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Abstract

A SPATIAL APPROACH TO THE POPULATION DYNAMICS OF THE MANILA CLAM TAPES PHILIPPINARUM

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The influence of spatial considerations on the population dynamics of sessile and sedentary organisms is explored using the Manila clam (Tapes philippinarum) as a model population. A plot of 8.4x7.2 m was censused once in a sandy beach in Puget Sound, Washington, extracting all the macrofauna and keeping record of their spatial coordinates.

Sediment characteristics and tidal level were highly correlated, so the latter was used to express the changes taking place along the intertidal gradient.

The spatial structure of the population was studied using contour maps and trend surface analysis. Every age group showed well defined patches. A graphical model was proposed to describe the interactions between age groups and the cycling of patches, and several predictions were tested statistically.

A stock-recruitment model was developed trying to reproduce the conflicting forces governing adult-larval interactions.

Changes in mortality, growth and recruitment with tidal level were analyzed, in an attempt to introduce the effect of a gradient in the population models.

It was assumed that mortality rates were a function of time of exposure to stress and to aquatic and terrestrial predators, which were a function of tidal level.

Recruitment and tidal level were related by a simple model which expressed the proportion of time a given level was covered by the tide.

Individual growth was studied using length at age data, growth ratios (length at age i+1)/(length at age i) and the von Bertalanffy model. For the latter, the parameters were related to tidal level, and combined in a single model expressing length as a function of age and tidal level.

Three indices of competition provided evidence of intraspecific competition in the stronger age classes. Food was considered the limiting resource.

Combining the models for growth and mortality, biomass per unit area was expressed as a function of age and tidal level. Maximization of long term yield based on the

concept of optimal rotation and a bioeconomic example were adapted from the forestry literature. Some applications of these results to aquaculture and harvesting of wild stocks were discussed.

A SPATIAL APPROACH TO THE POPULATION DYNAMICS OF THE MANILA CLAM (*TAPES PHILIPPINARUM*)

by

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INTRODUCTION

One of the key tools in modern fisheries management is the descriptive model representing the dynamics of a resource. Most of these models were developed for pelagic fisheries, or more generally, for fish populations. Although criticized, such a model provides the basis to understand some of the processes that control production in aquatic environments and the effects of exploitation.

The characteristics of the resources considered constitute an integral part of the set of assumptions required for the validity of a model, although they are seldom explicitly stated as such. Mobility is one of these characteristics. Pelagic fishes can roam freely within a large environment so that the stock itself and the effect of exploitation on it may be considered as "homogeneously" distributed over a large area. "Homogeneously" in this case means that any subarea experiencing local depletion from the fishery or any other cause would be rapidly reoccupied by adjacent members of the population; a redistribution of density would follow, and the impact would be absorbed by the whole stock. Local differences and any spatial component are negligible and ignored.

These assumptions are not always true for fish, and they are clearly false for a group of resources which could be called "space-related species". These must include: sessile and sedentary organisms (mussels, clams, seaweeds), species with low mobility (scallops, sea urchins), and territorial animals of any questions have addressed themselves to either a very large scale (biogeography) or a very specific methodological problem (description of pattern). Originally those studies were limited to the description of an instant in time; the dynamics of the processes were generally ignored, probably because of the difficulties inherent in the simultaneous consideration of time and space. One of the basic needs to bridge that gap is the development or adaptation of quantitative methods capable of incorporating that dual nature as an element of the problem. Many methods have already been developed in other sciences which deal frequently with spatial problems (geography, geology) or with the management of sessile resources (agriculture, forestry). However, fishery biologists facing the need to study sessile or sedentary populations have traditionally turned their attention to the methods employed in studies of pelagic fisheries, failing to recognize the closer resemblance of their problems with those faced by scientists working in those seemingly more distant disciplines (e.g.foresters). In spite of the deficiencies of the techniques available and of the vagaries of nature, it seems necessary to try to develop a quantitative approach to the management of these populations. This probably requires some adaptations of the classical methods plus the introduction of new points of view.

When an individual requires a space to survive and reproduce, many features of its biology and ecology will be determined by that requirement. To search for a site, to maintain control of it (competing with neighbors and trying to exclude invaders), and to reproduce, an individual must experience a complex set of *biological interactions*. Once in a site, the individual faces a particular set of *abiotic conditions*; these conditions may change even over short distances when for instance, a strong gradient is present.

There are five main aspects to consider under the two sets mentioned above; "space-related species" differ from more mobile ones in all five of them:

1) An animal linked to a space is forced to endure the micro-environment of the site; there may be no option to move to "greener pastures". A population therefore occupies a range of habitat conditions but each individual is exposed to a single set of such conditions, perhaps throughout its life. This results in a wide variation in the values of many population parameters over the habitat range. In the particular case of intertidal organisms, the existence of a well

defined gradient generates a variety of conditions in a usually limited space.

2) In most cases, the lack of mobility generates a reproductive constraint; the search of a mate has to be relegated to the gametes which are transported more or less passively in a fluid environment (air, water). The need to increase the chances of encounter between gametes is probably the driving force in the development of patchiness in many space-related species.

3) If the access to the food supply and the probability of successful reproduction require the control of a space, the dispersal unit has to find an adequate site to settle. Habitat selection by these units is likely to consist of a more or less complex set of behavioral responses to environmental clues, which are used to gather information on site quality. Of all the clues, the only type that provides some basic assurances of long term habitat suitability is the presence of adults of the same species. This is an additional factor contributing to patchiness and also the origin of intense interactions between dispersal units and adults.

4) At the time of settlement, the dispersal unit (larvae, spore, seed) must avoid or overcome the

defenses used by individuals already present to maintain control of a space. After settlement in turn, the recruits to the beach must try to prevent further colonization of the space they control. These two processes probably generate intense interactions between age groups.

5) If the supply of food (photons, particles, etc.) depends on the control of a space, competition becomes a predominantly local phenomenon, a neighborhood effect. Individuals are affected by crowding (sensu LLOYD, 1967), not by total numbers, biomass or mean density. Competition depends on the spatial configurations of competitors surrounding each individual of the population. The concept applies both to interspecific and intraspecific competition (within and between age classes).

The objective of this work is to study from a spatial point of view, some of those biological interactions and abiotic conditions in a model population. As the methods available to tackle spatial problems are scarce and not always adequate, a second objective is to adapt or develop some quantitative methods.

With these objectives in mind, the next step is the choice of a convenient model population. Intertidal molluscs seem especially adequate for that role. To begin with, intertidal animals inhabit a strong environmental gradient; within a few meters it is possible to find their optimum and their extreme conditions for growth, survival, reproduction. Although many have studied growth and mortality of molluscs at different tidal levels (STEPHEN, 1928; HALLAM, 1967; SEED, 1969b; TREVALLION et al., 1970; SUTHERLAND 1970; VERMEIJ, 1972; BEUKEMA et al., 1977; READING, 1979; GRIFFITHS, 1981), their studies are mostly based on a gross subdivision in higher and lower fractions of the beach, and they do not provide an easy way to include the effect of tidal level (a spatial gradient) on the parameters investigated. This is believed to be an important component in any model describing the biomass of an intertidal population.

As most of the information available comes from epifaunal species , it was considered convenient to select an infaunal species, to help fill the gap that exists in our knowledge of these populations. For similar reasons a soft bottom was preferred over a rocky shore. Within these constraints, clams were thought to be the more convenient model organisms.

The presence of growth rings in the shells allows reasonable easy access to information on age and growth. Many clams live in patches in an environment which is also patchy for most other characteristics, including other species (WOODIN, 1976; FINDLAY, 1981). Of all the clam species present in the Puget Sound, the Manila clam <u>Tapes philippinarum</u> has the best combination of ecological features for this study (abundance, access, etc).

The final step is to decide on a methodology that could provide the information sought. This thesis attempts to develop or adapt new methods to analyze the dynamics of a population from the information contained in a single "snapshot" of its spatial configuration. The snapshot consists of a complete census and map of a population in an area. Map in this case means a two-dimensional representation of the <u>individual locations</u> for all members of the population censused. As clams preserve part of their history in their shells, additional information on age and growth can also be related to their spatial location.

Perhaps the most serious inconvenience of the design proposed is the fact that material limitations impose a scale which may not be adequate; it would be extremely cumbersome to study the number of patches that could give a good representation of habitat types, etc. or to census an area large enough to be sure that sample size is not an issue. By replacing extensive and prolonged surveys with an intensive census, it will be possible to obtain detailed spatial information but at the expense of generality. In spite of this, it seems necessary to gain some insight into the small-scale spatial structure of a population before proceeding to a more refined and more general treatment of the subject.

SAMPLING PROGRAM

The stated objectives required detailed information on the spatial configuration of the population and a good description of the habitat in problem is quite different from the one considered here because of the mobility of the scallops. Another very different but also interesting approach was the study of the dynamics of patches in a mussel population (PAINE and LEVIN, 1981). This approach however, cannot be used for infaunal species. In the first place, the presence and type of patches cannot be ascertained by simple observation; it is necessary to carry out intensive sampling programs to achieve a reasonable description of the condition of the system at a given time. In the second place, the sampling process in itself generates a disturbance that cannot be reversed, so continuous observations of the same space at different times are not possible. An analogous problem is faced by paleontologists, trying to infer the dynamics of a population after finding a snapshot of its history created by a sudden catastrophe (volcanic eruption, mudslide).

There are no precedents of intensive surveys of the type described for infaunal invertebrates, and only a few studies that we could consider parallel to this in other environments such as a tropical forest (HUBBELL,1979), the soil (HAIRSTON et al., 1976) or in tree stands under exploitation (several papers in J.FRIES (ed), 1974; ARNEY, 1972; EK and

MONSERUD, 1974).

The lack of literature on this topic together with the lack of specific information concerning patch sizes in the Manila clam prevented the use of standard sampling designs, and because of that, several arbitrary decisions had to be made with respect to sample size, shape, etc.

CHOICE OF TARGET SPECIES

Among the many clam species present in Puget Sound, the Manila clam, *Tapes philippinarum*, seemed the most adequate for the objectives pursued. Even though it is an introduced species (QUAYLE,1941), it now has an important economic role and is a solid candidate for aquacultural development in the future (LUCAS, 1976, 1977; MILLER et al., 1978; ANDERSON et al., 1982).

Sexes are separate; the individuals reach sexual maturity within their first year of life, and spawning takes place in late spring and summer (HOLLAND, 1972). The planktonic larval stage lasts 2-4 weeks (YOSHIDA, 1953; QUAYLE and BOURNE, 1972).

The species is a filter-feeder and lives quite high in the intertidal (up to +8 ft on this beach), thus allowing for long sampling periods during low tides. It forms practically pure populations, with only a small number of individuals from other species of the macrofauna present. It prospers in gravelly areas which are suitable for sampling, and it does not bury itself very deeply (usually less than 15 cm, QUAYLE and BOURNE, 1972); both of these factors make sampling relatively easy. A recent bibliography of the genus is available (PARTRIDGE, 1977). Several studies on different aspects of the biology and ecology of the species, many performed in the Puget Sound region, provide abundant information (OHBA, 1956,1959a,1959b; NOSHO, 1971; HOLLAND, 1972; NOSHO et al., 1972; JONES, 1974; MILLER et al., 1978; GLOCK, 1978,1979; WILLIAMS, 1978,1980a,1980b; MILLER, 1982; MILLER et al., 1982; ANDERSON, 1982; ANDERSON et al., 1982). At present, there is some confusion concerning its specific name; Tapes, Ruditapes and Venerupis are used as generic names, usually combined with japonica or philippinarum.

CHOICE OF THE SITE

It was believed from the start that in order to appreciate the natural dynamics of a population, it would be desirable to work on a site as free as possible of human interference. In this way, factors such as recreational or commercial digging which probably have a strong impact on the spatial structure of the populations could be eliminated.

Many locations were explored throughout the Puget Sound and neighboring areas, searching for a site that has not been utilized in a long period, preferably close to twice the maximum life span of the organisms present in the area (2x7 = 14 years). This would insure that even the oldest animals present have lived free from human interference.

Availability and access were also requirements, considering the intensity of the sampling proposed. Populations low in the beach or in muddy areas made access very limited in time or very difficult. Even if access was adequate, the digging technique required for mapping the population could not be applied unless the substrate was rather firm and free from flooding.

