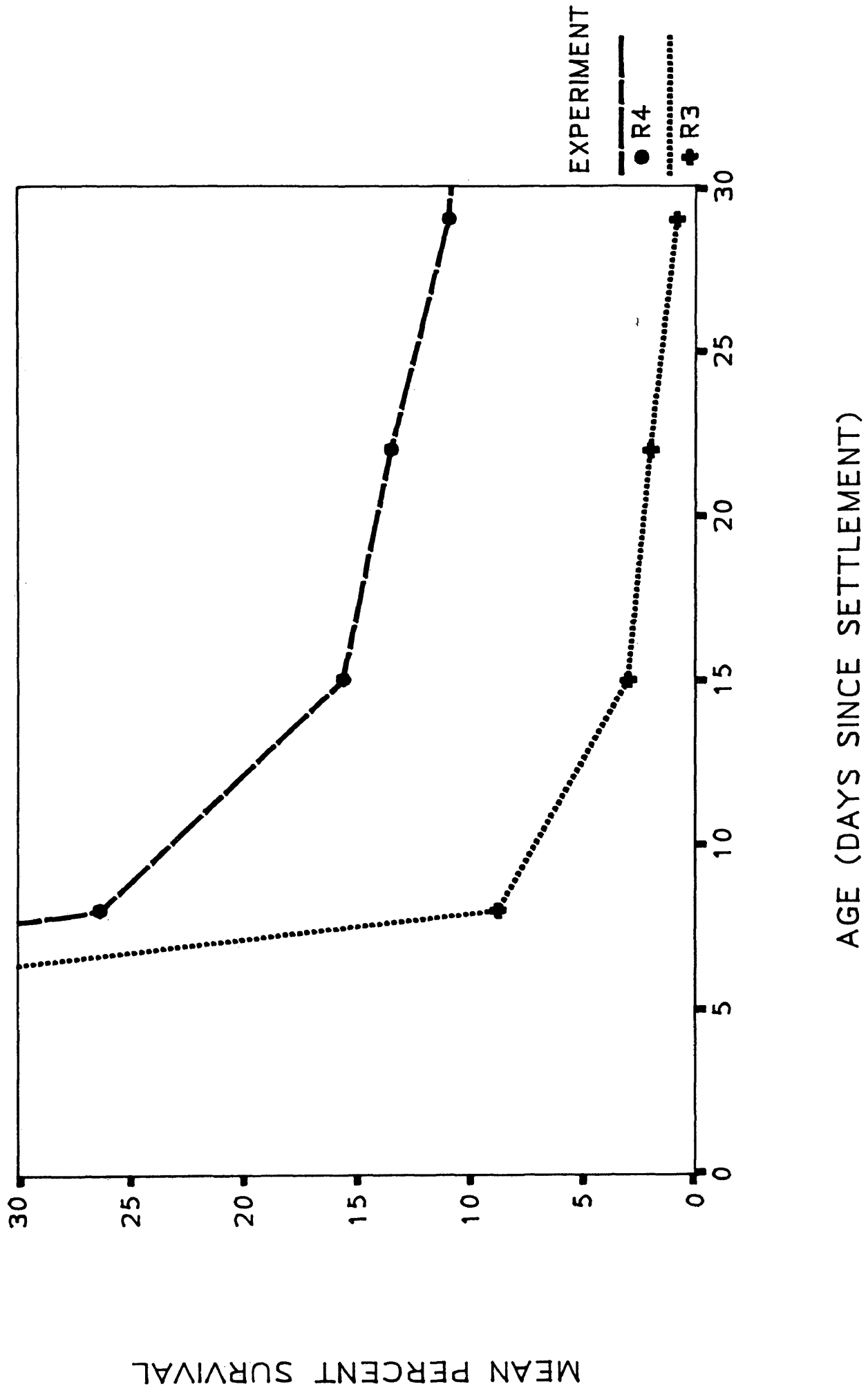
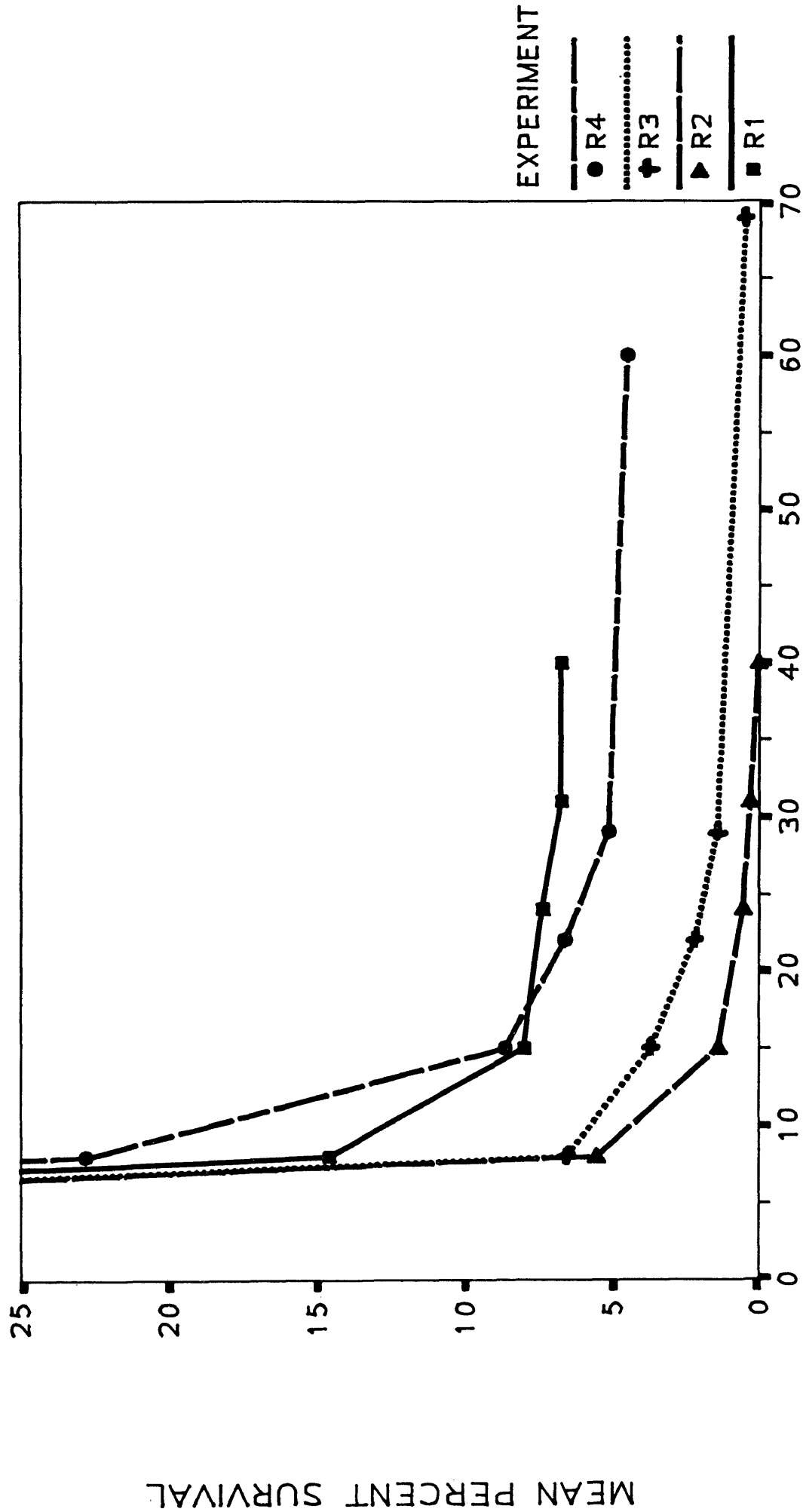


Figure 24: Seasonal percent survival by post-settlement age.
-75 cm level. Experiments R1 to R4 are shown.



AGE (DAYS SINCE SETTLEMENT)

TABLE 16: POST-SETTLEMENT SURVIVAL: TWO-WAY ANOVA
Transformed Proportional Survival by Experiment, Date

+25 cm, TPS x EXP(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	120			
Constant	1	321.04	0.000	***
EXP	2	133.18	0.000	***
SD	3	43.58	0.000	***
EXP x SD	9	5.29	0.000	***

MLW, TPS x EXP(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	118			
Constant	1	541.20	0.000	***
EXP	2	17.23	0.000	***
SD	3	14.26	0.000	***
EXP x SD	9	0.19	0.995	NS

-25 cm, TPS x EXP(3,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	54			
Constant	1	258.76	0.000	***
EXP	1	74.06	0.000	***
SD	3	5.57	0.002	**
EXP x SD	9	0.06	0.979	NS

-75 cm TPS x EXP(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	117			
Constant	1	216.55	0.000	***
EXP	3	19.09	0.000	***
SD	3	8.50	0.002	***
EXP x SD	9	0.92	0.507	NS

TPS: Transformed proportional survival; DF: Degrees of freedom; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant); SD: Sample date; EXP: Experiment.

TABLE 17: POST-SETTLEMENT SURVIVAL: ONE-WAY ANOVA
Transformed Proportional Survival by Experiment

+25 cm Level: TPS x EXP(1,4)

SD	N	F	P	SIG
2	34	17.63	0.000	***
3	34	64.71	0.000	***
4	34	88.34	0.000	***
5	34	91.96	0.000	***
6	34	69.53	0.000	***

MLW Level: TPS x EXP(1,4)

SD	N	F	P	SIG
2	33	4.55	0.001	**
3	34	4.81	0.007	**
4	34	4.24	0.013	*
5	33	3.93	0.018	*
6	24	6.90	0.005	**

-25 cm Level: TPS x EXP(3,4)

SD	N	F	P	SIG
2	16	9.81	0.007	**
3	16	24.87	0.000	***
4	15	33.44	0.000	***
5	15	44.79	0.000	***

-75 cm Level: TPS x EXP(1,4)

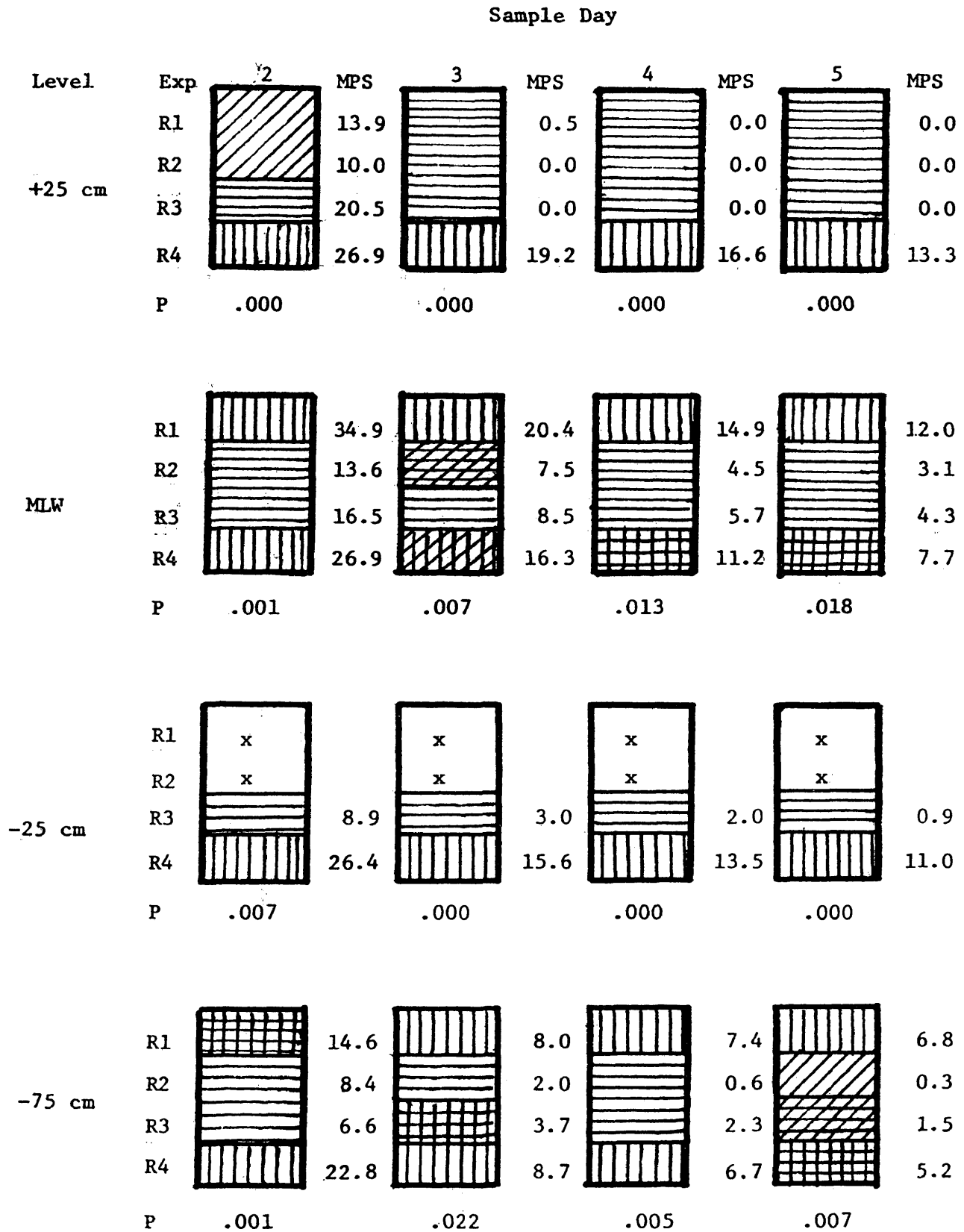
SD	N	F	P	SIG
2	33	7.12	0.001	**
3	34	3.71	0.022	*
4	34	5.34	0.005	**
5	33	4.95	0.007	**
6	34	7.99	0.001	**

TPS: Transformed proportional survival; N: Number of plates; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant); SD: Sample date; EXP: Experiment; TH: Tidal height.

Figure 25: Post-settlement survival by experiment and age. Results of Student-Newman-Keuls test for the determination of significantly different proportional survival values between levels for each date sampled. The significantly different groups are denoted by different stiple patterns. EXP: Experiment; MPS: Mean Percent Survival; SIG: Significance of ANOVA test.

SNK ANALYSIS

Mean Percent Survival - Experiment by Level



Instantaneous Mortality Rates

For each experiment, the mean daily percent mortality rate per sampling interval was computed. These data, along with the associated standard deviations, are presented in Table 20. In all cases, the mortality which occurred within the first week far exceeded that of any other period. The mortality rate also tended to decrease with time, falling to less than 1% day⁻¹ after the second week.

Survival Summary

In summary, post-settlement survival both within and between experiments was not uniform over the littoral-sublittoral zones. Recruitment failures always occurred at the +75 and +50 cm levels, and at the +25 cm level in Experiments R1, R2, and R3. In contrast, during Experiment R4 survival at the +25 cm level was high. The subtidal treatments tended to suffer higher mortalities than those at the MLW level, and these treatments often became statistically indistinguishable from zero. In Experiments R2 and R3, low overall recruitment coupled with heavy mortality reduced the number of plates bearing spat (thus influencing statistical results) and low yields were achieved. The survival rate was always lowest on the sample period following settlement, and survival over this interval never exceeded 40%.

Table 18: Mean daily mortality rate per sample interval.

E	TH	INTERVAL1		INTERVAL2		INTERVAL3		INTERVAL4		INTERVAL5	
		MMR	SD	MMR	SD	MMR	SD	MMR	SD	MMR	SD
R1	+25	12.87	1.73	1.35	1.69	0.06	0.	0.00	0.00	0.00	0.00
	MLW	9.31	1.58	1.80	0.89	0.61	0.40	0.37	0.36	0.20	0.30
	-75	12.20	1.45	0.94	0.73	0.07	0.12	0.09	0.16	0.00	0.00
R2	+25	14.14	0.27	0.15	0.27	0.00	0.00	0.00	0.00	0.00	0.00
	MLW	12.35	1.79	0.86	0.75	0.43	0.57	0.04	0.09	0.03	0.05
	-75	13.49	1.02	0.56	0.63	0.12	0.23	0.03	0.07	0.01	0.03
R3	+25	11.35	1.59	2.90	1.59	0.03	0.10	0.00	0.00	0.00	0.00
	MLW	11.92	2.01	1.15	1.10	0.40	0.46	0.20	0.28		
	-25	13.03	1.77	0.82	1.07	0.14	0.35	0.14	0.27		
	-75	13.34	1.31	0.41	0.57	0.21	0.38	0.11	0.18	0.03	0.05
R4	+25	9.17	2.52	2.37	1.61	0.37	0.37	0.48	0.37	0.06	0.07
	MLW	10.44	1.27	1.52	0.69	0.73	0.60	0.49	0.47	0.04	0.04
	-25	10.52	2.01	1.68	1.66	0.47	0.55	0.23	0.25	0.09	0.10
	-75	11.03	1.24	2.02	0.61	0.26	0.44	0.21	0.33	0.03	0.04

E: Experiment; TH: Tidal height; MMR: Mean daily percent mortality rate per sample interval; SD: Standard deviation.

Size

The size of spat were measured as area (cm^2) on each sampled day. Tables 19-22, contain the results summarized for each level per sampled day. Figures 26-29 show the mean size per level for each sampled day (note the ordinate scales).

The results of a three-way ANOVA (size x experiment, level, sampled date) are presented in Table 23. All main effects and interaction terms are highly significant. Significant F ratios are also found in the two-way ANOVA (size x level, sampled date) performed for each experiment except the interaction term in Experiment R2 (Table 24). Finally, Table 25 gives the results of the one-way ANOVA tests performed for each experiment on each sampled day, and the SNK results are graphically displayed in Figure 30.

The statistical tests were greatly fortified by the large number of individual spat measured; however, statistical differences delineated by the tests are not always of biological significance. For this reason, no size comparisons were made at the first day sampled (newly settled individuals); these are assumed to be of uniform area. Treatments which experienced complete mortality were removed from the analysis.

The one-way ANOVA test for Experiment R1 indicates significant differences in spat growth between treatment levels at all dates. After seven days of growth, spat at the MLW and +75cm levels were significantly larger than those at the +25 cm level. By the third sampled date, oysters at the -75 cm level had nearly twice the area as those grown at the MLW level, while the MLW and +25 cm grown oysters exhibited no significant differences in size; however, the +25 cm level

was represented by only one spat. At both 24 and 31 days post-settlement age, spat grown at the subtidal level continued to be twice the size of the intertidal spat. After 31 days of growth, the final mean size for the MLW spat was 0.656 cm^2 compared to 1.123 cm^2 for the subtidal treatment.

In Experiment R2, there were no survivors at the +25 cm level after the first week. Spat at the MLW and -75 cm levels had significantly different mean areas for the first two weeks but converged for the second two weeks. Initially, spat growing at the MLW level had achieved a much larger size than the spat at the subtidal level. This experiment suffered from low numbers of survivors, and the standard deviations were often greater than half of the mean. Final mean size for the MLW level was 0.529 cm^2 , while at the -75 cm level it was 0.460 cm^2 .

On SD2 of Experiment R3, there were significant differences between the mean sizes of spat at all treatment levels, with the MLW level having the greater size and the +25 level the least. By the next sampling date, the spat at the +25 cm level were extinct, while spat at the MLW level showed significantly greater size than those at the subtidal treatments. However, by the next week, growth rates of subtidally grown oysters had increased relative to those at the MLW level, and no difference between the levels was detected. By the final sampled date, the mean sizes of the subtidal spat surpassed that of oysters at the intertidal level: statistically only the sizes of the spat at the MLW level and the -75 cm level were different. Final areas achieved were 0.593 , 0.748 , and 0.950 cm^2 at the MLW, -25 and -75 cm levels, respectively.

In Experiment R4, the mean area of spat at the +25 cm level was significantly less than that of the other levels on each sampled day. Spat grown at the MLW and -25 cm levels were significantly smaller than those at the -75 cm level at SD8, but by SD15 all levels were different, with the mean size increasing with increasing depth. This pattern was repeated on the next sampled date, but only the +25 cm level oysters showed a significant difference in size. By the last sampled date, spat at the -25 cm level were significantly smaller than those grown at the MLW and -75 cm levels, and spat at all treatments were larger below the +25 cm level. The final sizes achieved were 0.195 cm^2 at +25 cm, 0.341 cm^2 at MLW, 0.273 cm^2 at -25 cm, and 0.348 cm^2 at -75 cm.

In summary, although the statistical significance varied, subtidal levels usually produced an equal or larger mean size of spat than those grown at MLW. The spat grown at +25 cm were always smaller than spat grown lower on the shore.

TABLE 19: SIZE SUMMARY STATISTICS

EXPERIMENT R1

TH	AGE	MSZ	SD	N	95% CONF.	INTER.
+25	1	0.0015	0.0008	20	0.0012	0.0019
	8	0.0032	0.0007	16	0.0028	0.0036
	15	0.0035	0.00	1		
0	1	0.0018	0.0005	208	0.0017	0.0019
	8	0.0088	0.0034	205	0.0083	0.0093
	15	0.0573	0.0241	120	0.0530	0.0617
	24	0.2866	0.1783	78	0.2464	0.3268
	31	0.6563	0.3166	53	0.5690	0.7436
	40	1.2740	0.6476	41	1.0696	1.4784
-75	1	0.0016	0.0005	53	0.0014	0.0017
	8	0.0091	0.0049	53	0.0077	0.0105
	15	0.1009	0.0545	29	0.0802	0.1217
	24	0.5512	0.3156	25	0.4209	0.6815
	31	1.1232	0.5814	22	0.8654	1.3809
	40	2.0116	1.0388	21	1.5388	2.4845

TH: Tidal height (cm relative to MLW); AGE: Age (Days) from Settlement;
MSZ: Mean Area (cm²); SD: Standard Deviation; N: Number of Spat;
95% CONF. INTER.: 95 Percent Confidence Interval.

TABLE 20: SIZE SUMMARY STATISTICS

EXPERIMENT R2

TH	AGE	MSZ	SD	N	95% CONF. INTER.	
+25	1	0.0006	0.0001	5	0.0005	0.0006
	8	0.0011	0.0004	5	0.0006	0.0015
MLW	1	0.0008	0.0002	108	0.0008	0.0008
	8	0.0137	0.0054	188	0.0129	0.0145
	15	0.0507	0.0335	102	0.0441	0.0573
	24	0.1566	0.1062	56	0.1282	0.1850
	31	0.5199	0.4189	18	0.3116	0.7282
	59	2.6195	1.4808	6	1.0655	4.1734
-75	1	0.0006	0.0002	20	0.0005	0.0007
	8	0.0063	0.0037	117	0.0056	0.0070
	15	0.0214	0.0127	46	0.0176	0.0251
	24	0.1284	0.0958	22	0.0859	0.1708
	31	0.4598	0.3642	13	0.2397	0.6799
	59	3.9836	3.7993	2	-30.1516	38.1188

TH: Tidal height (cm relative to MLW); AGE: Age (Days) from Settlement;
MSZ: Mean Area (cm²); SD: Standard Deviation; N: Number of Spat;
95% CONF. INTER.: 95 Percent Confidence Interval.

TABLE 21: SIZE SUMMARY STATISTICS

EXPERIMENT R3

TH	AGE	MSZ	SD	N	95% CONF.	INTER.
+25	1	0.0009	0.0003	267	0.0009	0.0009
	8	0.0018	0.0009	267	0.0017	0.0019
	15	0.0006	0.00	1		
MLW	1	0.0011	0.0003	107	0.0010	0.0011
	8	0.0140	0.0069	347	0.0133	0.0147
	15	0.1162	0.0677	128	0.1044	0.1281
	22	0.2587	0.1251	69	0.2287	0.2888
	29	0.5925	0.2823	47	0.5096	0.6754
-25	1	0.0008	0.0003	149	0.0008	0.0008
	8	0.0087	0.0051	149	0.0078	0.0095
	15	0.0715	0.0475	55	0.0586	0.0843
	22	0.2986	0.2003	32	0.2264	0.3708
	29	0.7476	0.4664	13	0.4658	1.0295
-75	1	0.0010	0.0003	132	0.0009	0.0010
	8	0.0118	0.0077	250	0.0109	0.0128
	15	0.0790	0.0761	145	0.0665	0.0915
	22	0.3284	0.2572	87	0.2736	0.3833
	29	0.9501	0.5612	41	0.7729	1.1272
	69	2.3941	1.4164	16	1.6394	3.1489

TH: Tidal height (cm relative to MLW); AGE: Age (Days) from Settlement;
MSZ: Mean Area (cm²); SD: Standard Deviation; N: Number of Spat;
95% CONF. INTER.: 95 Percent Confidence Interval.

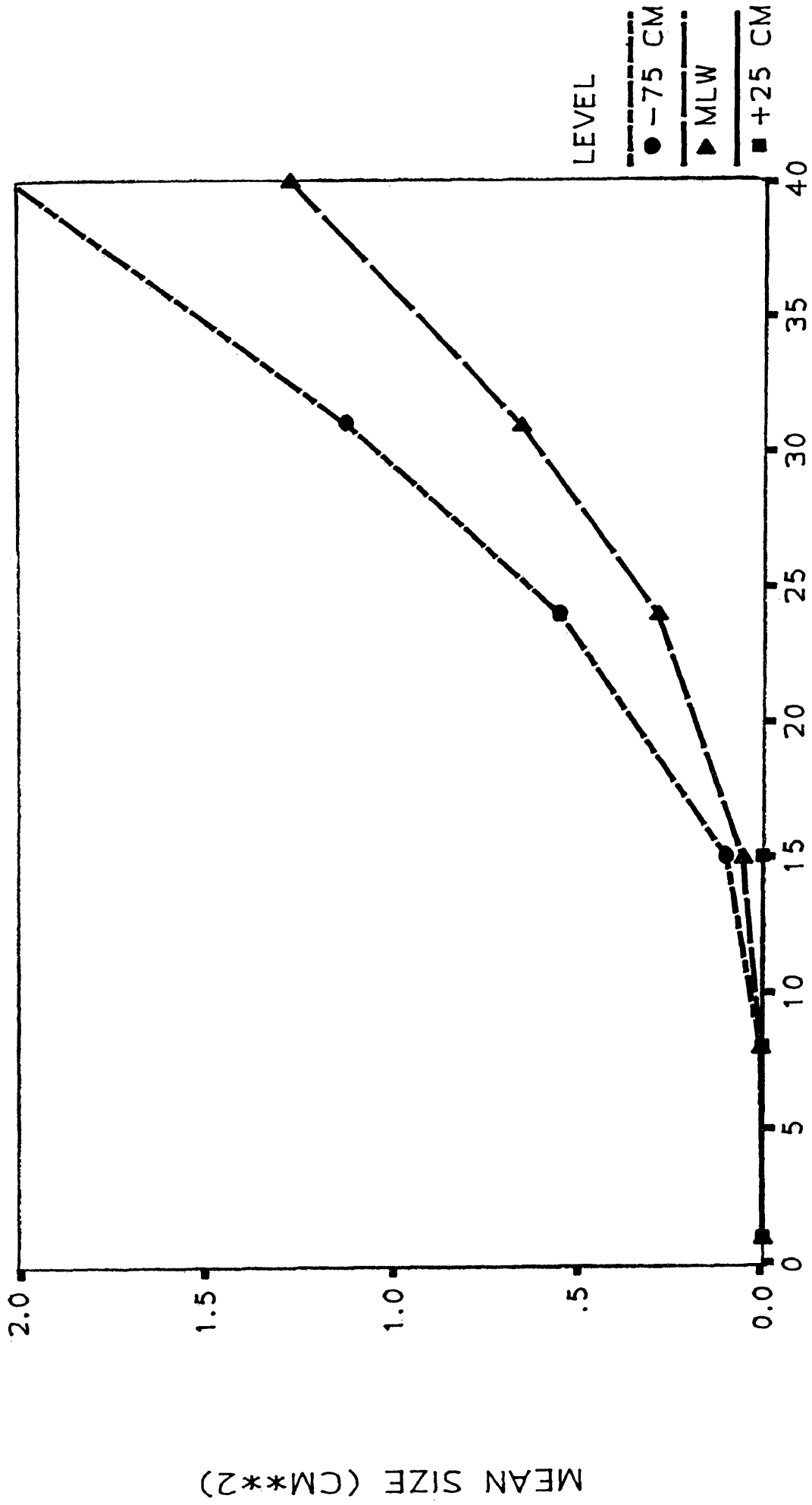
TABLE 22: SIZE SUMMARY STATISTICS

EXPERIMENT R4

TH	AGE	MSZ	SD	N	95% CONF. INTER.	
+25	1	0.0018	0.0005	242	0.0018	0.0019
	8	0.0042	0.0019	266	0.0040	0.0045
	15	0.0243	0.0111	172	0.0226	0.0259
	22	0.0620	0.0277	141	0.0574	0.0666
	29	0.1935	0.1055	110	0.1735	0.2134
	60	0.5543	0.2508	86	0.5006	0.6081
0	1	0.0015	0.0006	404	0.0015	0.0016
	8	0.0136	0.0055	407	0.0131	0.0141
	15	0.0486	0.0287	243	0.0450	0.0522
	22	0.1745	0.0977	142	0.1583	0.1907
	29	0.3614	0.1665	97	0.3278	0.3949
	60	0.9818	0.4205	70	0.8816	1.0821
-25	1	0.0011	0.0004	202	0.0010	0.0011
	8	0.0130	0.0056	162	0.0121	0.0139
	15	0.0593	0.0390	99	0.0515	0.0671
	22	0.1471	0.0964	60	0.1222	0.1720
	29	0.2733	0.2063	57	0.2186	0.3281
	60	0.8543	0.5797	41	0.6713	1.0373
-75	1	0.0015	0.0004	219	0.0015	0.0016
	8	0.0176	0.0072	220	0.0166	0.0186
	15	0.0745	0.0347	102	0.0677	0.0813
	22	0.1549	0.0876	63	0.1328	0.1769
	29	0.3475	0.2004	40	0.2834	0.4116
	60	1.0017	0.5197	31	0.8111	1.1924