After sampling in more than 30 locations in the region, a beach in upper Carr Inlet was selected (Fig. 1). The particular cove in Henderson Bay is very narrow , opening to the west side of Carr Inlet (Fig. 2). An aerial photograph of the cove shows the broad features of the sampling area (Fig. 3). A well marked spit on the South and another less prominent point on the North side mark the entrance of the cove whicht runs in a general East-West direction with its minimum width

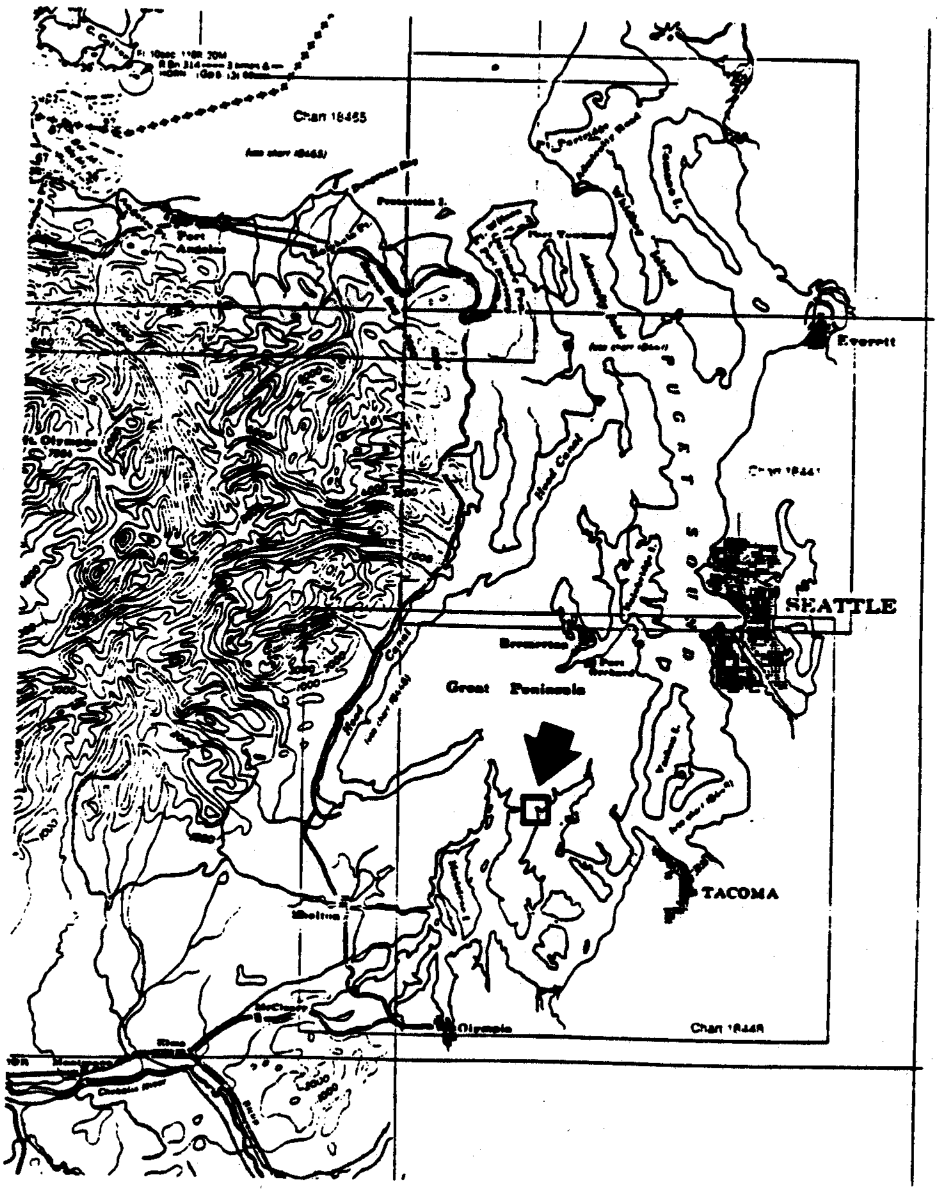


FIG. 1 : Map of Puget Sound showing the location of the study area.

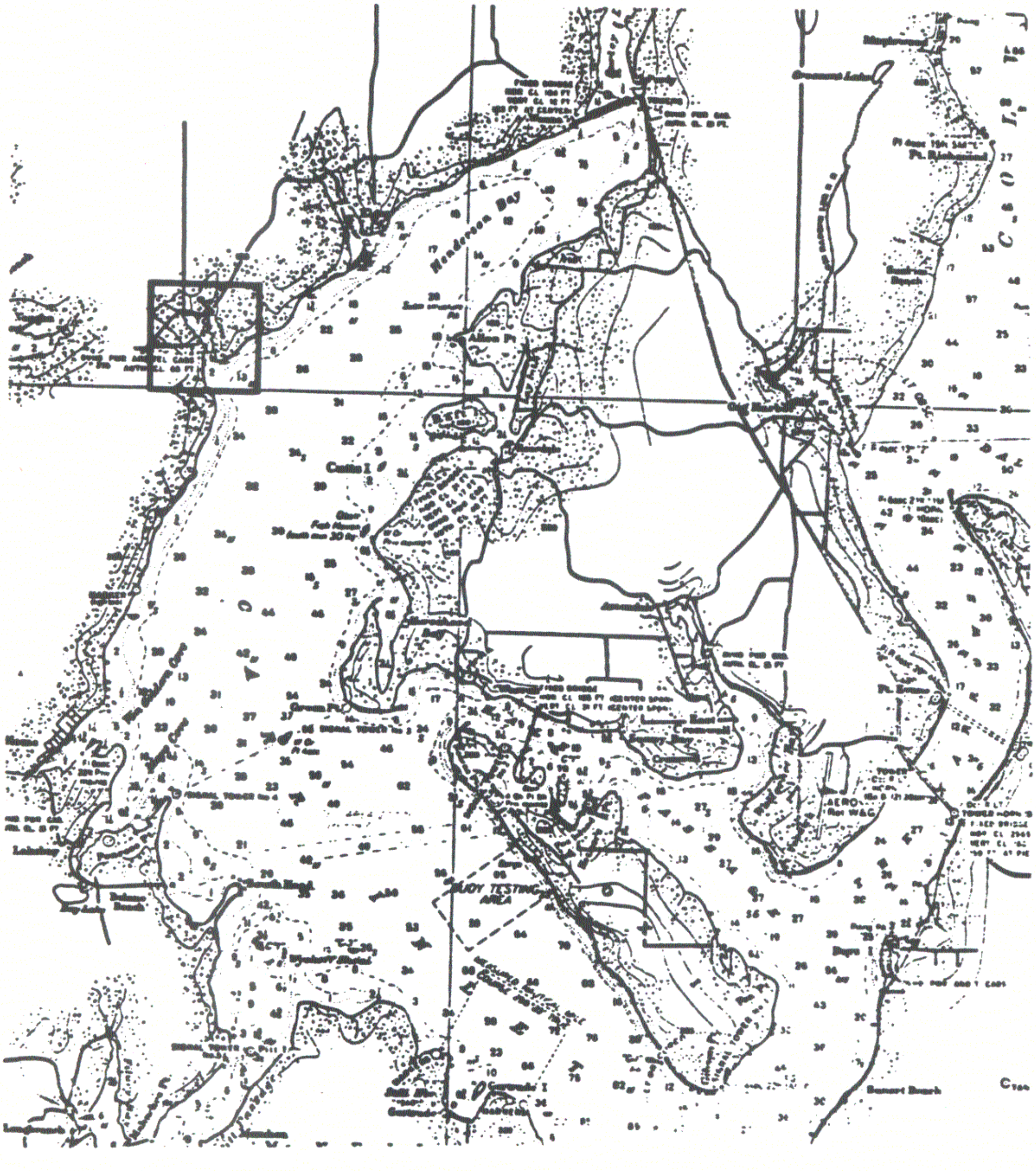


FIG. 2 : Detail of Henderson Bay showing the orientation of Glencove.

FIG. 3 : Aerial photograph of Glencove. Scale 1:12000.

being roughly half way to the head . It is very shallow, and in minus tides the whole cove has a depth of less than 90 cm. The sea condition is very calm; even outside the mouth wave heights are quite low (ANON., 1977).

Human activities in the area are mostly restricted to canoeing and sailing at or near the small pier from the YMCA Camp Seymour in whose property the plot is located. Motor boat traffic, which may create waves, is not significant in spite of the presence of a marina in the west end; in a peak summer day the number of boats going in or out is not greater than 20; on most other days, the activity is restricted to fewer than 5 boats. There is no evidence of pollution or disturbances arising from this source.

All beaches in the cove are privately owned and their use is far from intensive. In particular, the site chosen has explicit prohibitions concerning clam digging. Year-round personnel from the Camp enforces these regulations. Apparently, the requirement of a prolonged period without disturbance was satisfied for the last 12 years with certainty and quite possibly for 4-5 more years. It can then be assumed quite safely that the population under study is as close as possible to a "pristine" condition. In regard to natural catastrophes, there is no record of any massive mortality nor disruption of the beach by storms, etc. The combination of a narrow mouth with spits on both sides, the orientation of the cove and its shallowness provide excellent protection against wind and waves. Fig. 4 shows some aspects of the site studied.

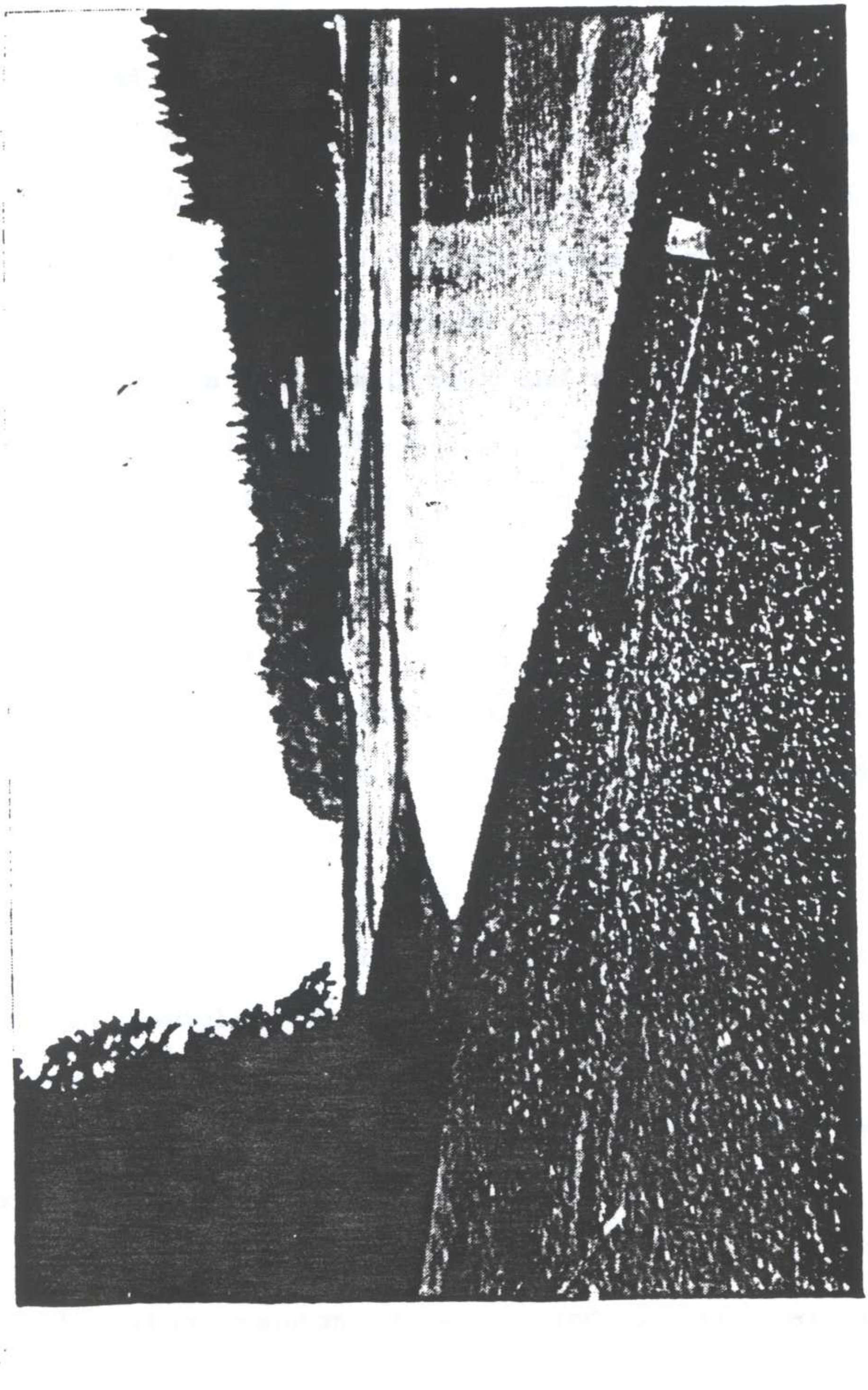
CHOICE OF THE TIME

Because low tides in winter are nocturnal, the sampling period was the summer (1980). Collections were taken daily during all days in which the tides allowed access to the plot (roughly 12 out of every 14).