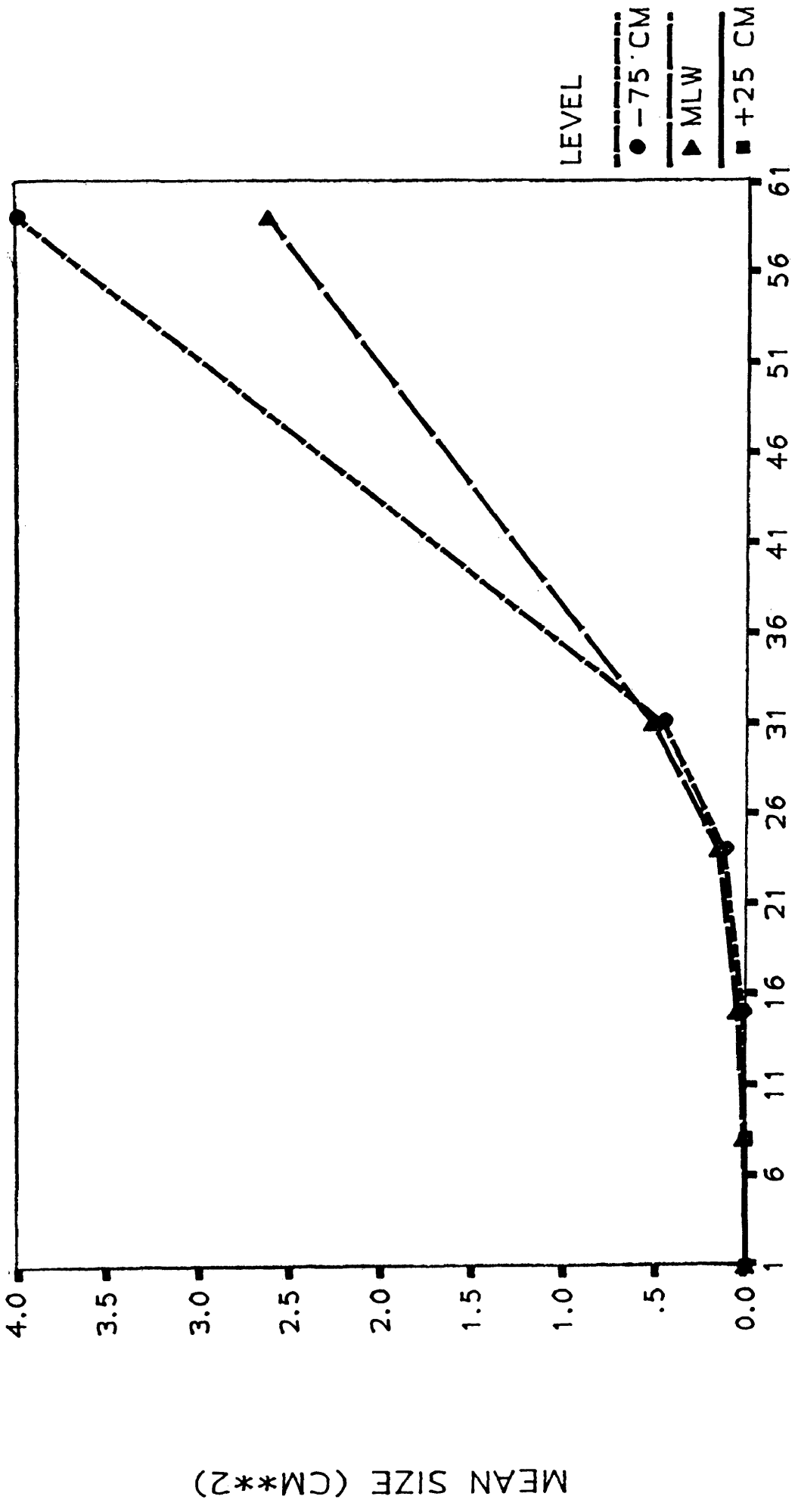
TH: Tidal height (cm relative to MLW); AGE: Age (Days) from Settlement;
MSZ: Mean Area (cm²); SD: Standard Deviation; N: Number of Spat;
95% CONF. INTER.: 95 Percent Confidence Interval.

Figure 26: Mean size (cm^2) by post-settlement age.
Experiment R1. Tidal levels +25, MLW, and -75
are shown.



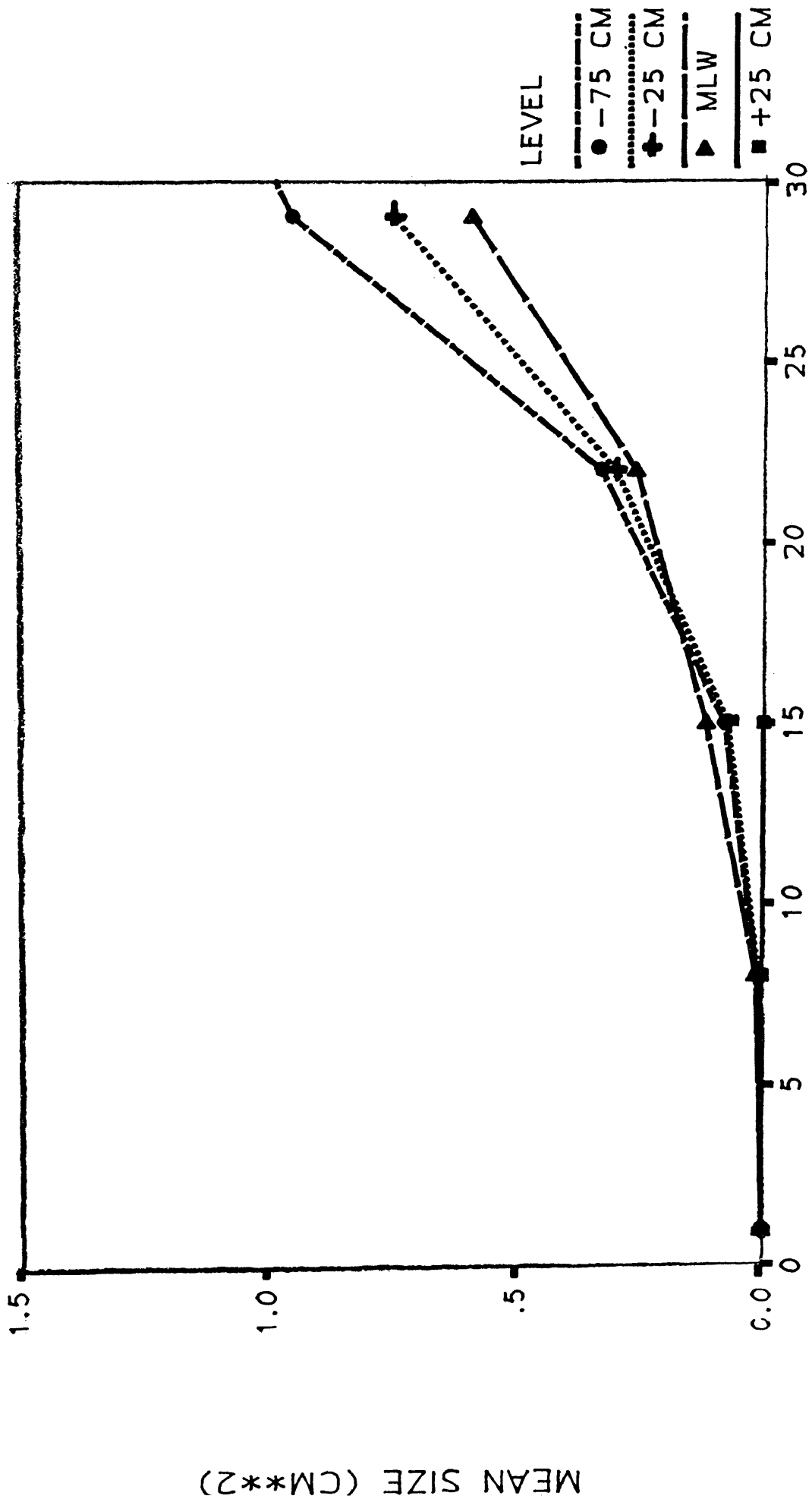
AGE (DAYS SINCE SETTLEMENT)

Figure 27: Mean size (cm^2) by post-settlement age.
Experiment R2. Tidal levels +25, MLW, and -75
are shown.



AGE (DAYS SINCE SETTLEMENT)

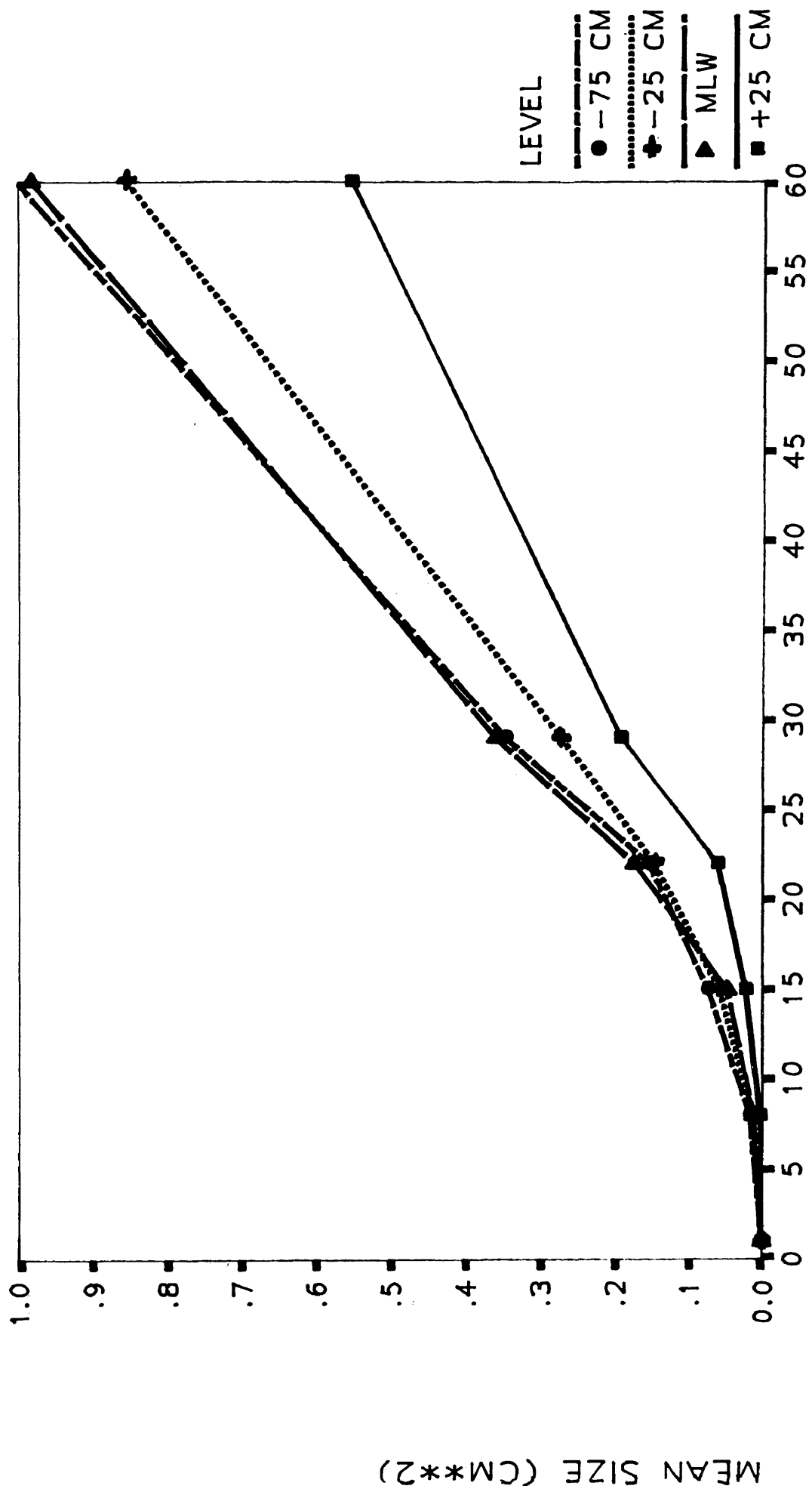
Figure 28: Mean size (cm^2) by post-settlement age.
Experiment R3. Tidal levels +25, MLW, -25, and
-75 are shown.



AGE (DAYS SINCE SETTLEMENT)

MEAN SIZE (CM**2)

Figure 29: Mean size (cm^2) by post-settlement age.
Experiment R4. Tidal levels +25, MLW, -25, and
-75 are shown.



AGE (DAYS SINCE SETTLEMENT)

TABLE 23: SIZE STATISTICS: THREE-WAY ANOVA
 MSZ x EXP(1,4), TH(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	5014			
Constant	1	58.10	0.000	***
EXP	3	28.91	0.000	***
TH	3	49.73	0.000	***
SD	3	54.20	0.000	***
EXP x TH	7	36.05	0.000	***
EXP x SD	9	14.73	0.000	***
TH x SD	9	20.60	0.000	***
EXP x TH x SD	14	21.73	0.000	***

MSZ: Mean size (cm²); SD: Sample date; EXP: Experiment; Tidal height; DF: Degrees of freedom; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant).