SAMPLING

The upper limit of the sampling area was defined by the upper limit of the vertical distribution of the clams (at a tidal level of approx. +2.4 m (+8 ft)). The lower end was determined after finding a change in the slope of the beach that resulted in a flatter, muddier area, at a tidal level of +1.5 m (+4.5 ft). The slope of the section studied was 7 degrees. The width of the plot was left open to "grow" as sampling progressed, with time constraints ultimately limiting it. This area was divided into quadrats 90x60 cm for

FIG. 4 : View of the study site.

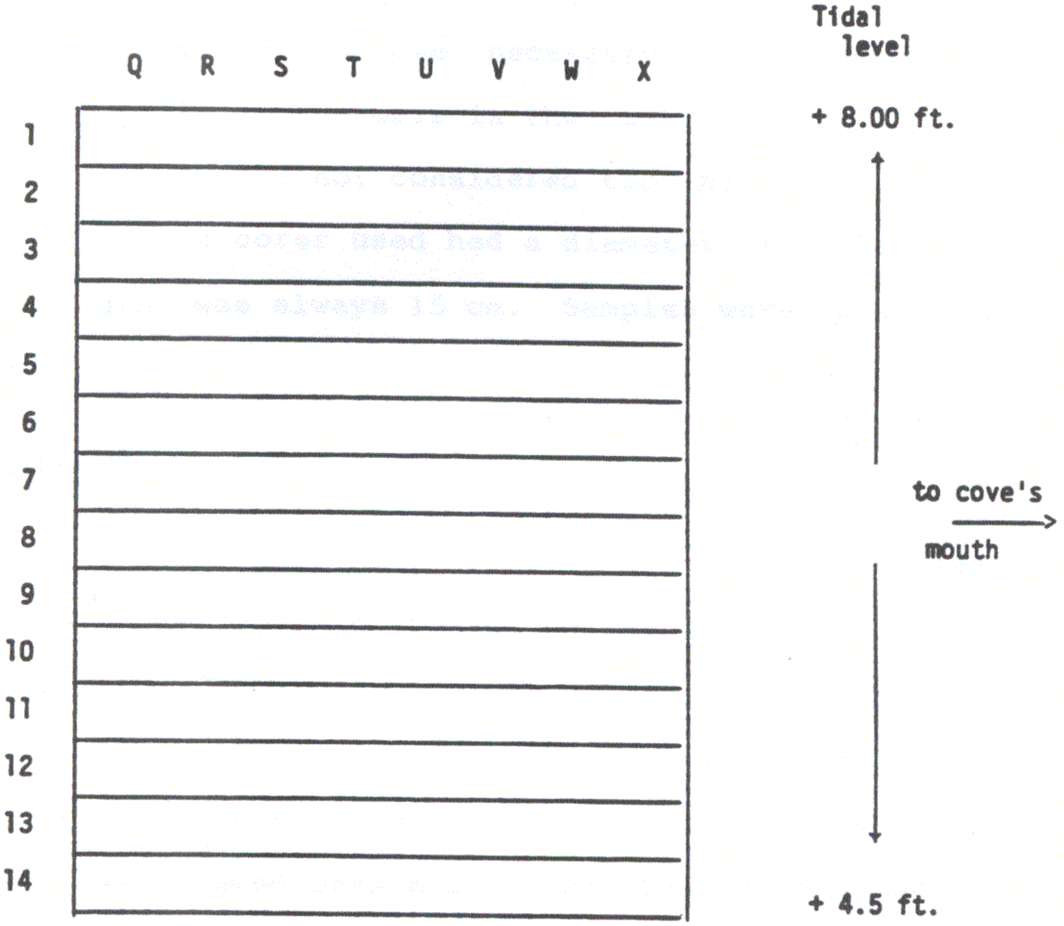


convenience; these quadrats were used only as "administrative" units. As <u>locations of individuals</u> were used for most analysis, the size or shape of the quadrats had no bearing on the results, and they were replaced by other subdivisions whenever it seemed convenient to do so. The final layout is shown in Fig.5; the plot divided into 8 columns perpendicular to the shoreline by 14 rows parallel to it. Columns were identified by the letters Q to X and rows by the numbers 1 (highest level) to 14 (lowest level). Total area sampled was 7.2x8.4 m = 60.48 sq.m (24x28 ft = 672 sq.ft).

SAMPLING THE SEDIMENTS

In order to obtain some measure of the heterogeneity of the habitat, a series of sediment samples were taken by corer throughout the beach as it was not possible to gather continuous data along the gradient. The design used was a double systematic sample, chosen to provide even coverage of the plot. Cores were taken from one out every two quadrats following a checkered pattern (e.g. Q1,Q3,Q5,.....Q13, R2,R4,R6,........R14 ... in the notation of Fig.5) . After that, 15 quadrats were selected using random numbers, and additional cores taken from the centers of these if they had not been

Fig. 5 : Layout of study area.



Columns : Q to X, 8 columns 3 feet wide each; total width 24 ft.
(90 cm.) (7.2 m.)

Rows : 1 to 14, 14 rows 2 feet long each; total length 28 ft.
(60 cm.) (8.4 m)

TOTAL AREA : 672 sq.ft. (60.48 sq.m.)

extracted already in the systematic samples. This second set provides a random sample of quadrats in case some estimation would become necessary. The cost of flexibility is an increase in the number of samples to process, but it was not considered too high.

The corer used had a diameter of 12.5 cm and core length was always 15 cm. Samples were preserved frozen.

SAMPLING THE POPULATION

To determine the coordinates for each individual the following technique was used: an aluminum ruler 1 m long with two holes separated by exactly 90 cm was placed in such a way that the protruding section of two buried stakes fitted inside them. As the ruler itself was screwed onto a L-shaped piece of aluminum , an axis was defined this way. Over this system, a right angle ruler (longer arm = 60 cm) could be positioned in

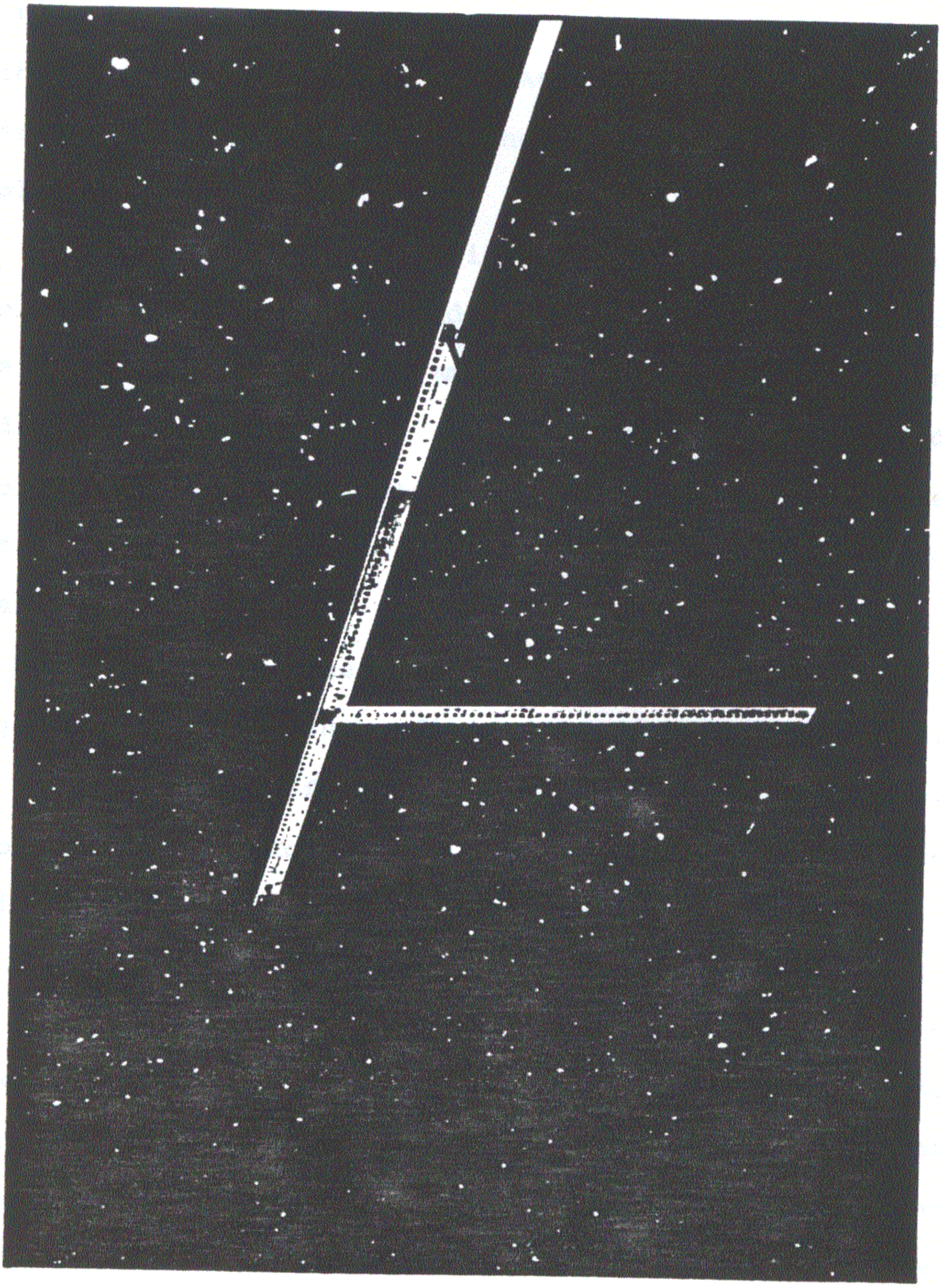


FIG. 6 : Measuring device used to record spatial cordinates.

focus was to gather information on patchiness of the settlers in the absence of an adult population.

PROCESSING THE SEDIMENT SAMPLES

After thawing, samples were split in two to preserve a back-up sample. The half chosen to process was then split repeatedly until reaching 500-600 g , discarding the rest. A fraction of 500 g was used for particle size analysis, another of 15 g for the determination of organic matter.

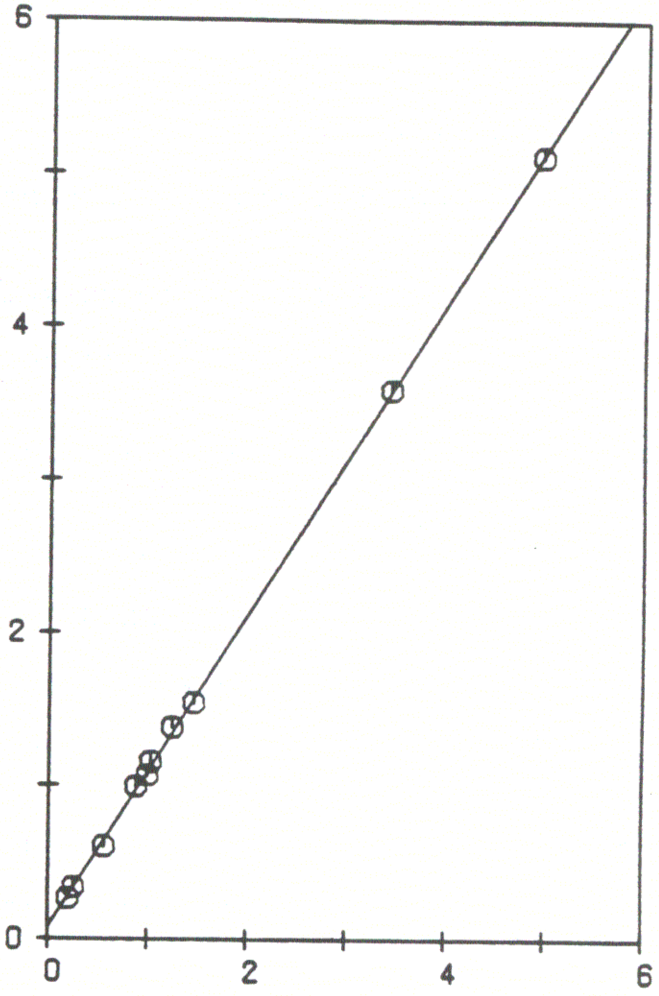
PARTICLE SIZE ANALYSIS: The following description is provided to indicate some of the deviations from standard procedures that were needed because of the gravel content of the samples:

The sediment sample was dried at 103-105° C overnight. The whole was sieved by hand into 3 fractions corresponding to sizes -3, -2 and -1 or less in the Wentworth scale. In this scale, the values used are the negative logarithm of base 2 of the particle size in mm (called phi units). The larger fractions were then weighed and discarded; the remaining fraction was split to yield 30-60 g of material for further sieving. The rest of the process was performed using a mechanical shaker and the traditional techniques. The fractions considered went from -3 to +4 phi units, all material smaller than +4 was pooled in a single category. Table A-1 in Appendix A provides the particle size distribution for all samples in percent weight. [All Tables in which the letter A precedes the number will be found in that Appendix].