TABLE 24: SIZE STATISTICS: TWO-WAY ANOVA
Mean Size by Tidal Height, Date

EXPERIMENT R1: MSZ x TH(1,3), SD(2,5)

SOURCE	DF	F	P	SIG
Within	592			
Constant	1	17.85	0.000	***
TH	2	56.82	0.000	***
SD	3	65.11	0.000	***
TH x SD	4	25.59	0.000	***

EXPERIMENT R2: MSZ x TH(1,3), SD(2,5)

SOURCE	DF	F	P	SIG
Within	558			
Constant	1	110.13	0.000	***
TH	2	3.30	0.037	*
SD	3	158.45	0.011	*
TH x SD	3	0.92	0.431	NS

EXPERIMENT R3: MSZ x TH(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	1617			
Constant	1	58.02	0.000	***
TH	3	30.87	0.000	***
SD	3	52.07	0.000	***
TH x SD	7	23.46	0.000	***

EXPERIMENT R4: MSZ x TH(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	2365			
Constant	1	5453.59	0.000	***
TH	3	168.87	0.000	***
SD	3	1283.22	0.000	***
TH x SD	7	35.94	0.000	***

MSZ: Mean size (cm²); TH: Tidal height. SD: Sample date DF: Degrees of freedom; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant);

TABLE 25: SIZE STATISTICS: ONE-WAY ANOVA
Mean Size by Tidal Height

EXPERIMENT R1 ANOVA = MSZ x TH(1,3)

SD	N	F	F	SIG
2	273	18.05	0.000	***
3	149	23.30	0.000	***
4	102	27.68	0.000	***
5	74	20.10	0.000	***

EXPERIMENT R2 ANOVA = MSZ x TH(1,3)

SD	N	F	F	SIG
TH(2,3) 2	304	169.8	0.000	***
3	147	33.15	0.000	***
4	77	1.17	0.281	NS
5	31	0.17	0.681	NS

EXPERIMENT R3 ANOVA = MSZ x TH(1,4)

SD	N	F	F	SIG
2	1012	232.80	0.000	***
TH(2,4) 3	327	12.90	0.000	***
TH(2,4) 4	187	2.16	0.118	NS
TH(2,4) 5	99	7.27	0.001	**

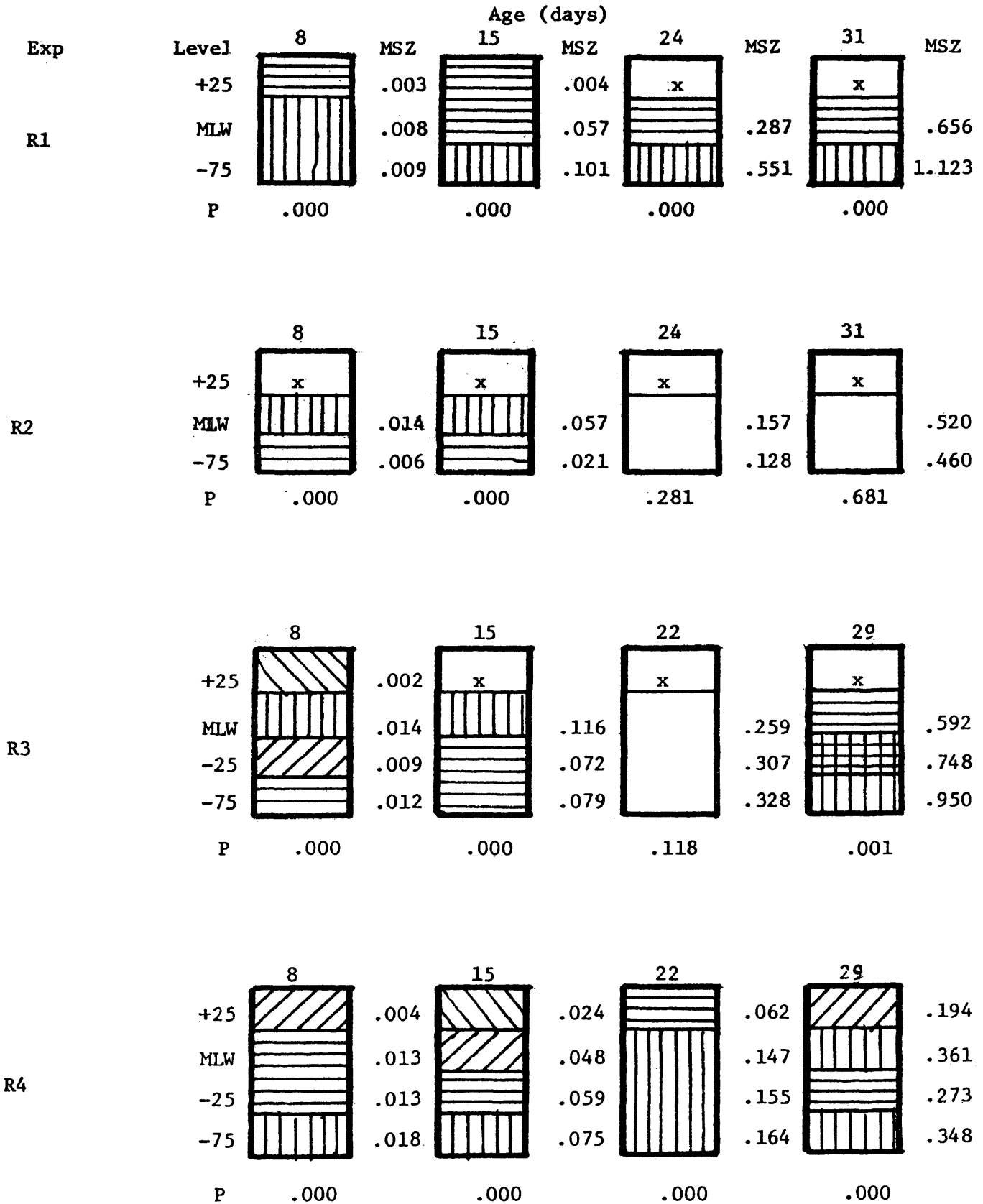
EXPERIMENT R4 ANOVA = MSZ x TH(1,4)

SD	N	F	F	SIG
2	990	283.10	0.000	***
3	578	74.96	0.000	***
4	388	48.57	0.000	***
5	302	21.08	0.000	***

MSZ: Mean size (cm²); TH: Tidal height; DF: Degrees of freedom; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant);

Figure 30: Mean size by experiment and age. Results of Student-Newman-Keuls test for the determination of significantly different mean size values between levels for each date sampled. The significantly different groups are denoted by different stiple patterns. EXP: Experiment; MSZ: Mean Size; SIG: Significance of ANOVA test.

SNK ANALYSIS
Mean Size (cm²) - Level by Experiment



Seasonal Sizes

The sizes achieved by spat at each treatment level were compared across experiments in an analogous fashion to the seasonal percent survival comparisons. Thus, the same constraints apply for interpreting the results. The mean sizes per tidal level are shown in Figures 31-35.

Two-way ANOVA's testing mean size x experiment, sampled day indicate significant differences for all main effects and interaction terms except for the +25 cm level, where only sampled date was significant. These results are presented in Table 26. The one-way analyses conducted for each level on each sampled date are presented in Table 27, and the corresponding SNK analyses are displayed in Figure 35. Spat sizes were significantly different across all experiments except -25 cm, sampled date 3 (Experiments 3 and 4 only were compared).

At the +25 cm level, comparisons were only made at SD2 since only one survivor occurred for Experiments R1 and R3, and none during Experiment R2. Thus, all experiments were different.

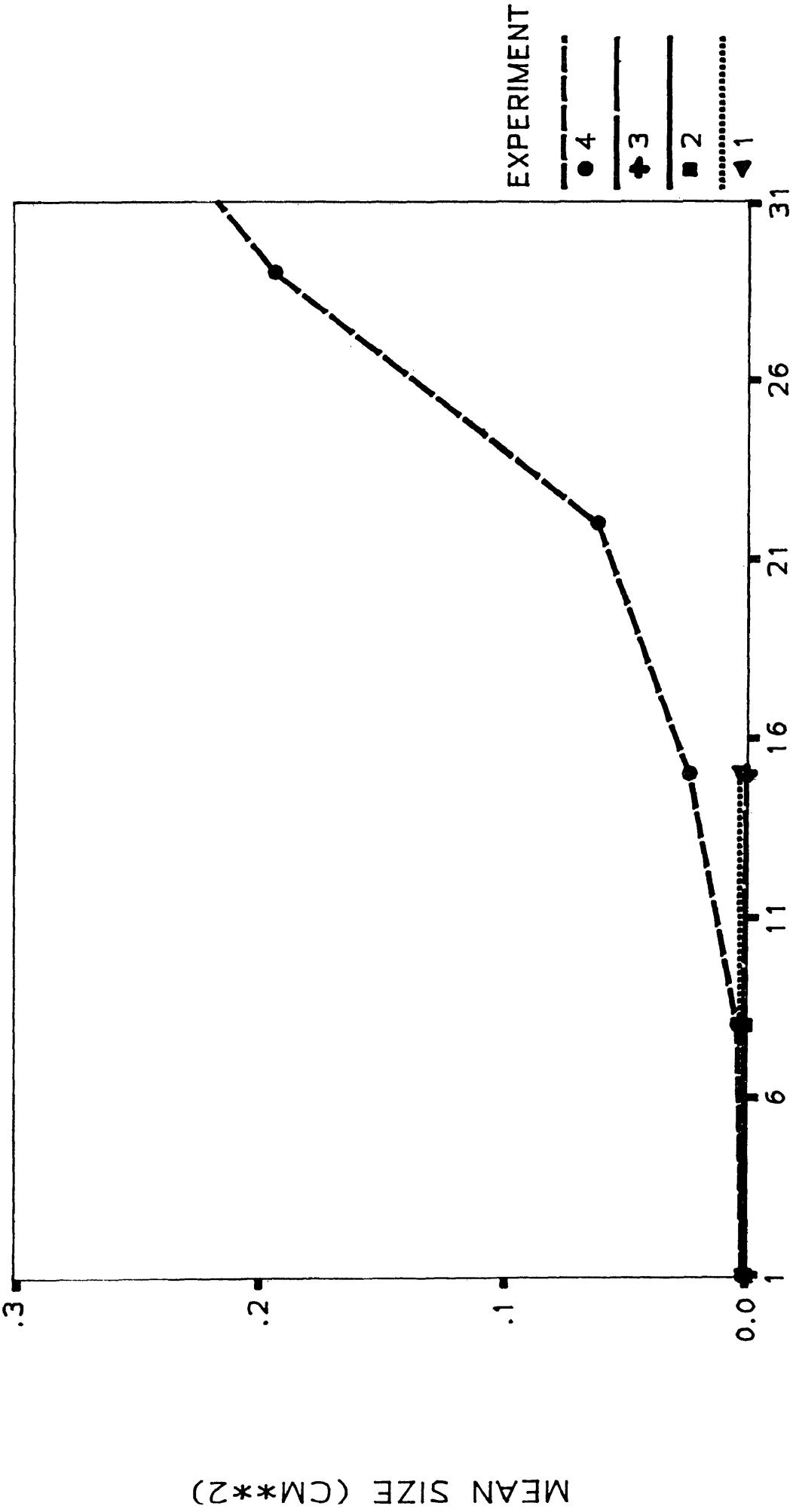
The SNK analysis revealed two significantly different sized groups at each sampled date at the MLW level, but these groups were not consistently ranked by season. By the second sampled day, Experiment R1 was significantly smaller than the other experiments, but by the next date sampled it was not different from Experiments R2 or R4, all of which were smaller than the spat grown during Experiment R3. By the fourth sampled date, Experiments R1 and R3 were significantly larger than Experiments R2 and R4, while at the last sampled date the only difference was Experiment R4, which was smaller than the others. Thus Experiment R1, which had the smallest initial mean size grew the most while Experiment R4 tended to be smaller than the other experiments.

The mean size of spat grown during Experiment R3 was consistently in the group with the larger size. Experiment R2 was always in the larger group except at the fourth sampled date. These results indicate the possibility of differing growth rates, although differential survival may also have occurred.

The -25 cm level was only compared for Experiments R3 and R4. The mean size of spat for the former was smaller than the latter at the second sampled date, but no significant difference was found by SD 15. Thereafter, the mean sizes of the spat grown during Experiment R3 were the larger.

The -75 cm level had the greatest amount of significantly different sized groups. At SD 8, all experiments had different sizes, with the ranking (from smallest to largest) the same as the order of the experiments. A week later, however, the only significantly different group was Experiment R2, which was smaller. At the next week, all groups were once again different, with the ranking of experiments (from smallest mean size to the largest) R2, R4, R3, and R1, respectively. The final sampled date revealed two groups, with Experiments R1 and R3 having larger mean sizes than Experiments R2 and R4.

Figure 31: Mean size (cm^2) by post-settlement age. +25 cm level. Experiments R1 to R4 are shown.