DETERMINATION OF ORGANIC MATTER: This analysis was performed by ignition in a muffle furnace at 600°C for an hour, following the standard technique in A.P.H.A.(1971). The calibration was run with a standard of glucose (GROSS, 1971). Fig. 7 shows the calibration function for 10 samples. As can be seen, the relationship is linear within the range of the data. The values of r^2 (0.99986) and the standard deviation about the regression (0.0274) show the close approximation of both measures. The slope (1.0199) indicates a tendency to overestimate the actual concentration. Table I shows the corresponding statistics.

STATISTICAL PROCESSING OF SEDIMENT DATA

The statistical analysis of the results was



Concentration in standard (%)

FIG. 7 : Organic matter calibration. Loss upon ignition versus glucose concentration in standard.

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  TABLE  I : Organic matter calibration

     y = concentration measured (%)

     x = concentration standard (%)

         y = 0.0704 + 1.0199 x

        S.E.(b)  = 0.0060

        S.E.(a)  = 0.0125

        S.Deviation = 0.0274

        r2 = 0.99986

    The slope is not significantly different from 1.
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sorting, etc. based on the size distribution (Trask values, Inman values, etc.). Of these, the Folk and Ward values were chosen because they are considered the most adequate in the case of bimodal distributions prevailing in most of these samples (TRASK, 1930; INMAN, 1952; FOLK and WARD, 1957; FOLK, 1966). Table A-2 shows the statistical results obtained using SEDAN: Percent gravel, sand and silt, Sand/Mud ratio, and the mean, deviation, skewness and kurtosis according to Folk & Ward formulas (Table A-3).

The values of the different parameters are shown for all samples in the beach in Tables A-4 I to A-4 VI.

The mean phi value is a measure of the particle size in the sample. The deviation, measuring spread around the mean is used as a coefficient expressing the degree of sorting. Skewed distributions arise when some selective agent operates against one of the tails of the distribution. Kurtosis can also be related to sorting; leptokurtic distributions would correspond to the better sorted samples.

The bimodality observed in the frequency distribution of particle size is usually ascribed to the action of 2 transport agents, each one imposing its own characteristics in the size composition (FRIEDMAN and

SANDERS, 1978). Considering the size of the particles in both modes (see Table A-1), we can speculate that the gravel fraction is probably of glacial origin, while the smaller-sized mode is probably due to hydrodynamic factors. In this region, the combination of modes observed is typical of the Vashon till (ANON., 1977).

PROCESSING THE BIOLOGICAL SAMPLES

Samples were thawed at room temperature. After washing, sorting and drying, all the animals were weighed and measured. For the Manila clam, growth rings were identified under a binocular microscope, and the length at each ring was also measured. Other authors (OHBA, 1959) had difficulties with the location of growth rings in Japanese populations of this species, but in the material analyzed they were quite distinct. The annual periodicity of the rings was verified by comparison with mark-recapture experiments and with individuals of known age from other studies in the same area (ANDERSON, 1982). In what follows, the age of an animal will be expressed as a number of rings even though the first ring is usually laid down at approximately 6 months from settlement (QUAYLE, 1952; JONES, 1974). An age 3 for instance, indicates that an animal has already laid down its third ring, not that it is actually 3 years old. Chronological age was used in the growth models, and later in the biomass model.

Initially, weight of meat, shell and total were recorded separately, but due to the constancy in the proportions of different parts it was decided to measure only total individual weight. Table II provides information on these relationships.

Weights and lengths were recorded for a total of close to 7000 individuals belonging to 4 bivalve species. The other 3 species present were the native littleneck (*Protothaca staminea*), the horse clam (*Saxidomus nuttalli*) and *Cryptomya californica*. Less than 5 % of the total number belonged to these other three species.

BRIEF SKETCH OF THE COMMUNITY

Besides the 4 species of bivalves mentioned above, only a few macrofauna components were found. Among the infauna only the ghost shrimp (*Upogebia pugettensis*) appeared in the samples. Its presence was not quantified because of the difficulty of assessing whether tubes were occupied or not without digging much deeper than was usually necessary for the clams.

When the tide is low, we can observe an epifauna composed of small barnacles and mussels attached to pebbles, and a few crabs (*Hemigrapsus sp*)

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TABLE II : Regressions to verify relationships between total weight (TW), meat weight (MW) and shell weight (SW) for the Manila clam. $n = 170$

i) $TW = -3.79 + 1.76(SW)$ $r^2 = 0.9927$ $p < 0.001$
S.E.(b) = .0117 S.E.estimate = 17.64

ii) $TW = 10.37 + 2.55(MW)$ $r^2 = 0.9885$ $p < 0.001$
S.E.(b) = .0213 S.E.estimate = 22.16

iii) $SW = 9.66 + 1.43(MW)$ $r^2 = 0.9702$ $p < 0.001$
S.E.(b) = .0194 S.E.estimate = 20.21

****

seeking shelter under occasional cobbles. Both in numbers and in biomass they are not significant ; their impact on the population is not clear, but they are known to prey on juvenile bivalves (BOURNE and LEE, 1973). During low tides crows and often some dominican seagulls prey in the exposed area.

Although no direct observations are available during high tide, it can be inferred from the presence of individuals or other evidence that moon snails (Polinices lewisii), red rock crabs (Cancer productus) and some flatfish probably prey on this population when it is accessible to them (MILLER, 1982; ANDERSON et al., 1982; ANDERSON, 1982). The impact of a very dense population of Pacific staghorn sculpin (Leptocottus armatus) present in the area is not easy to ascertain; they prey on bivalves, but they seem to prefer other types of prey (MILLER, 1982; THORNBURG, 1978; WINGERT et al., 1979). A kingfisher (Megaceryle alcyon) is the most frequently observed predator on the sculpins, probably limiting their use of the shallower areas of the beach. This sketch of the community is obviously incomplete with observations limited to low tides, daylight hours and during a single season.

ANALYSIS OF SITE EFFECTS

The first step in the analysis of the problem must be the identification of those environmental variables with a significant impact on the population.

As a result of the sediment analysis, a set of 6 variables describing different aspects of the physico-chemical characteristics of the beach was produced : Organic matter content (OM), particle size (PHI), sorting coefficient (DEV), skewness (SKEW), kurtosis (KURT) and percentage of gravel in the sample (GRAV).

To these, we must add the tidal level (TL) as another descriptor of the environment in which the animals are living. This is probably a complex variable, that is to say one which represents several sources of variation. For instance, the tidal level is clearly correlated to the amount of time intertidal animals spend submerged during the whole tidal cycle. The way this time changes with tidal level has been studied by several authors (HEWATT, 1937;DOTY, 1946,1957; RICKETTS and CALVIN, 1952). This in turn translates into changes in the following processes:

a) The amount of time available for feeding

b) The amount of time exposed to aquatic and terrestrial predators.

c) The degree of exposure to environmental stresses : extreme temperatures or salinities, dessication, etc.

d) The degree of accessibility for larvae attempting settlement.

Tidal level is likely to affect most population processes for possibly different reasons. Some of these effects will generally be confounded in the analysis, unless specific experiments are performed to isolate the sources.

An accurate analysis of these factors requires a detailed study which is beyond the scope of this work. However, an assessment of the relative influence of each one of them, and a determination of the degree of redundancy within the system of sedimentary characteristics measured should help to reduce the number of variables.

The approach chosen is to identify a set of population characteristics that could be affected by the environmental variables mentioned and to measure their covariation. These population characteristics had to be averaged over quadrats for which measures of sedimentary variables were available. This requirement introduces some problems: a) some population parameters cannot be

* * *

TABLE III : Correlation matrix between sediment properties and population parameters, n=53. (PARTITIONED FOR PRESENTATION)

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

a) Sedimentary properties and tidal level

	OM	PHI	DEV	SKEW	KURT	GRAV	Y
OM	--	.38	.44	-.28	-.26	-.28	.46
PHI	**	--	.74	-.95	-.57	-.94	.72
DEV	***	***	--	-.55	-.53	-.67	.59
SKEW	*	***	***	--	.46	.90	-.70
KURT	ns	***	***	***	--	.70	-.50
GRAV	*	***	***	***	***	--	-.64
Y	***	***	***	***	***	***	--

b) Population parameters

	L1	R2/R1	R3/R2	L3	N1
L1	--	-.14	.08	.82	.23
R2/R1	ns	--	.06	-.05	-.17
R3/R2	ns	ns	--	-.08	.04
L3	***	ns	ns	--	.35
N1	ns	ns	ns	*	--

c) Sedimentary properties, tidal level and population parameters.

	L1	R2/R1	R3/R2	L3	N1
OM	.37 **	-.06 ns	.07 ns	.34 *	.11 ns
PHI	.56 ***	-.12 ns	.05 ns	.63 ***	.31 *
DEV	.24 ns	.08 ns	-.10 ns	.46 ***	.38 **
SKEW	-.61 ***	.17 ns	-.01 ns	-.63 ***	-.23 ns
KURT	-.39 **	.26 *	-.04 ns	-.52 ***	-.41 **
GRAV	-.52 ***	.18 ns	-.03 ns	-.57 ***	-.34 *
Y	.83 ***	.00 ns	.07 ns	.89 ***	.35 **

* * *

other variables. It is fairly obvious that there is some redundancy present and possibly some spurious correlations.

In order to explore these alternatives, a matrix of partial correlations was prepared, controlling for tidal level (TABLE IV). The choice of tidal level as the control variable is based on the considerations made concerning its multiple impact on the populations, and on the fact that some sedimentary variables are known to vary according to the level of the beach (e.g.particle size, sorting, etc).

After this step, most of the significant correlations disappeared, indicating their spurious character. The few left are :

i) the negative correlations between the coefficient of sorting and size of animals in their first year (length).

ii) the positive correlation between kurtosis and the growth ratio R2/R1.

iii) the negative correlation between number of recruits and kurtosis.

An attempt to control a second variable (particle size) did not improve the results obtained in the previous step, so it was omitted. Both kurtosis and the coefficient of sorting can be considered as measures

****

TABLE IV : Partial correlations between population parameters and sediment properties controlling for tidal level.

	L1	R2R1	R3R2	L3	N1
OM	-.02	-.07	.05	-.20	-.06
	ns	ns	ns	ns	ns
PHI	-.11	-.17	.00	-.05	.08
	ns	ns	ns	ns	ns
DEV	-.56	.09	-.17	-.19	.23
	***	ns	ns	ns	ns
SKEW	-.09	.24	.05	-.03	.02
	ns	ns	ns	ns	ns
KURT	.05	.30	.00	-.19	-.29
	ns	*	ns	ns	*
GRAV	.03	.24	.02	.01	-.16
	ns	ns	ns	ns	ns

****

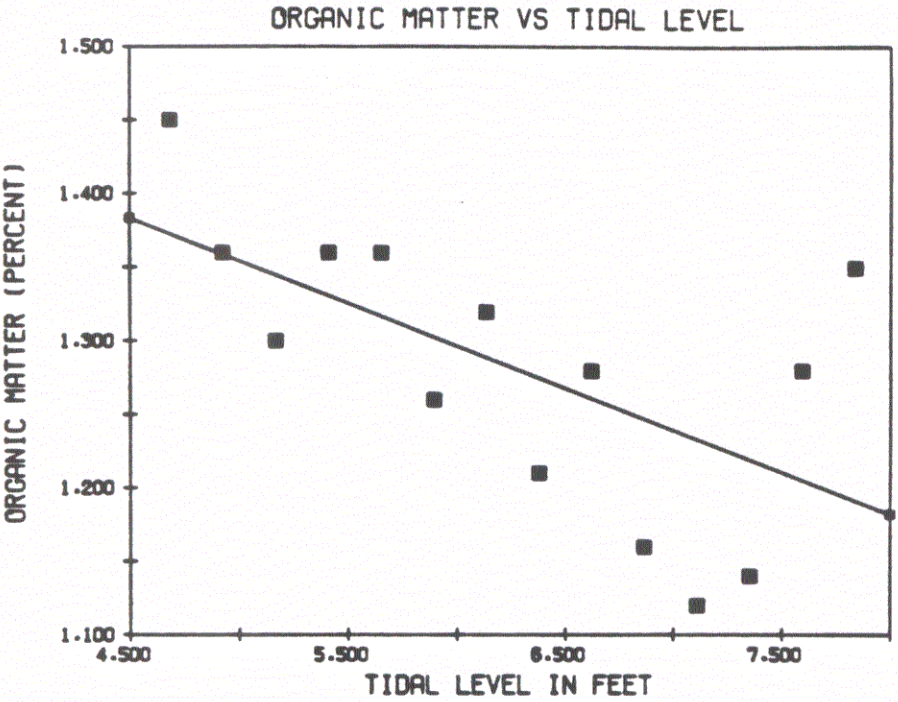
of homogeneity in the particle size distribution and they usually increase at lower tidal levels.

The most likely explanation for the remaining significant correlations can be found in Figs. 8 to 13 which show the changes in some sedimentary properties with tidal level. In a partial correlation, we control the effect of one variable by eliminating a linear component attributed to that source. It is quite obvious that the effect of the tidal level is not linear (DOTY, 1946,1957). The nonlinear components present in the system leave a portion of the variation due to the control variable still in place. As the coefficient of sorting and the kurtosis are also nonlinear functions of tidal level, their remnants correlate with the remnants of some other variables, especially those that follow more closely the true tidal level effect.

It could be possible to modify the analysis to allow for the non-linear behavior of some of the functions, but it does not seem really necessary. Even the raw approach utilized eliminates most of the variation in the system, so the redundancy is quite evident. This fact, and the impossibility to establish true causal relationships from this type of analysis suggest a simplified approach.

FIG. 8 : Organic matter (loss upon ignition) % versus tidal level in feet.

FIG. 9 : Particle size (phi units) versus tidal level in feet.


ORGANIC MATTER VS TIDAL LEVEL
1.500
1.400
1.300
1.200
1.100
ORGANIC MATTER (PERCENT)
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET

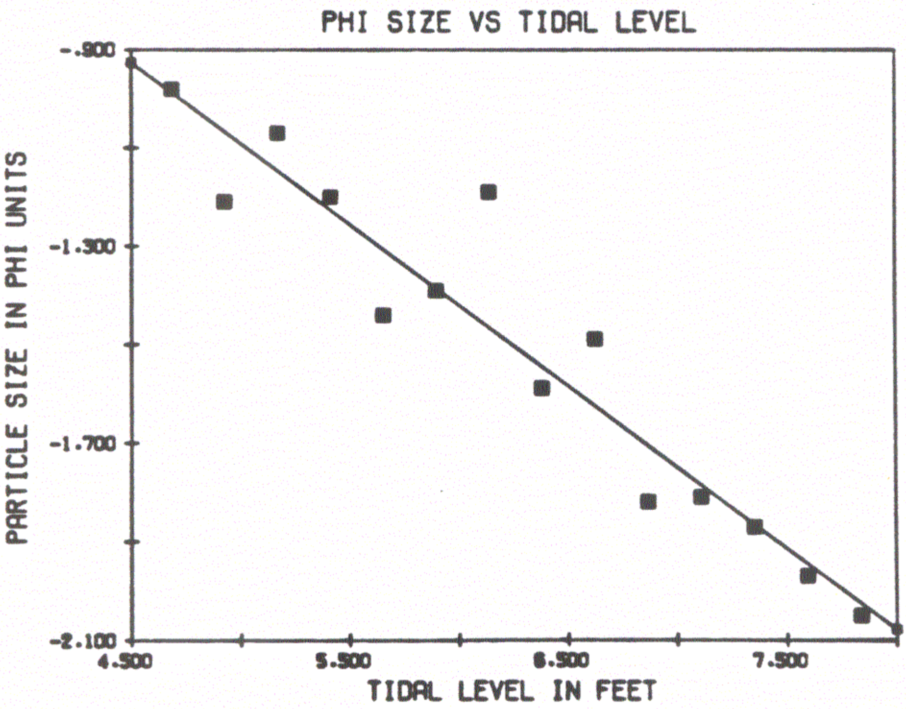
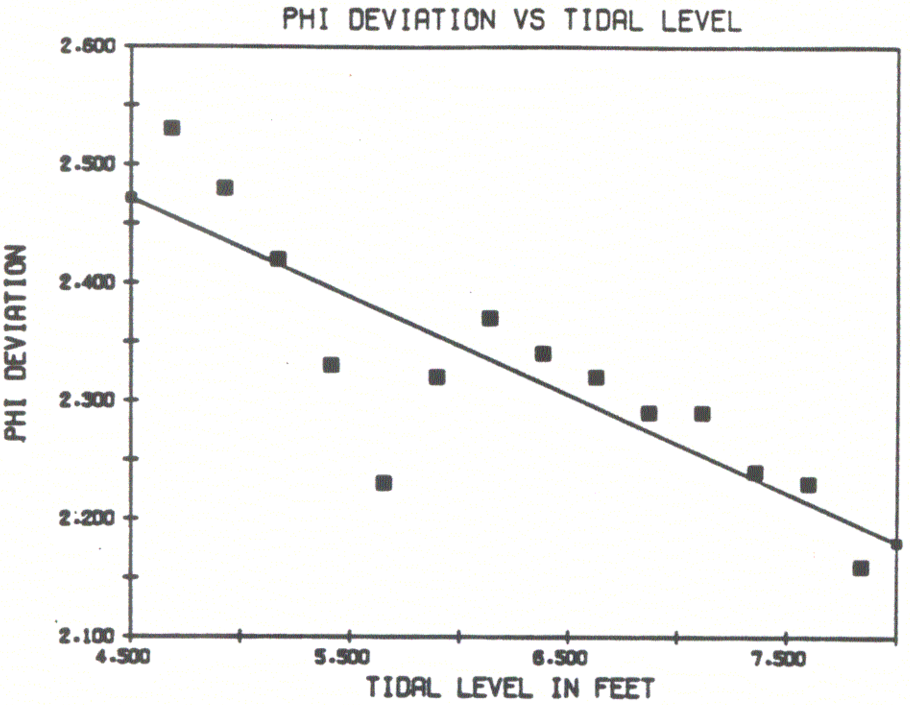

PHI SIZE VS TIDAL LEVEL
-.900
-1.300
-1.700
-2.100
PARTICLE SIZE IN PHI UNITS
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET

FIG. 10 : Phi deviation versus tidal level in feet.

FIG. 11 : Phi skewness versus tidal level in feet.


PHI DEVIATION VS TIDAL LEVEL
2.600
2.500
2.400
2.300
2.200
2.100
PHI DEVIATION
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET

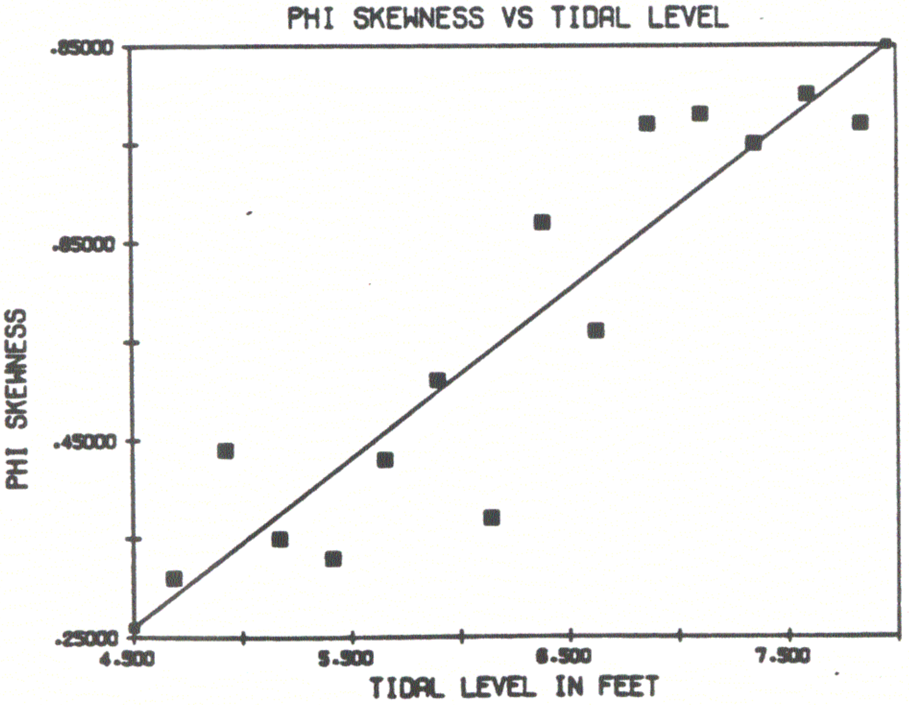
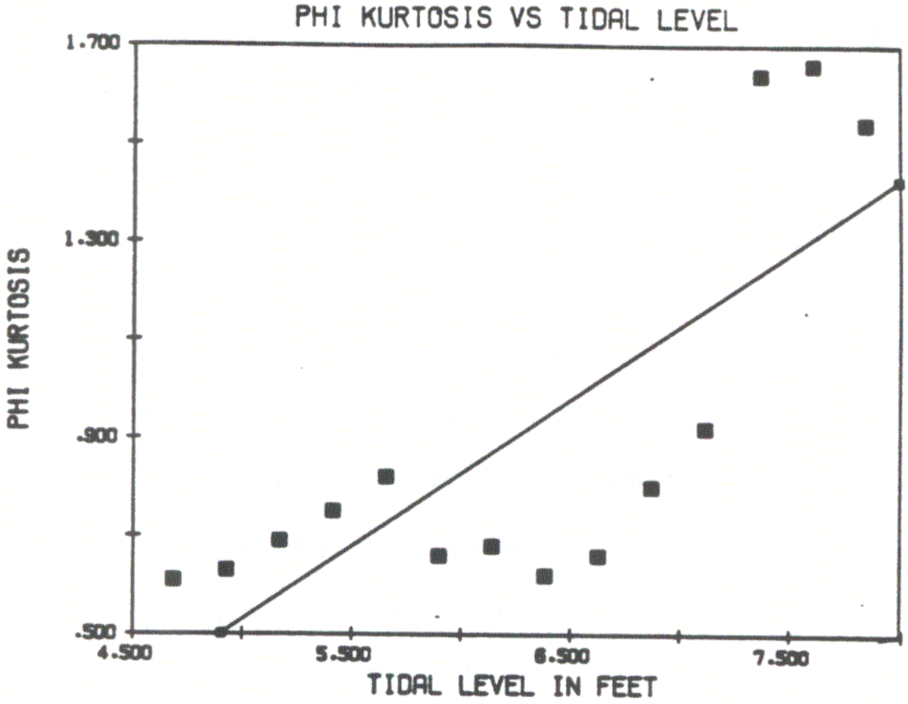
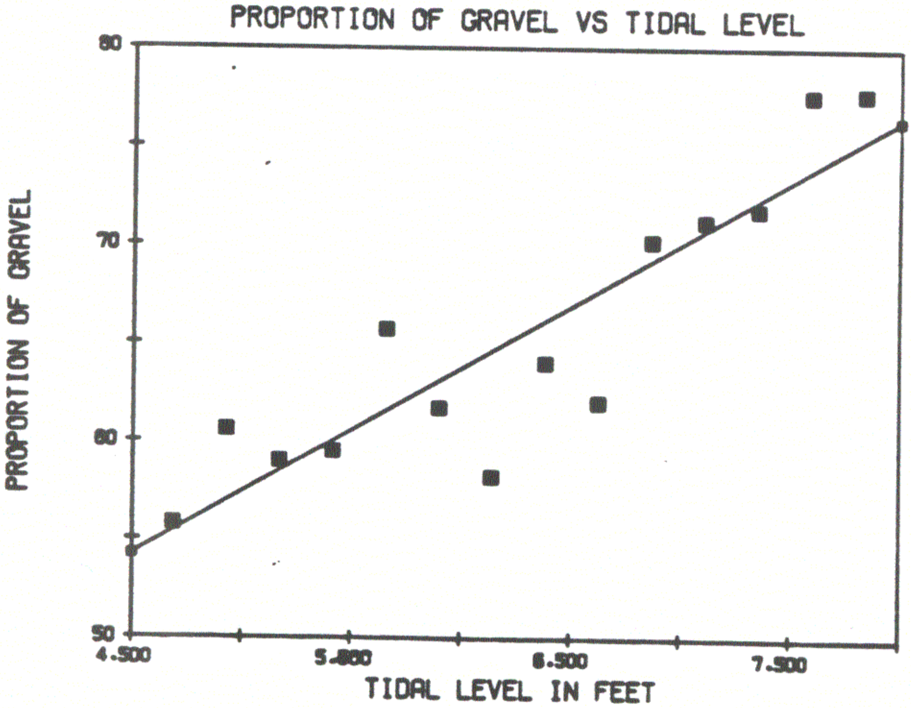

PHI SKEWNESS VS TIDAL LEVEL
.85000
.65000
.45000
.25000
PHI SKEWNESS
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET

FIG. 12 : Phi kurtosis versus tidal level in feet.