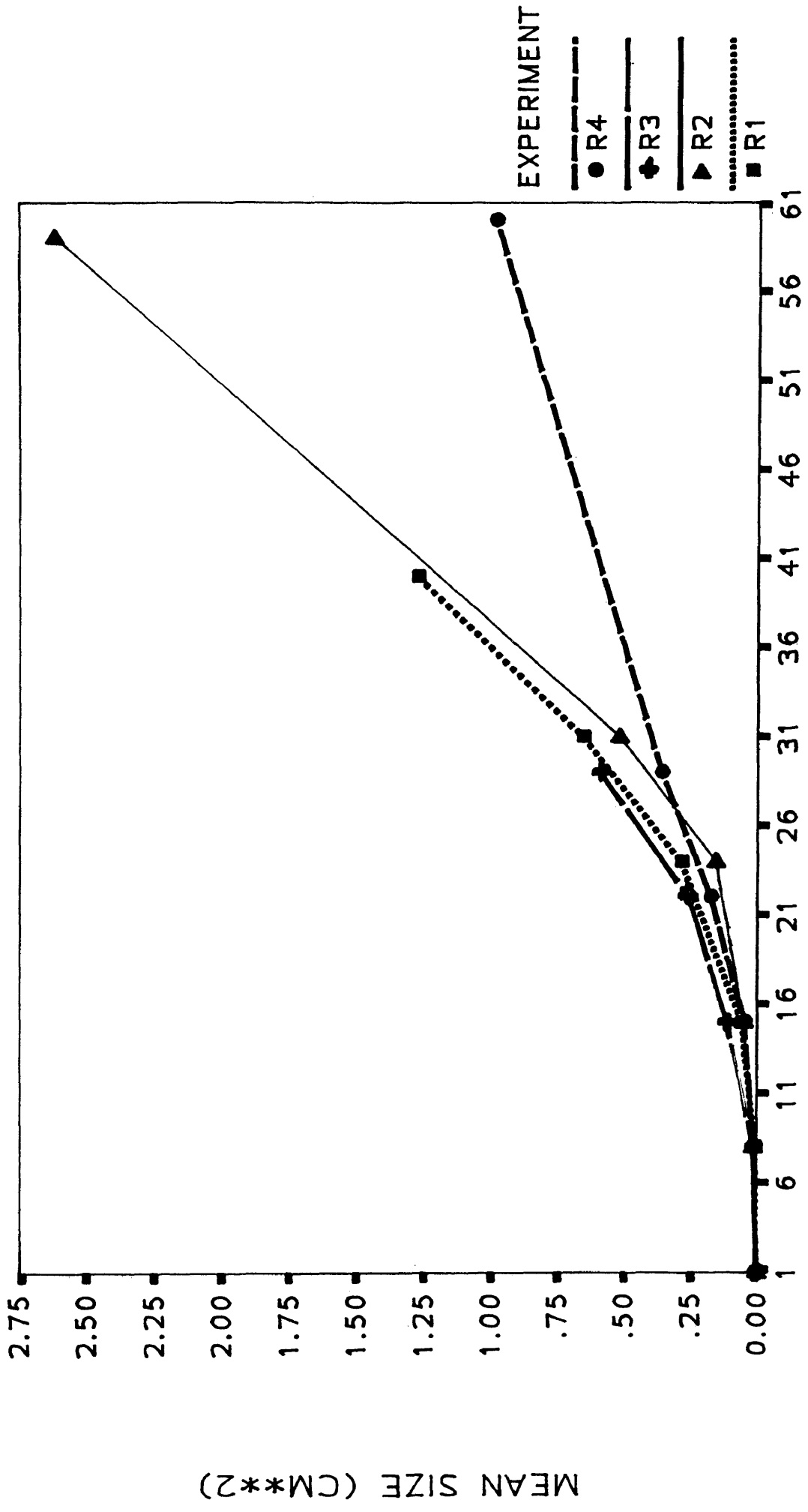


AGE (DAYS SINCE SETTLEMENT)

MEAN SIZE (CM**2)

EXPERIMENT
 ● 4
 ◆ 3
 ■ 2
 ▲ 1

Figure 32: Mean size (cm^2) by post-settlement age. MLW level. Experiments R1 to R4 are shown.



AGE (DAYS SINCE SETTLEMENT)

MEAN SIZE (CM**2)

EXPERIMENT
 ● R4
 ◆ R3
 ▲ R2
 ■ R1

Figure 33: Mean size (cm^2) by post-settlement age. -25 cm level. Experiments R3 and R4 are shown.

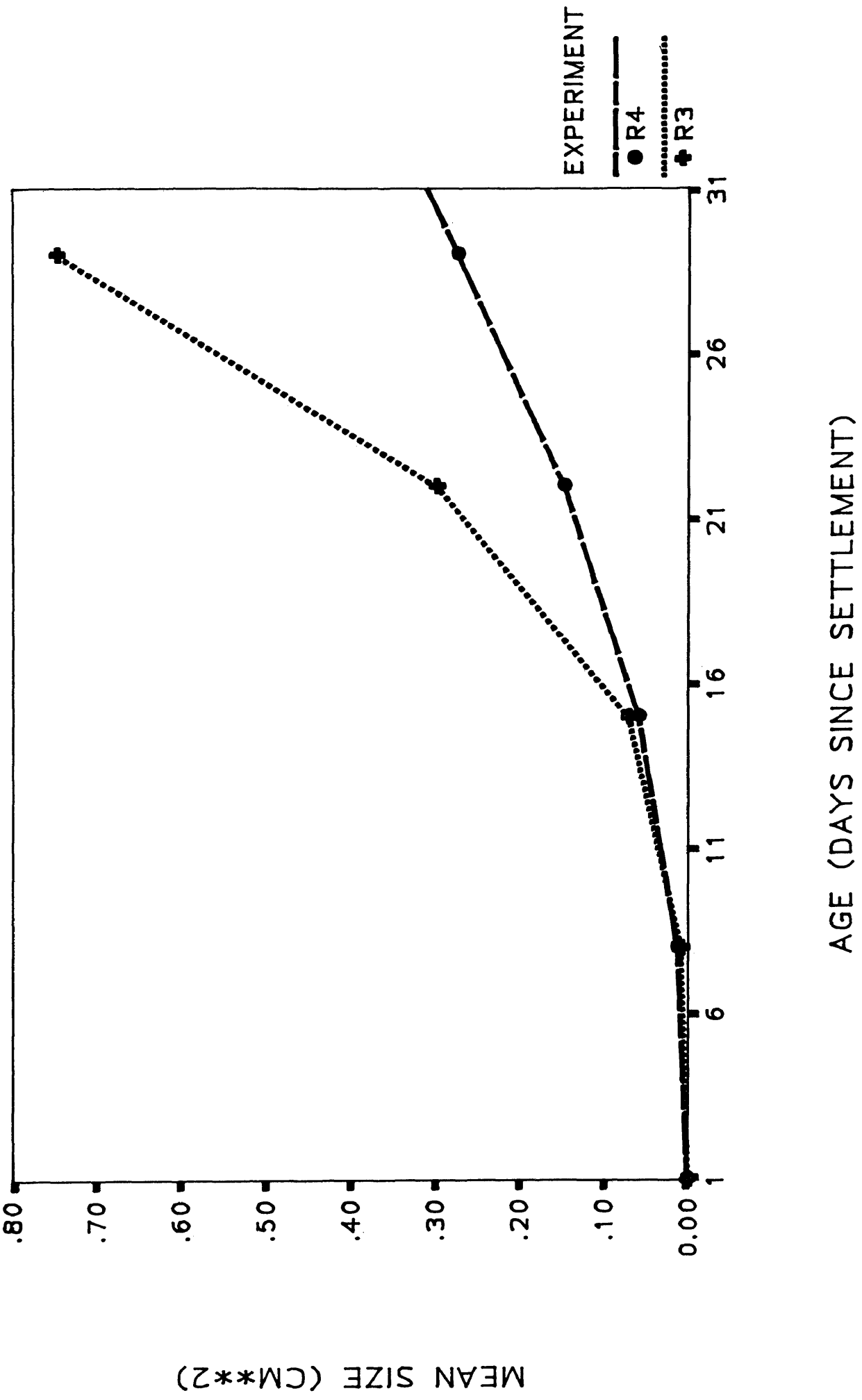
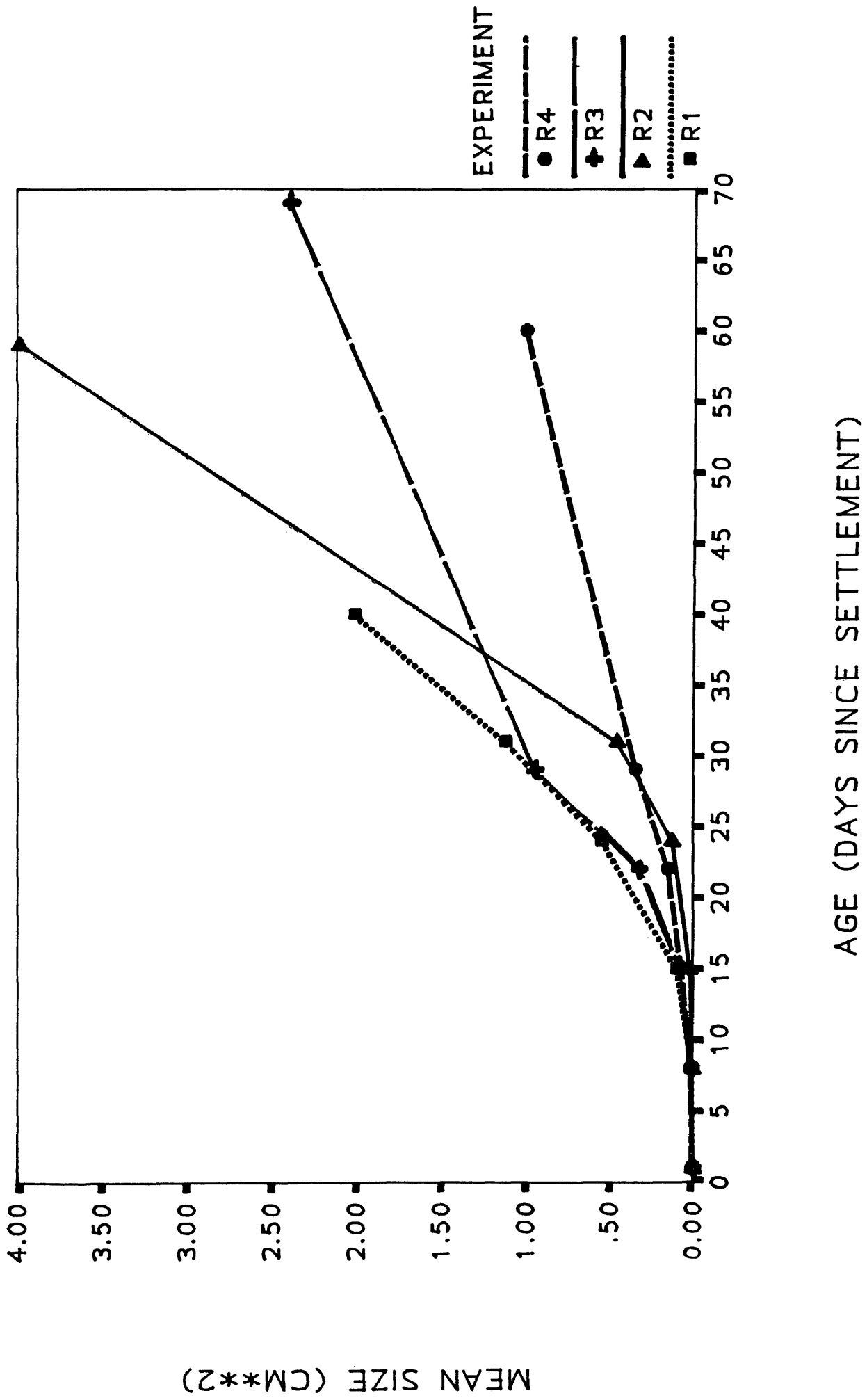


Figure 34: Mean size (cm^2) by post-settlement age. -75 cm level. Experiments R1 to R4 are shown.



MEAN SIZE (CM**2)

AGE (DAYS SINCE SETTLEMENT)

EXPERIMENT
 ● R4
 ▲ R3
 ▲ R2
 ■ R1

TABLE 26: SIZE STATISTICS: TWO-WAY ANOVA
Mean Size by Experiment, Date

+25 CM Level: MSZ x EXP(1,3), SD(2,5)

SOURCE	DF	F	P	SIG
Within	970			
Constant	1	1.62	0.201	NS
EXP	3	0.44	0.866	NS
SD	3	151.20	0.000	***
EXP x SD	2	0.29	0.750	NS

MLW Level: MSZ x EXP(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	2284			
Constant	1	5915.06	0.000	***
EXP	3	124.08	0.000	***
SD	3	1486.06	0.000	***
EXP x SD	9	44.05	0.000	***

-25 CM Level: MSZ x EXP(3,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	619			
Constant	1	1251.39	0.000	***
EXP	1	191.68	0.000	***
SD	3	320.99	0.000	***
EXP x SD	3	69.90	0.000	***

-75 CM Level: MSZ x EXP(1,4), SD(2,5)

SOURCE	DF	F	P	SIG
Within	1259			
Constant	1	1864.85	0.000	***
EXP	3	141.75	0.000	***
SD	3	552.96	0.000	***
EXP x SD	9	50.53	0.000	***

MSZ: Mean size (cm²); SD: Sample day; EXP: Experiment; DF: Degrees of freedom; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant);

TABLE 27 SIZE STATISTICS: ONE-WAY ANOVA
Mean Size by Experiment

+25 CM Level: MSZ x EXP(1,3)

SD	N	F	P	SIG
2	548	189.22	0.000	***
3	173	3.97	0.021	*

MLW Level: MSZ x EXP(1,4)

SD	N	F	P	SIG
2	1082	4.20	0.000	***
3	555	83.18	0.000	***
4	327	21.68	0.000	***
5	214	17.27	0.000	***

-25 CM Level: MSZ x EXP(1,4)

SD	N	F	P	SIG
2	469	70.35	0.000	***
3	246	0.39	0.579	NS
4	149	26.43	0.000	***
5	81	41.01	0.000	***

-75 CM Level: MSZ x EXP(1,4)

SD	N	F	P	SIG
2	639	80.41	0.000	***
3	321	15.16	0.000	***
4	196	26.00	0.000	***
5	113	19.89	0.000	***

MSZ: Mean size (cm²); EXP: Experiment; SD: Sample Date; N: Number of spat; F: F Ratio; P: Probability value; SIG: Significance of P (***: P<0.001; **: 0.001<P<0.010; *: 0.010<P<0.050; NS: Not significant).

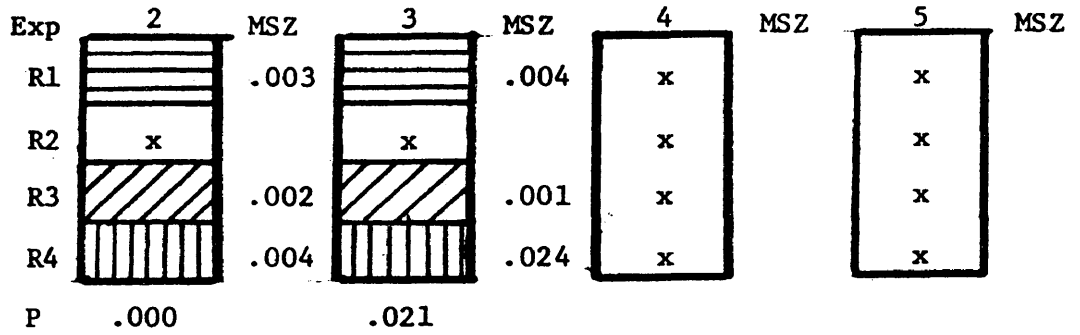
Figure 35: Mean size by tidal level and age. Results of Student-Newman-Keuls test for the determination of significantly different mean size values between experiments for each date sampled. The significantly different groups are denoted by different stiple patterns. EXP: Experiment; MSZ: Mean Size; SIG: Significance of ANOVA test.