FIG. 13 : Proportion of gravel versus tidal level in feet.


PHI KURTOSIS VS TIDAL LEVEL
PHI KURTOSIS
1.700
1.300
.900
.500
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET


PROPORTION OF GRAVEL VS TIDAL LEVEL
PROPORTION OF GRAVEL
80
70
60
50
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET

In what follows it will be assumed that the tidal level is a reasonably appropriate measure of the characteristics of a site. If its explanatory value looked insufficient, additional variables could be included, but only after failing with the most parsimonious approach.

species is a potentially interesting area of the many that had to be put aside during this work.

2) After the reduction in the set of environmental variables considered, we have left only the tidal level to represent the different effects caused by this gradient and its confounded variables. Another objective in the study of the spatial components affecting the dynamics of populations is <u>to introduce the effects of an environmental gradient in the basic models</u>.

With these objectives we proceed to the analysis.

SPATIAL STRUCTURE OF THE POPULATION

One of the objectives of this work is to study the spatial distribution of age groups. The information available concerning this subject is scarce, and in most cases indirect. A typical example is provided by O'CONNOR and BROWN (1977), who show that "Within each site, annual differences in the location of feeding effort (by oystercatchers) were correlated with year-to-year variation in the location of second-winter cockles". No explanation is attempted for the observed change in location of the cockles themselves.

Although several authors have studied patchiness in sessile organisms (e.g.LEVINS, 1976; WIENS, 1976; WHITTAKER and LEVIN, 1977; CROWLEY, 1981; PAINE and LEVIN, 1981) , the characteristics of patches (size, age structure, etc.) are not well known. Occasionally, studies on recolonization of cleared areas provide some indirect evidence for massive influx of an age group to a restricted space (SAVAGE, 1956; KRISTENSEN, 1957; DARE, 1976; TIMKO, 1979).

In spite of this lack of knowledge, most surveys utilize data arising from quadrats which are assumed to be representative of larger areas. In population studies quadrat samples are used for many purposes such as estimation of abundance or biomass, growth parameters, mortality coefficients, etc. This type of approach has always been popular because of its convenience; it provides the researcher with a wealth of information covering most population processes with a very simple sampling design.

Much has been said on the effect of quadrat shape or size, or on how to place them (GREIG-SMITH, 1952,1964; MEAD, 1974; ROGERS, 1974; LUDWIG, 1979). In contrast, there is a general lack of awareness of the assumptions underlying the validity of the approach (representativeness of the quadrat) and of the effect of different non-random patterns of age groups in space. It is a peculiar gap if we consider the emphasis placed in benthic ecology during the 1970ies on subjects related to the problem such as: competitive interactions, stock-recruitment relationships, interactions in dense assemblages, etc.(RHOADS and YOUNG, 1970; HANCOCK, 1973; WOODIN, 1974, 1976, 1979; GRAY, 1981).

The data to be presented will show some problems of the traditional approach. Two techniques were used to describe the spatial distribution of age groups: contour maps and trend surface analysis (TSA). Both of them smooth the data in order to show the main features present, TSA being the more drastic of the two. A brief description of them is given together with the results observed.

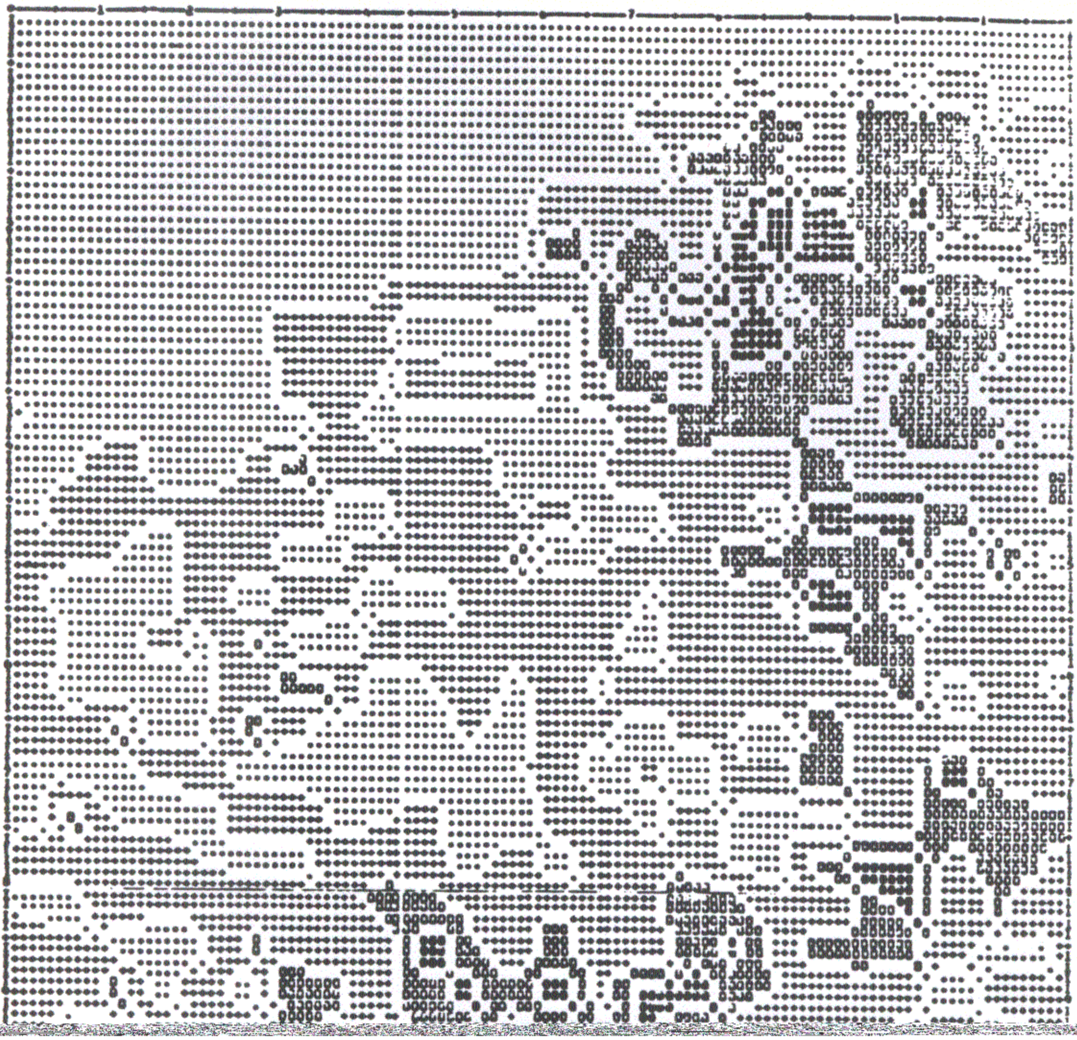
1) Contour maps

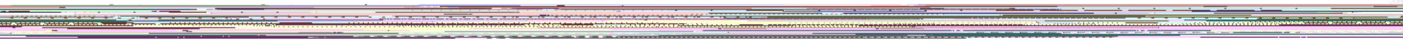
Fig. 14 shows a contour map of total density for the whole plot, after dividing the area in small (30x30cm) quadrats. For each quadrat, the density of each age group was calculated, and the values were then analyzed using the SYMAP package (DOUGENIK and SHEEHAN, 1977). The corresponding program traces contour lines based on a polynomial system of interpolation. These lines define areas of different densities which are represented by a shading system. In order to standardize the plots, the shading system is based on relative abundances, that is to say all points are expressed as a percent of the maximum value observed for each age group. Five intervals, each comprising 20% of the total range of values, were used for ages 1 to 5; four were used for the 6's and three for the 7's according to their range of variation.

Even though there are a few areas with higher densities, it does not seem to be an extremely patchy distribution. Figs. 15 to 21 show the results obtained

FIG. 14 : Contour map of total density.
Intervals have the following densities (unit area = 30x30 cm^2) :

darkest	29 - 36
	22 - 28
	15 - 21
	8 - 14
lightest	0 - 7





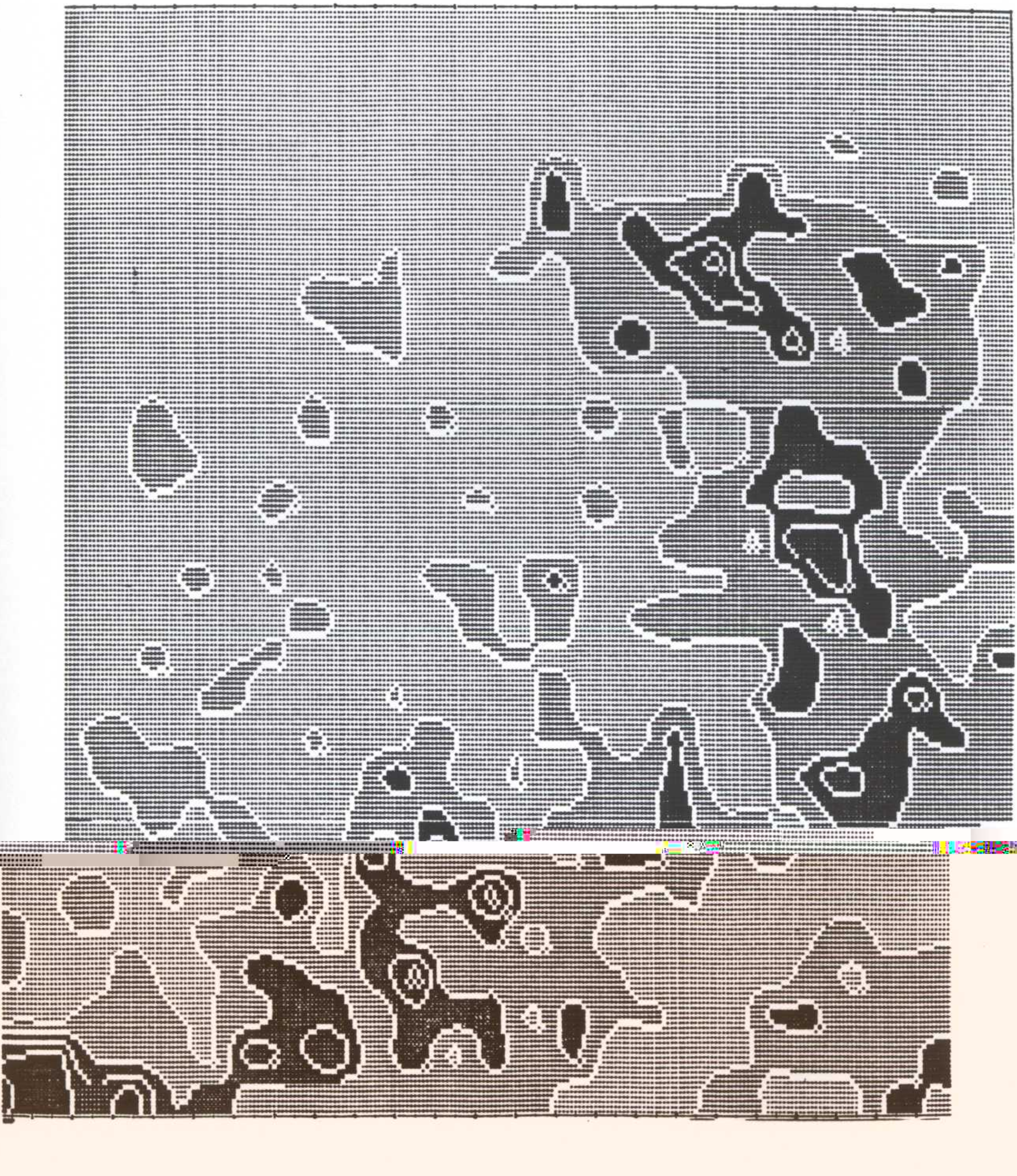
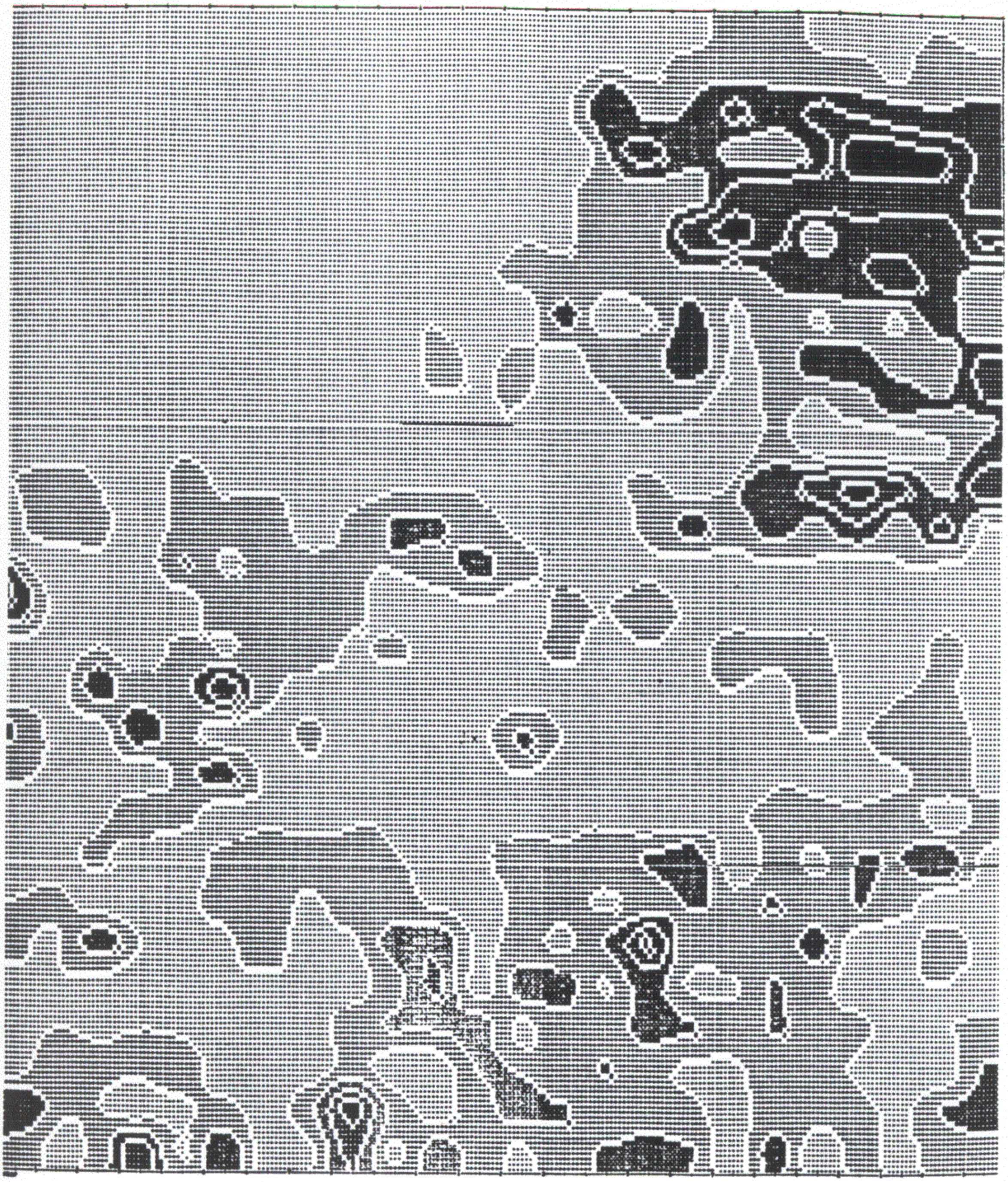