SNK ANALYSIS

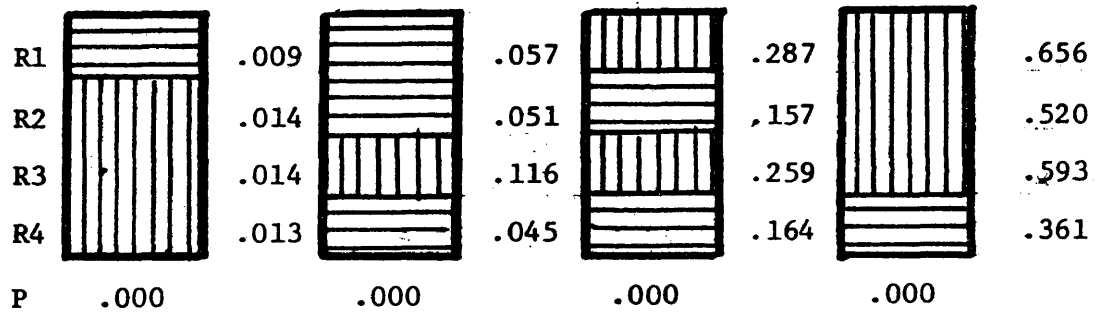
Mean Size (cm²) - Experiment by Level
Sample Day

Level

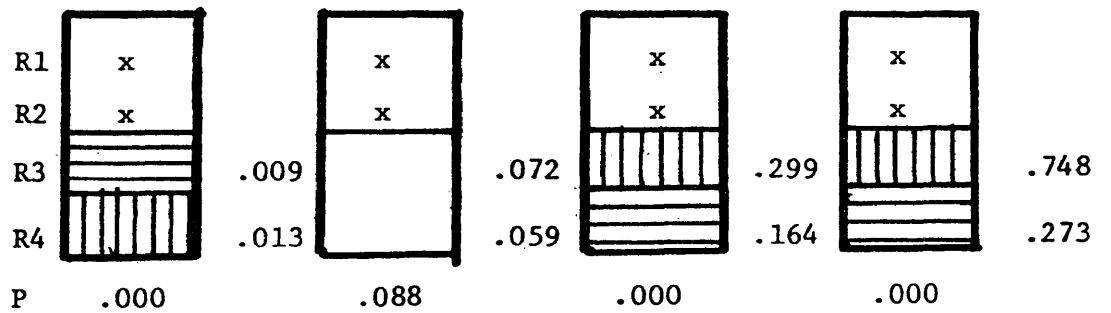
+25 cm



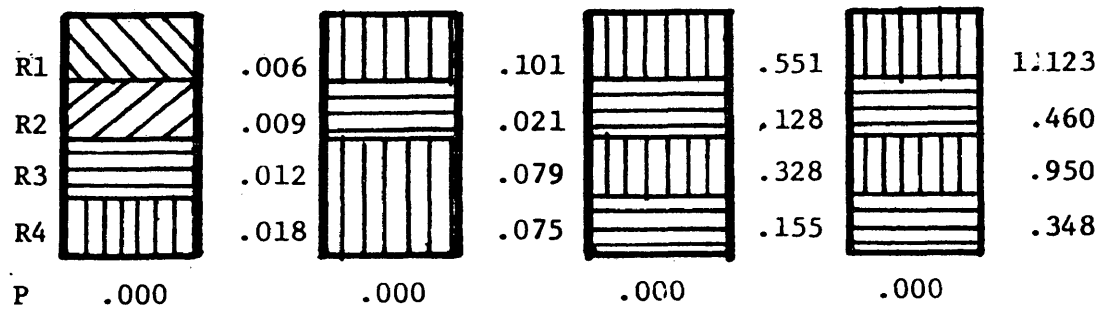
MLW



-25 cm



-75 cm



Instantaneous Growth Rates

The mean instantaneous growth rates for each experiment were computed (Tables 28-31). In Experiment R1, the subtidal growth rates for each interval can be seen to exceed those of the MLW level. Experiment R2 exhibited a higher rate in the intertidal until the last interval, when the subtidal oysters (two individuals) grew faster. In Experiment R3, the MLW and -75 cm levels generally had higher rates than the -25 cm level. In the final experiment, the +25 cm level spat were growing much slower than those at the other treatments, which exhibited very similar growth rates. In each case, the mean growth rate increased each interval for the first month, but the rate computed for the second month (when available) had decreased.

Table 28: Mean instantaneous growth rates. Experiment R1.

TH	GI	D	MGR	SD	NP	%E
+25 cm	1	7	0.0002	0.0001	3	24.5
	2	7	0.0000	0.0000	1	38.5
MLW	1	7	0.0009	0.0002	6	4.7
	2	7	0.0080	0.0017	6	2.1
	3	9	0.0270	0.0105	7	1.7
	4	7	0.0544	0.0146	7	3.7
	5	9	0.0747	0.0350	7	5.8
-75 cm	3	7	0.0011	0.0004	6	0.0
	3	7	0.0130	0.0050	6	0.0
	3	9	0.0502	0.0150	6	0.0
	3	7	0.0787	0.0246	6	0.0
	3	9	0.0970	0.0314	6	0.0

TH: Tidal height (cm relative to MLW); GI: Growth interval; D: Duration of growth interval (days); MGR: Mean growth rate (cm²/day); SD: Standard deviation; NP: Number of plates with surviving spat; %E: Percent exposure per interval.

Table 29: Mean instantaneous growth rates. Experiment R2.

TH	GI	D	MGR	SD	NP	%E
+25 cm	1	7	0.0001	<.0001	2	29.2
	1	7	0.0010	0.0006	4	2.6
	2	7	0.0041	0.0021	5	1.7
MLW	3	7	0.0143	0.0020	4	3.7
	4	9	0.0482	0.0104	3	5.3
	5	28	0.0761	0.0820	2	8.5
	1	7	0.0006	0.0004	2	0.0
	2	7	0.0022	0.0001	2	0.0
-75 cm	3	7	0.0153	0.0000	1	0.0
	4	9	0.0368	0.0000	1	0.0
	5	28	0.1259	0.0000	1	0.0

TH: Tidal height (cm relative to MLW); GI: Growth interval; D: Duration of growth interval (days); MGR: Mean growth rate (cm²/day); SD: Standard deviation; NP: Number of plates with surviving spat; %E: Percent exposure per interval.

Table 30: Mean instantaneous growth rates. Experiment R3.

TH	GI	D	MGR	SD	NP	%E
+25 cm	1	7	0.0001	<.0000	10	40.1
	2	7	-0.0002	0.0000	1	47.4
MLW	1	7	0.0021	0.0010	6	6.8
	2	7	0.0148	0.0068	7	9.4
	3	7	0.0226	0.0091	7	5.2
	4	7	0.0478	0.0177	7	9.9
-25 cm	1	7	0.0010	0.0005	5	0.0
	2	7	0.0082	0.0031	4	0.0
	3	7	0.0229	0.0126	4	0.0
	4	7	0.0389	0.0403	3	0.0
-75 cm	1	7	0.0019	0.0009	3	0.0
	2	7	0.0135	0.0087	4	0.0
	3	7	0.0439	0.0185	4	0.0
	4	7	0.0828	0.0211	4	0.0
	5	40	0.0542	0.0365	4	0.0

TH: Tidal height (cm relative to MLW); GI: Growth interval; D: Duration of growth interval (days); MGR: Mean growth rate (cm²/day); SD: Standard deviation; NP: Number of plates with surviving spat; %E: Percent exposure per interval.

Table 31 : Mean instantaneous growth rates. Experiment R4.

TH	GI	D	MGR	SD	NP	%E
+25 cm	1	7	0.0003	0.0001	8	32.8
	2	7	0.0029	0.0009	9	30.7
	3	7	0.0042	0.0021	9	29.7
	4	7	0.0199	0.0066	9	16.7
	5	31	0.0138	0.0055	9	31.9
MLW	1	7	0.0017	0.0003	10	1.0
	2	7	0.0053	0.0021	10	1.0
	3	7	0.0155	0.0073	9	2.1
	4	7	0.0283	0.0147	9	0.0
	5	31	0.0190	0.0040	9	7.3
-25 cm	1	7	0.0016	0.0005	8	0.0
	2	7	0.0057	0.0043	7	0.0
	3	7	0.0148	0.0094	7	0.0
	4	7	0.0243	0.0216	8	0.0
	5	31	0.0199	0.0098	9	0.0
-75 cm	1	7	0.0017	0.0010	10	0.0
	2	7	0.0069	0.0032	8	0.0
	3	7	0.0133	0.0075	7	0.0
	4	7	0.0233	0.0165	6	0.0
	5	31	0.0221	0.0100	6	0.0

TH: Tidal height (cm relative to MLW); GI: Growth interval; D: Duration of growth interval (days); MGR: Mean growth rate (cm^2/day); SD: Standard deviation; NP: Number of plates with surviving spat; %E: Percent exposure per interval.

Effect of density

Recent studies have indicated the interest in the effects of density of settlers or recruits on subsequent survival and growth (Connell, 1985). The possibility of density dependent mortality with this data set was examined through the use of regression analysis. Theoretically, one would expect the effects of density dependant mortality to increase with time as competing organisms are increasingly subjected to space and food limitations. Regressing the initial number of settled organisms with the number of survivors for each date sampled should thus show a trend of decreasing correlation (measured as r^2 and P values) with time. The results of this analysis is shown in Table 32. The data are equivocal. The MLW level appears to follow expected pattern for density-dependent mortality, while the other levels do not. Thus, the data do not strongly indicate the presence of density dependent mortality.

Table 32: Regression analysis for the determination of density-dependent mortality: Number of survivors at each sampled date was regressed against number of initial settlers. Data is from Experiment R4.

AGE	<u>Tidal Height</u>							
	+25		MLW		-25		-75	
	R	P	R	P	R	P	R	P
8	0.939	0.000	0.673	0.004	0.691	0.001	0.796	0.001
15	0.923	0.000	0.673	0.004	0.773	0.004	0.829	0.000
22	0.920	0.000	0.555	0.013	0.888	0.001	0.895	0.000
29	0.934	0.000	0.310	0.095	0.663	0.014	0.920	0.000
60	0.800	0.000	0.206	0.188	0.598	0.014	0.636	0.006

AGE: Age of post-set; R: correlation coefficient; P: Probability value.

Biological Interactions

The experiments previously discussed were not specifically designed to test the effect of predators or competitors on oyster growth or survival. The surfaces afforded by the experimental plates and trellises, however, quickly became foci for the settlement of various sedentary invertebrate larvae and algal spores, as well as mobile species, and the importance of the biotic interactions could not be ignored. Thus, during photosampling and the analysis of each time series of photographs on the image analyzer, observations on the structure and extent of competitors and predators were made. Periodic surveys of the pilings were also conducted. It must be emphasized that during photosampling the plates were often "weeded", and thus, with the exception of serpulids and cirripeds, each sampling constituted a removal of the epibiota. This was necessary in order to have clear photographs of the spat.

The recruitment of organisms onto the primary space of the plates was heterogeneous in time and space, and was especially varied in relation to vertical zonation. The following account will describe recruitment patterns in relation to these aspects.

The following species were the dominant occupiers of primary space on experimental plates: the cirripeds Chthamalis fragilis Darwin, Balanus eburneus Gould, and Balanus improvisus Darwin; the ascidian Molgula manhattanensis (DeKay); the algae Ulva lactuca Linneaus and Enteromorpha spp; and erect hydrozoans and bryozoans.

Vertical Zonation.

Aerial exposure most consistently delineated settlement distribution and recruitment success. No organisms recruited into the +75 cm level. Molgula was confined to the subtidal zone (-25 to -75

cm), while the hydroids and the bryozoans were able to colonize plates up to the sublittoral fringe (MLW). Green algae (Ulva and Enteromorpha) ranged from +50 to -25 cm, but were most abundant between MLW and +25 cm. Barnacle settlement occurred at each level except the +75 cm. Although it was not possible to distinguish between the Balanus species, Chthamalis was restricted to intertidal recruitment.

Spatial Heterogeneity.

Adjacent plates within a treatment level were often composed of different compositions of the dominant fouling organisms. The densities of settling barnacles especially were observed to vary greatly among replicate plates, ranging from nearly zero individuals to complete cover. Algal, hydrozoan, and bryozoan covers were also patchy. Oyster valves were not immune to settlement: all of the above organisms used oysters for attachment. This was especially true with Molgula, which in contrast to having a heterogeneous distribution, tended to cover all surfaces, including oysters and barnacles, with a near continuous mat at levels below -5 cm. Other organisms, most notably the algae Ceramium spp and Polysiphonia spp, and the various hydroids and bryozoans, as well as isopods and annelids, lived as epibionts on the Molgula or within the associated organic debris. This "Molgula community" only developed after the weekly sampling had been completed, when the plates were not frequently disturbed. (Although cleaning the plates prohibited the quantification of these areas, the image analyzer would be a useful tool for an investigation designed to measure percent cover of fouling organisms.) An organic layer mixed with inorganic materials was often a conspicuous component of the percent cover.

Temporal Heterogeneity.

The recruitment of fouling organisms in this study also varied over the two time scales measured: the short weekly to monthly sampling scale within an experiment and the longer seasonal scale between experiments. Within these temporal frameworks, there were changes in the variations between the vertical zonation and spatial considerations.

On the shorter scale, various densities of barnacles settled onto the plates within the first week, and secondary settlements onto oysters, other barnacles, and primary space were also common. Where recruitment was successful, barnacles grew rapidly, and within two to three weeks could occupy all available space. Mortality, however, often began to occur within four weeks and included smothering from other organisms, mechanical damage, exfoliation through intraspecific interactions in crowded conditions, and, presumably, predation. The result was a renewal of primary space. The hydroids, bryozoans, and algae were usually somewhat slower in colonizing the plates, and became prominent only after two to three weeks. The density of ascidians remained constant and low during the weekly sampling, when removal of the trellises resulted in mass mortalities (in addition to cleaning the plates). When undisturbed, however, Molgula quickly dominated all surfaces below -5 cm.

Variations over the seasonal scale concerned both species composition and vertical range. In the latter regard, Experiment R4 exhibited a significant range extension of organisms shorewards. In Experiments R1 through R3, barnacle cyprids (along with dead oyster settlers of experimental origin) were usually noted at the +50 cm level, and both settled and newly metamorphosed barnacles and oysters could be found at the +25 cm level. None of these individuals survived. Green algae colonized the +25 cm level in these experiments by the second or

third week and in Experiment R1, lightly colonized the +50 cm level by the fifth week. Experiment R4, in contrast, exhibited barnacle recruitment and algal colonization at the +25 cm level after one week and at the +50 cm level after three weeks.

Experiment R4 was also subjected to significantly less fouling by Molgula. By the end of the September, the ascidian mats were sluffing off substrates, and by the last sample in November most ascidians were solitary.

Predators.

Two main invertebrate predators were observed at the study site, and were observed to be responsible for oyster spat mortality. Oyster drills, Urosalpinx cinerea (Say) and Eupleura caudata (Say), were found during Experiments R1, R2, and R3 on the -75 cm level. A high percentage of spat at this level were found to have been drilled, and egg cases from the gastropods were found on experimental plates. The portunid crab Callinectes sapidus Rathbun was common on surrounding pilings as well as on the trellises. On August 13, a crab was observed feeding on a spat at the MLW level of Experiment R2. The crab had crushed the spat and, in the process, broke the plate in two.

DISCUSSION

Settlement

The settlement pattern recorded during the microcosm experiments did not reflect the observed zonation patterns of adults at this locale. The settlement of the vast majority of the larvae in the lowest possible subtidal site within the settlement tubes suggests the larvae have a strong geopositive tendency. In contrast, the adult oyster populations at the study site are mostly confined to the intertidal zone.

These results correspond well to the few previous studies which compared intertidal and subtidal recruitment of oysters on time scales short enough to distinguish between settlement and post-settlement mortality. (Many early studies sampled over monthly, or greater, time scales (Galtsoff and Luce, 1930; Loosanoff, 1932; Mackin, 1946), and thus actually measured long term survival patterns.) McDougall (1942), in a study at Beaufort, N.C., evaluated settlement on ceramic plates over one to two week intervals and found subtidal settlement to be substantially greater than intertidal settlement, with the heaviest settlement occurring near the bottom. Chestnut and Fahy (1952) found similar results from week-long shellstring studies which measured settlement at depths between +3 to -15 feet relative to MLW at several sites in Bogue Sound, N.C. Nichy and Menzel (1967), in a recruitment study at Alligator Harbor, Florida, observed greater subtidal than intertidal settlement. Hidu and Haskin (1971), in Delaware Bay, found settlement patterns between inshore and offshore sites to be related to

temperature and hydrographic processes. Intertidal settlement was very high at the inshore site where suitable subtidal habitats were scarce, but settlement was typically subtidal at the deep, off-shore sites. An exception, however, can be found in McNulty (1953), who found intertidal settlement to exceed subtidal settlement in two-week long shell bag experiments in Wadmalaw, S.C. At all of these sites adult populations occur in the intertidal zone.

The present study differed from those described above by the use of hatchery-reared larvae exposed to field conditions in microcosms, as opposed to relying on the presence of natural larval abundances. The use of cohorts of larvae spawned from known genetic stock and grown to a comparable developmental stage is advantageous for experimental research because biological variation is limited. The similarity of the results between experiments indicates little possibility of a cohort effect.

The exact influence of the microcosm tubes on the settlement behavior of the oyster larvae is unknown. Personal observations of the behavior of larvae in tubes in the laboratory do not reveal important detrimental factors other than some swimming inhibition at high larval densities. Conditions within the tubes differ from the natural environment in the lack of horizontal currents in the tubes. At the study site, these currents can approach 30 cm sec^{-1} . Barnacle cyprid settlement has been shown to be influenced by currents (Crisp, 1976), and settlement patterns of Mercenaria mercenaria (L.) have been demonstrated to change in response to increasing flow velocities (Butman et al., 1988). There is also evidence that oyster larvae distinguish between hydrographic regimes (Hidu and Haskin, 1971; Bushek, 1988). Studies have indicated that larvae of many species may

actively regulate their vertical position in the water column in accordance to tidally-forced changes in current velocity, salinity, or temperature (Wood and Hargis, 1971; Mann, 1986). Such a planktonic zonation may contribute to the estuarine retention of oysters (Pritchard, 1952; Wood and Hargis, 1971; Seliger *et al.*, 1982; Andrews, 1983; Mann, 1988; Ruzecki and Hargis, 1989) as well as possible site selection for settlement (H. Hidu, pers. comm.). In the shallow, well-mixed, and vertically homogeneous water column at the study site, larvae may not be able to vertically stratify in the water column until slack water. In contrast, the calmer conditions in the settlement tubes would allow the larvae to actively depth regulate. The observed distribution of settled oysters thus probably reflects larval behavior patterns and not those imposed passively by hydrographic conditions. The composition of the biological exudates within the tube may also have affected the settlement distribution (Crisp, 1967; Weiner and Colwell, 1982; Hadfield, 1984; LeTourneux and Bourget, 1988; Raimondi, 1988).

Post-settlement Survival

The results of the survival experiments reveal significant differences between the survival of oysters grown at different tidal levels both within and between experiments. The variability of the data tended to be high, not unexpectedly, especially in cases of low settlement and high mortality, but several prominent trends are present.

First, the highest mortality rates occurred within the first week. The initial mean percent survival values ranged from a low of 0% (recruitment failure) to a high of 35.8%. The cause of this initial mortality could not be clearly determined because survival was ascertained by the presence or absence of an individual in relation to

the initial settlement. Thus survival rates may be somewhat inflated if individuals noted as present were actually dead (for example, the +25 level of Experiment R3). Competency of the larvae to successfully complete metamorphosis, the "early post-set mortality" of MacKenzie (1970), is the most likely cause of this low initial survival, although predation and physical factors (disruption) are also probably important.

Second, the upper and mid-littoral zones (+75 and +50cm) suffered complete mortalities within this initial period. Additionally, oysters placed at the low littoral (+25 cm) level always died within two weeks of post-settlement age except during Experiment R4 in September. Conversely, mean percent survival was greater at this level than at any other treatment. Thus, barring the former exception, no significant recruitment occurred in the intertidal zone. The initial survival at the MLW (sublittoral fringe subzone) and subtidal levels varied between experiments but was generally higher at the MLW level than lower on the shore.

All experiments had high variation between replicates within a level, which tended to reduce the significance of differences between levels. Certain trends in recruitment patterns, however, are apparent. When comparing oysters grown over the first four weeks at the MLW level with those at the subtidal levels, -25 and -75 cm, the MLW level always had higher recruitment than the other levels although the significance of the statistical tests varied. The -75 cm levels often had the lowest survival; however, the MLW level often had the higher mortality rates after the third week.

Finally, a comparison of the experiments indicates the importance of the initial survival on the subsequent population patterns. Oysters grown at or below MLW during Experiments R1 and R4 had relatively high

initial survival that translated to higher recruitment over time than those of Experiments R2 and R3, where low initial survival resulted in low overall recruitment. This effect is appreciated when comparing Experiments R1, R2, and R4: Experiments R1 and R2 were initiated only nine days apart in June, while Experiment R4 was conducted three months later in September, under different environmental conditions. Those levels with the lowest initial mean daily mortality rates (Table 19) resulted in the highest recruitments: all mean mortality rates after this time were of the same magnitude and decreased with time. The factors affecting the initial survival thus are important in determining the magnitude of the recruitment.

Growth

The mean sizes and growth rates of oyster spat were found to vary temporally and spatially. Along the vertical transect, the intertidal oysters were always found to grow at a slower rate than oysters grown at the MLW level or subtidally. This is especially evident during Experiment R4, in September, where the mid intertidal treatment grew only about half as fast as the subtidal treatments.

A comparison between the growth rates of subtidally grown oysters and those grown at the sublittoral fringe, however, do not indicate consistent trends. Growth at the MLW level was substantially less than that at the -75 cm level during Experiment R1 in June, and during Experiment R3 in July after the second growth interval. In September, in contrast, the growth rates of oysters at the MLW, -25, and -75 cm levels were generally of the same order. There was also no consistent trend to the growth of oysters located at the -25 cm level.

Seasonally, spat grown during September tended to be smaller than the spat in the other experiments. The sizes of spat at the MLW level

after a month of growth were greater when grown in June and July than during September. Spat grew faster at the -25 cm level during July, and Experiments R1 and R3 had faster growing spat than Experiments R2 and R4 at the -75 cm level.

Effect of Physical Parameters

The effects of water temperature and salinity could not be demonstrated to directly influence survival or growth of oysters during this study. The ranges of these physical parameters were well within the tolerance limits of oysters, and although variations occurred between experiments, these variations could not be correlated with differences in growth or survival. This is mainly due to the high variability between replicates. In contrast, air temperatures, modified by length of exposure periods, significantly affected both the recruitment and growth of intertidal oysters. The influence of aerial exposure was wholly negative at periods greater than 10% emersed.

Water temperature obviously has an effect on oyster growth, as many studies have indicated. During this study, with the exception of the second month of Experiment R4, the water temperature varied by only 10°C. The lowest temperatures of this period were recorded in June, when some of the the fastest growth occurred. By the time the water temperatures declined rapidly in October, the oysters of Experiment R4 were already significantly smaller than oysters grown in the other experiments. The highest temperatures were experienced during Experiment R3, but few significantly different mean sizes with Experiment R1 were recorded. Thus water temperature differences alone do not account for differences in growth.

Oysters are euryhaline organisms, and can withstand a wide range of salinity (Galtsoff, 1964). During this experiment, the salinity values measured were well within the tolerance limits of oysters (Ingle and Dawson, 1952), and salinity thus probably did not directly impact survival. Salinity is known to affect the growth of oysters, with relatively faster growth rates occurring at higher concentrations (Galtsoff, 1964). Chanley (1957) reported optimum growth of new recruits over six weekly samples at 15-22.5 o/oo, although salinities higher than 27 o/oo were not tested. Although the experiments reported here were conducted under somewhat differing salinity regimes, the range of the mean values was only about 6 o/oo, and growth and salinity variations did not appear to be correlated. The growth rates of the oysters grown at the -75 cm level during Experiments R1 and R3 were nearly identical although the salinity regime was different. Experiment R4 had the highest salinity and the lowest growth rates. Thus the salinity ranges experienced during this experiment do not account for the observed differences in growth rates. Similarly, the salinity differences noted probably did not directly impact survival.

Indirectly, the salinity regime does control oyster distributions by influencing the distribution of oyster predators and competitors. Many of the invertebrates which affect oyster settlement, survival, and growth are relatively intolerant of low salinity, and are thus restricted in distribution (Galtsoff, 1964; Gosner, 1971); these ranges may be spatially and temporally variable, depending mainly on seasonal rainfall patterns. During this experiment, salinity was high enough to permit the activity of three of the oysters' primary predators (drills, blue crabs, and flatworms) as well as a host of competitors. The influence of some of these biota on the experimental oysters will be

discussed below. Thus, the effect of salinity was indirect and yet has major ramifications to oyster zonation.

High aerial temperatures had a significant affect on the intertidal oysters during this study. Oyster recruitment was completely curtailed in the intertidal zone during June and July, where the maximum air temperatures consistently ranged above 30°C. September air temperatures remained below 30°C after September 15, and recruitment at the +25 cm level, but not higher, occurred. Presumably, intertidal mortality was caused primarily by desiccation. These findings are consistent with field observations in which the natural oyster recruitment onto the pier pilings occurred only in September and October; additionally, the failure of barnacle cyprids to metamorphose and survive followed the experimental oyster recruitment.

The period of inundation, controlled by mainly tidal oscillations at this site, proved to be important in determining the severity of aerial exposure. Within experiments, oysters placed at the MLW level, with exposures less than 10% emersed, never exhibited significant reductions in recruitment over subtidal treatments, and in fact often had increased survival. In contrast, with the exception of Experiment R4, higher exposures resulted in complete mortalities. Growth was more variable, and during Experiments R1 and R3 was significantly less at the MLW level than at the -75 cm level after a month, while no difference was found during Experiments R2 and R4; however, significantly greater sizes at the MLW than at more subtidal treatments were measured over some sampling intervals. At higher exposure levels, growth rates were retarded in comparison to subtidal treatments. Growth at the +25 cm level during Experiment R4 was significantly less than the other

treatments at all dates sampled. This may reflect the consequences of reduced feeding times for intertidal spat (Peterson and Black, 1987).

Less clear were the direct effects of percent aerial exposure on oysters at the MLW level over the weekly sampling periods. Both within and between experiments, the exposure periods varied, but these variations could not be correlated to variations in growth rates or mortality rates. Indeed, during some periods enhancement of growth with increased exposure is indicated. During Experiment R1, with exposure at the MLW ranging from 1.7 to 5.8%, growth rates were always lower than oysters situated subtidally, while during the higher aerial exposures during Experiment R3, the growth rates at the MLW level were generally higher than those at the -25 cm level, but less than or equal to those at the -75 cm level. These differences may have resulted from variations in interspecific competition caused by the die-off of exposure-intolerant species. In contrast, the very short aerial exposures which occurred during Experiment R4 resulted in nearly identical growth rates at the subtidal and subtidal fringe zones. Thus, there is not good evidence for negative effects of aerial exposure at low levels of emersion. Because of this, the MLW level is more closely associated with the subtidal than intertidal zones.

Thus there was a clear difference in the effect of the measured physical parameters on oysters grown between intertidal and subtidal treatments. Subtidally, the salinity and water temperatures did not measurably affect survival or growth, although salinity is recognized to have important ecological repercussions. Intertidally, high aerial temperatures limited recruitment and stunted growth. Tidal inundation mitigated the effects of aerial exposure, and the short-period exposures which occurred at the MLW level may have contributed to the observed

enhanced recruitment over subtidal treatments, probably by limiting some negative biological factors (see below). Physical factors thus most affected the intertidal treatments, where air temperature and exposure proved to be the dominant influences on growth and recruitment patterns.

Effect of Biological Parameters

Significant biological interactions between oysters and other biota occurred along the tidal gradient, and to a lesser extent, seasonally. The biological parameters of importance were competition and predation.