FIG. 16 : Contour map of density for age 2.
Intervals have the following densities (unit area = 30x30 cm^2) :

darkest	10 - 12
	8 - 9
	5 - 7
	3 - 4
lightest	0 - 2



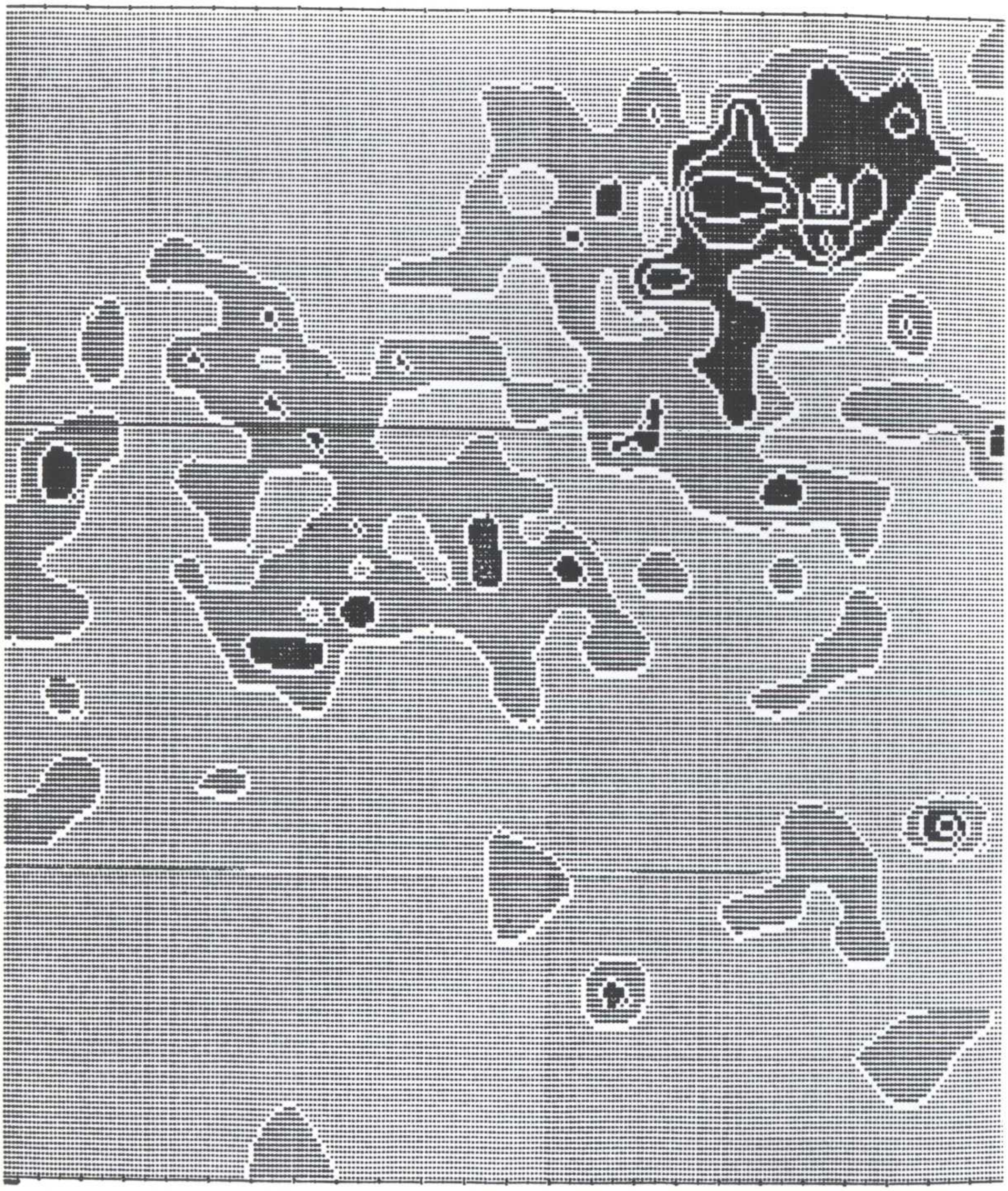


FIG. 18 : Contour map of density for age 4.
Intervals have the following densities (unit area = 30x30 cm^2).

darkest	4
	3
	2
	1
lightest	0

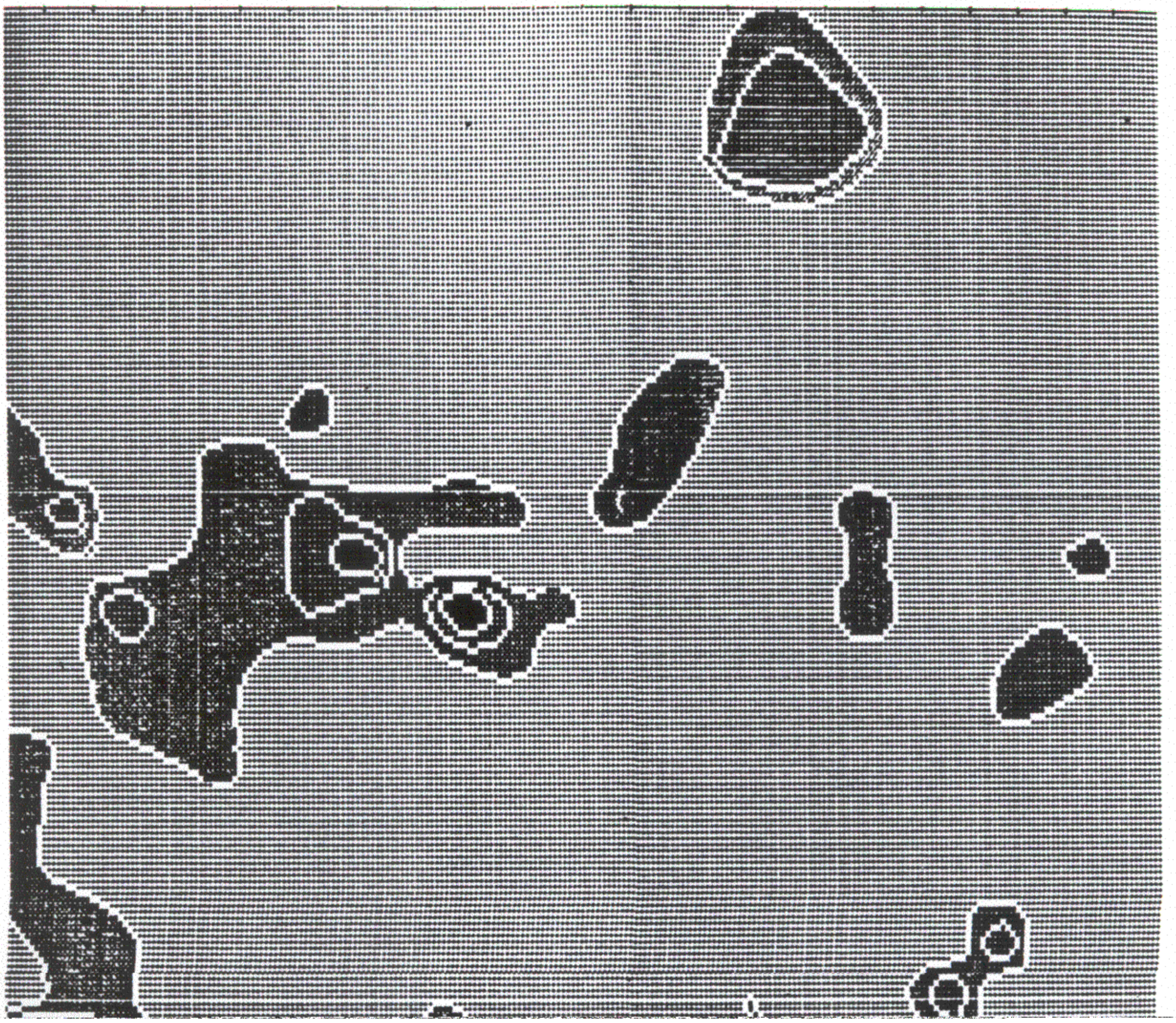


FIG. 19 : Contour map of density for age 5. Intervals have the following densities (unit area = 30x30 cm^2).