Competition for space is considered to be a major influence on biological distributions on hard substrates, where space is generally a limiting resource (Connell, 1985). In this study, this was found to be true only subtidally, as the intertidal zone usually had a substantial amount of unoccupied space. Subtidal competition for space, however, could be intense, and involved both inter- and intraspecific components.

The hypothesized intraspecific competition, which should be manifested as increasing density-dependant mortality with time, was not supported by a comparative regression analysis performed on Experiment R4 (Table 33). Comparisons of the regressions between high and low density plates within a treatment were also unconvincing, although observations indicate that mortality caused by competitive overgrowth does occur, especially in dense aggregations. Over the time scales of this experiment, it appears that density independent mortality predominated.

Interestingly, the negative effects of high density settlements were ameliorated to some extent by the growth patterns of oysters. Oysters growing in contact with one another could change the direction of growth to reduce competitive interactions. This was frequently observed during the "time lapse" analysis of the photographs. The

change of orientation could occur in three dimensions. Chance events were also important in determining the survivors of high density settlements, both in the relative position and orientation of a spat in relation to its neighbors, and also in the survival of the neighbors. Neighboring spat which settled with umbones facing the same direction were less likely to coexist than those which either faced away or towards each other, because overgrowth most frequently occurred as one spat grew over the relatively static hinge region of the other spat. Interaction between the growing posterior shell margins more readily resulted in competitive interference between the margins and changes in the growth axis. Overgrowth was not always advantageous: spat which grew on objects other than the primary substrate or which projected into space were much more likely to be dislodged than spat adhering closely to the substrate.

The effects of competition on oyster growth and survival are difficult to quantify, both because the experiments were not designed to measure these effects and because of the variations in the intensity and composition of the recruitment of fouling organisms between replicate plates, coupled with cleaning the plates during photosampling. Observations illuminate some aspects of the interactions. Interspecific competition with barnacles usually began during the first week of each experiment, and was a factor throughout all experiments and all treatments. Generally, oysters outcompeted barnacles at all levels by overgrowing them, and, combined with barnacle mortality from other causes (smothering and Stylochus ellipticus (Girard) and Urosalpinx cinerea predation), this usually resulted in a reduction of the competitive interactions by the fourth week. However, oysters were vulnerable to barnacles when both species were small. The rapid growth

rates of barnacles surrounding a spat could result in the spat being lifted from the substrate. This action appeared to be dependent on high density barnacle recruitments. When a barnacle survived to grow to a large size, it was often able to prevent overgrowth and so interfere with oyster growth. Barnacle settlements frequently occurred on oyster valves. It is unknown how barnacle densities affected oyster growth rates, but no obvious correlations between differing densities on replicate plates were noted.

On the experimental structures, the dominant space competitor subtidally was the ascidian Molgula manhattanensis, which did not require primary space for attachment. This organism was kept in check during the month of primary sampling, but dominated all surfaces below -5 cm afterwards. Molgula is very susceptible to aerial exposure, and was not recorded at the MLW level. It is also seasonally abundant, and became less prevalent in September. Molgula commonly smothered barnacles, but the effect of overgrowth on oysters was not pronounced. The flow of water to oysters may not have been greatly reduced, while barnacle cirral activity would certainly be hampered. The impact of hydroids and bryozoans on oyster growth and survival could not be determined.

Predation on oyster spat by the oyster drills Urosalpinx cinerea and Eupleura caudata and the crab Callinectes sapidus was directly observed. The presence of drills, drill egg cases, and drilled spat was first recorded on July 7; the drills were confined to the bottom portion of the trellis during these experiments, but this may have been an artifact of sampling. The effect of blue crab foraging was observed only once, but the high proportion of fairly large spat, often in groups, which were simply missing ("exfoliated") from the plate may

indicate crab predation. A host of other mobile predators may also have been responsible (Edwards et al., 1982). Alternatively, this effect may have been due to mechanical damage or wave stress.

The cleaning of the experimental plates certainly led to an artificial state which probably aided oyster survival by reducing the impacts of predators and competitors. Indeed, the subtidal zone on the pilings is dominated by several species of large, persistent sponges (primarily Microciona prolifera Ellis and Solander and Halichondrina bowerbanki Burton), mortality-enhancing shell-boring sponges (Cliona spp), and other species which were not noted to recruit on any experimental structures. Thus the effect of the biological interactions on oyster growth and survival are probably understated in these experiments. Alternatively, the time scales may simply have been too short to have registered the final results of the biological interactions.

Thus, the biological interactions were significant and varied along the vertical transect. The most intense competition and predation occurred subtidally, although these were moderated by the sampling regime. The aerial exposure which occurred at the MLW level was sufficient to limit the survival of several competitors, most notably Molgula. Predatory activities by gastropods may also have been reduced. A very limited biota was able to colonize the intertidal zone until fall. Predation by drills was confined to lower levels, and were never observed intertidally, though crabs had no such constraint.

To my knowledge, there are few experimental studies in the literature which have compared recruitment patterns of artificially produced spat placed in the intertidal zone over comparable temporal scales. Several studies have been performed in which recruitment of

natural oyster populations over various time scales has been monitored, however. Loosanoff (1932), in Chesapeake Bay, found recruitment throughout the tidal gradient in the James and Corrotoman Rivers, with the best survival near the bottom and good survival intertidally. At Wachapreague, however, most survival was intertidal, and drill predation below MLW was determined to be the cause. The sample periods of these studies ranged from 3 to 3.5 months. Mackin (1946), repeating this work at Wachapreague over periods between 1 and 4 months, found comparable results. Growth intertidally was found to be negatively correlated with exposure time, while drill activity was sharply reduced above MLW. In Beaufort, N.C., McDougall (1943) conducted a study which monitored the settlement of organisms on cleaned plates at 1 to 2 week intervals as well as recruitment of organisms on uncleaned plates over biweekly periods. All unprotected subtidal oysters were killed, presumably through competitive interactions (Urosalpinx and Cliona) were absent), while intertidal oysters survived. Ortega (1981) compared the intertidal distributions of fouling organisms between protected and wave-exposed sites in Beaufort, N. C. Oysters were outcompeted by the mussel Brachidontes exustus at the exposed sites due to differential tolerance to wave stress. Crassostrea virginica dominated at protected sites because of superior recruitment and faster growth rates. Predation was found to be unimportant to the structuring of the intertidal communities because drills were not active in the intertidal zone. It seems a serious flaw, however, to state that predation was of limited importance on the basis of low activity of one possible predator (Edwards et al, 1982), especially when crabs, obvious components of the macrofauna of the area, are abundant (Kranz and Chamberlin, 1978). Chestnut and Fahy (1952) also attributed predation and competition to

the prevalence of intertidal oysters in Bogue Sound, N.C. In Georgia, Bahr and Lanier (1981) concluded that boring sponges caused the high subtidal mortality, and considered growth orientations which afforded mutual shading to be important for reducing heat mortality in the intertidal zone. Further south, Nichy and Menzel (1967) concluded that the intertidal distributions of oysters were maintained by heat mortality at the upper levels and by predation subtidally. When compared with the results of the settlement monitoring studies cited previously, it can be noted that the subtidal areas where most settlement occurs are not the areas where survival occurs. The evidence thus supports the hypothesis that the intertidal zonation of oysters in the areas studied are controlled by physical factors in the intertidal zone and biological factors subtidally.

There are also few studies which quantitatively document the growth rates of juvenile Crassostrea virginica over short sample durations, although there are many studies which have measured growth rates of larger oysters over longer periods (i.e. Loosanoff and Nomejko, 1949; Butler, 1952; Beaven, 1952; Andrews and McHugh, 1957; Shaw and Merrill, 1966; others). Fewer workers have examined growth rates in relation to exposure levels. Additionally, the indices used for growth include length measurements, wet or meat weights, condition indices, and percent increases (none utilizing area). Despite these problems, the results of previous studies, some involving other oyster species, will be evaluated.

The evidence in the literature for reduced growth with aerial exposure is mixed. Loosanoff (1932) measured natural recruitment over three and a half months in the James River, Virginia, and found the intertidal oysters to be smaller than subtidal oysters, although he

attributed this difference to the differential settlement of the intertidal oysters. Ingle and Dawson (1952), working with Crassostrea virginica in Florida, found slower growth in the intertidal zone, and no differences in the growth rates of oysters placed at different subtidal depths. It is not clear for which sizes (or ages) of oysters this applies. For Crassostrea gigas Thunberg in the Pacific there are some data indicating a functional response of exposure and growth. Sumner (1981) found superior growth in subtidally grown oysters over a three month period. Quayle (1988) discussed a strategy of oyster growers in the Pacific Northwest for moving seed to lower shore positions to increase growth. Studies by Wisely et al. (1979a), with Crassostrea commercialis Say in Australia, measured higher growth rates in off-bottom rafts than intertidal racks, although fouling and mortality were reduced intertidally (Wisely et al., 1979b). Walne (1958) demonstrated reduced growth rate with intertidal height with Ostrea edulis L. in Conway, Great Britain. All of these species of oysters have natural intertidal populations over some part of their range.

Dissenting results can be found in Gillmor (1982), who, in laboratory experiments with Crassostrea virginica, explained growth enhancement at simulated intertidal levels as a capacity adaption. This study is interesting and should be repeated. Littlewood (1988) measured the best growth and survival of spat of Crassostrea rhizophorae in the mid intertidal zone, although his tidal data is probably inaccurate.

CONCLUSIONS

The objectives of this study were first, to measure the vertical settlement patterns of oyster larvae; second, to determine the early recruitment and growth patterns of oysters in relation to vertical zonation; finally, to relate these findings to the distribution of oysters at the field site. The results support the hypothesis which explains intertidal zonation as the interaction of biological and physical stressors. The settlement patterns of larvae were shown to be concentrated at depth, with only a slight settlement in the intertidal zone. This is apparently mediated by behavioral factors. Recruitment was found to be both temporally and spatially variable. The high initial mortality which occurred at all sites is probably a function of larval quality. The high air temperatures resulted in total mortalities of the upper intertidal treatments during all experiments, as well as in the low littoral site during the summer. High recruitment in the low intertidal in fall is correlated with lower air temperatures. The oysters at the sublittoral fringe and subtidal treatments were not measurably affected by physical factors, and, although much of the mortality could not be qualified, predation intensity was greater subtidally. Drills were observed to be a major source of predation, and their activity was concentrated in the lower subtidal treatments; however, the effect of both predation and competition were moderated by the sampling procedure. Mortality rates are expected to be higher in undisturbed treatments. Finally, growth was shown to be reduced by long

exposures to air. Thus, the oysters at the field site are not living in optimum conditions.

These data indicate that the intertidal oysters are refuge populations which persist in areas of reduced prédation. Recruitment into this population is probably very low under natural conditions, and is dependent upon favorable, low aerial temperatures coupled with larval availability. Successful recruitment into the "survival zone" thus appears limited to a narrow environmental window. Given the temporal variation inherent in environmental factors, it is conceivable that recruitment into the survival zone may be an episodic event, and may fail to occur during unfavorable years. In 1988 at least, natural recruitment was very slight. But because oysters are relatively long lived and are competitively dominant in the intertidal, even a low level of recruitment will serve to maintain the observed zonal pattern.

These results must be placed within the context of the estuarine system and temporal variations in the factors affecting oyster distributions. For example, prédation intensity is highly dependant on salinity. A salinity-mediated decrease in predator activity could allow oysters to populate substrate lower on the shore and grow into a size refuge. Such a range extension may then persist for years, depending on factors affecting the survival of adults. Conversely, as seen during the summer of 1988, high air temperatures may eliminate recruitment in the intertidal zone for much of the settlement season, and, if coupled by long exposures, can result in increased mortalities of established individuals. This would result in a range contraction. Thus, the perpetuation of the intertidal zonation is a dynamic process.

Interestingly, the observed oyster zonation at this site is probably a result of ecosystem disturbance. Although there is a

correlation of intertidal oysters and salinity (Hopkins, 1954; Bahr and Lanier, 1981), the distribution of intertidal reefs within the Chesapeake Bay subestuaries was once extremely extensive, as the charts compiled by Moore (1909) for the James River clearly indicate. These highly productive intertidal areas appear larger in the higher salinity locations, but the reefs at this time were under heavy exploitation from the dredge fishery, and the differential distribution may thus reflect differential fishing pressures. In any case, the subtidal distribution of oysters far exceeded the intertidal area: the oysters were not restricted to the intertidal zone. This may reflect a predator-swamping effect, or perhaps oysters recruited into the intertidal zone and were later dislodged into the subtidal zone after reaching a size refuge. At the study site (where intertidal reefs once occurred), the predators now far outnumber the oysters, and subtidal oysters are scarce.

Some of the lower Chesapeake intertidal reefs existed as late as 1953 (Marshall, 1953), but at present, all are substantially subtidal, and most are no longer productive. The prime cause of the decline in vertical height has been the physical removal of shell material from the reefs, coupled with the well documented decline in recruitment from previously measured levels (Marshall, 1953; Haven et al., 1978; Haven and Whitcomb, 1983; DeAlteris, 1986; Hargis and Haven, 1986). Seliger and Boggs (1988) described a similar loss of subtidal reefs in Maryland; however, they attributed this loss to sedimentation. It is now clear that the decline of the oyster in Chesapeake Bay is due to overfishing coupled with disease epidemics and environmental degradation. This loss has been a long time coming, and it was not unforeseen. Ironically, the same recommendations for the preservation of the oyster reefs first made

over 100 years ago in response to overfishing are valid arguments today (Armstrong, 1879; Moore, 1909; Galtsoff and Luce, 1930; Loosanoff, 1932).

The loss of the productivity of the intertidal reefs is not merely an economic issue. The extensive reef systems in existence prior to this century likely had a profound influence on the ecology of the entire Chesapeake Bay system (Newell, 1989). Circulation patterns and reef formation are closely interdependent (Norris, 1953; Price, 1954; Scott, 1968). By regulating currents and gyres, the reefs must have affected not only oyster growth and recruitment but also the distribution and abundances of other organisms by influencing the dispersal of pelagic propagules (Pritchard, 1952; Seliger et al, 1982; Shanks and Wright, 1987; Wolanski and Hamner, 1988). Additionally, the sheer numbers of oysters must have significantly affected the pelagic-benthic coupling of energetics through their prodigious filtering and processing abilities (Bahr, 1974; Dame, 1971; Dame et al, 1984; Newell, 1989). Thus, it is probable that the entire ecology of the Chesapeake Bay has been substantially altered by the demise of the oyster. It is highly questionable that the system can be restored within a reasonable time scale.

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