darkest	6 - 7
	5
	3 -4
	2
lightest	0 - 1

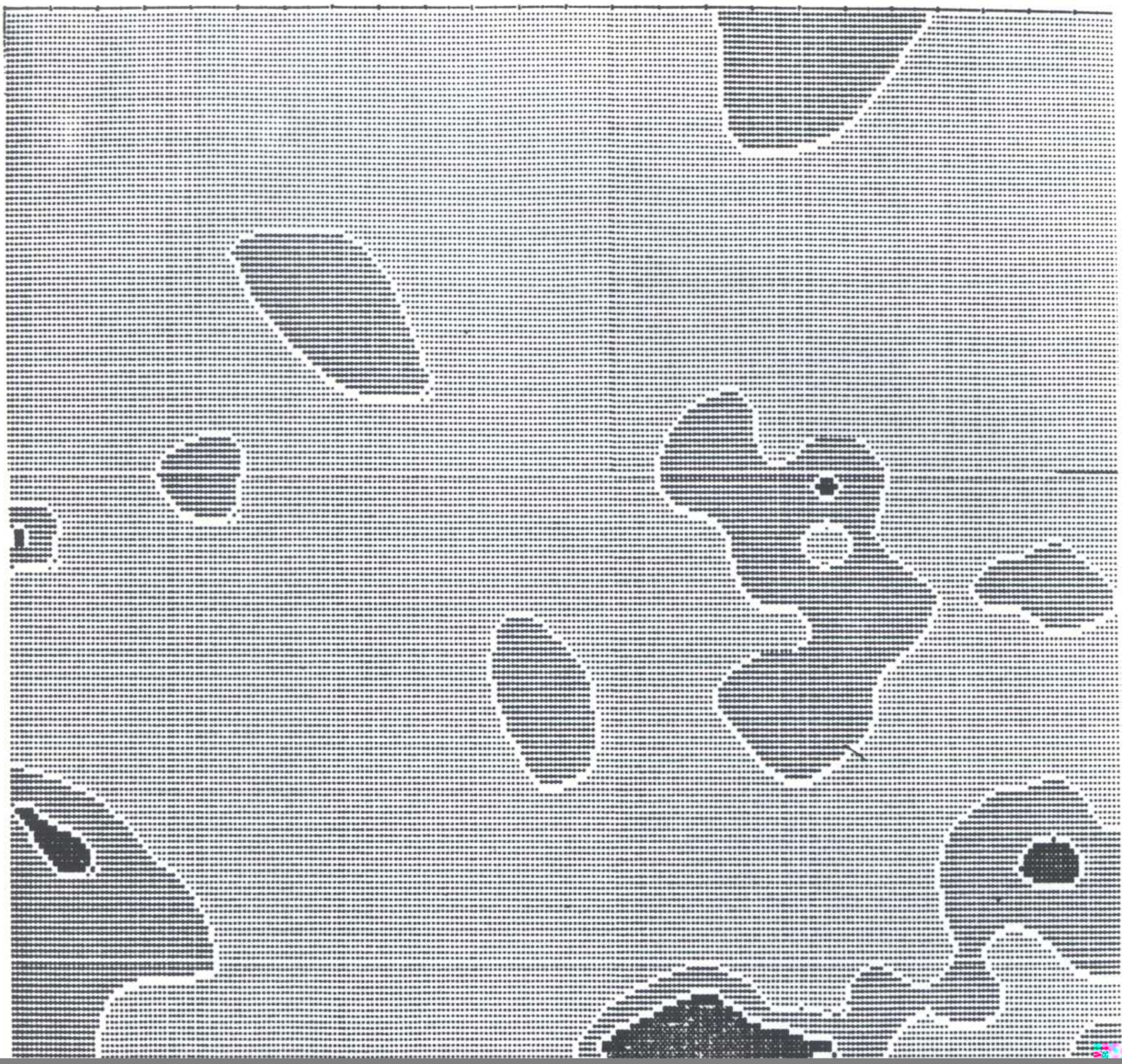


FIG. 20 : Contour map of density for age 6.
Intervals have the following densities (unit area = 30x30 cm^2)

darkest	3
	2
	1
lightest	0

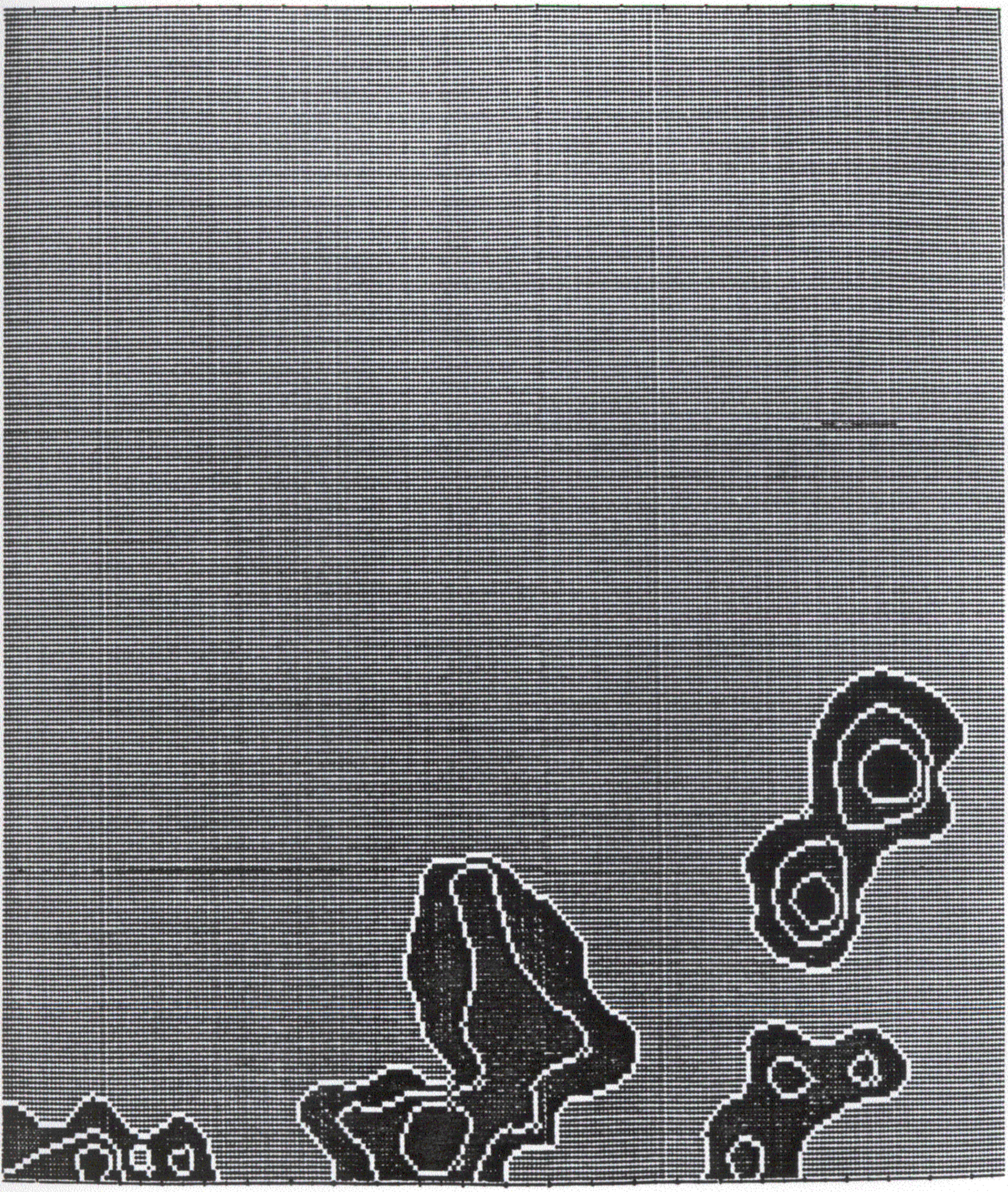
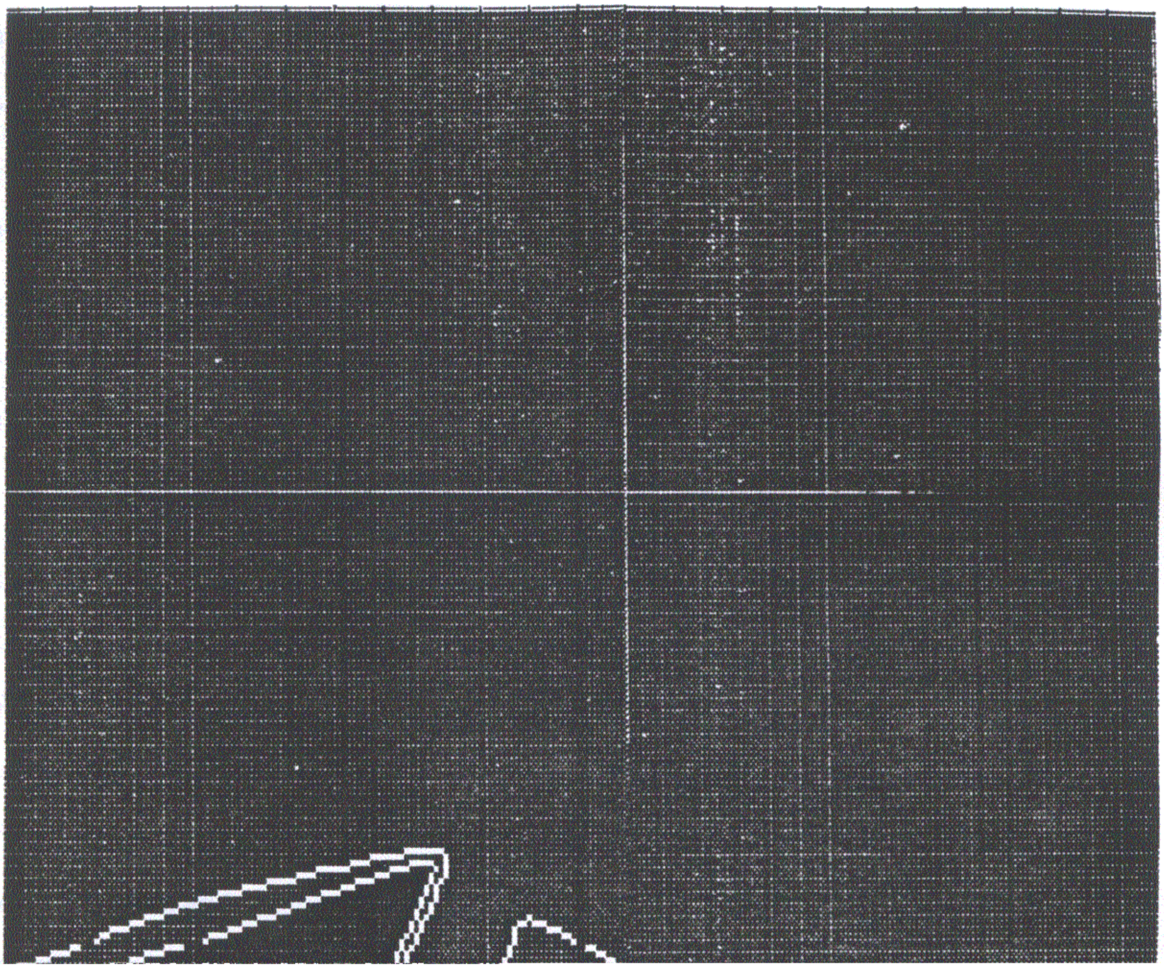


FIG. 21 : Contour map of density for age 7.
Intervals have the following densities (unit area = 30x30 cm^2).

darkest	2
	1
lightest	0



for age groups 1 to 7. If the distributions were random or uniform, these methods should fail to identify specific areas with density gradients. As we see, it is possible to define nuclei for each age group with quite precise location in the beach (darkest areas in figures). The age groups show a highly contagious pattern, occurring in patches of different sizes and shapes, but with a tendency toward ellipses with major axis parallel to the shore.

Within each patch, we observe a concentric density gradient (DAVIS, 1923), which may arise from differential mortality at the edge as compared to the center, or, more likely , from the pattern of larval settlement: The patchiness observed in the beach may reflect a) patchiness of the larvae in the water column, b) aggregation after settlement or c) differential mortality.

a) Plankton patchiness and its origins have been studied from different points of view (STEELE, 1976, 1977; LASKER, 1978; GREENBLATT, 1982). Some authors believe larvae are aggregated by hydrographic conditions (MATTHIESSEN, 1960; LABOURG and LASSERRE, 1980; DEAN, 1981). Others believe patchiness originates in differential survival (THORSON, 1966; LEHMAN and SCAVIA, 1982). The role of behavior in the generation and maintenance of aggregations is not well known (CLUTTER, 1969; HIDU and HASKIN, 1971; SHOW, 1979). In the particular case of larvae of benthic forms, two approaches have been used to verify the presence of patchiness:

1) direct observation of larval distribution in the water column (CARRIKER, 1951; WOLF, 1973; NORMANDEAU ASSOC., 1974). LOOSANOFF (1966) assumes the presence of larval patches in the water by the similarity in size and development of groups of larvae caught in a tow. Occasionally, laboratory experiences seem to furnish evidence for larval aggregation (MINAUR, 1969).

2) indirect evidence arising from patchiness of newly settled organisms (HIDU and HASKIN, 1971; WAUGH, 1972; HANCOCK, 1973; HIDU, 1978; READING, 1979; SEBENS, 1981,1982; CAFFEY, 1982). Rigorously however, it is not possible to separate the effects resulting from "the settlement of an aggregation of larvae" from those arising from "the aggregation of many individual settlers" or from a combination of both processes.

b) Aggregation at or after settlement: the mechanisms of aggregation have been reviewed by KNIGHT-JONES and MOYSE, 1961). Several authors believe that the patchiness observed originates at or after settlement

(TURNER, 1951; BAGGERMAN, 1953; SMITH, 1955; MATTHIESSEN, 1960; SUTHERLAND, 1982) either by passive transport or active migrations. In a way, all habitat selection mechanisms tend to aggregate larvae that share similar reactions to environmental factors (MEADOWS and CAMPBELL, 1972; CRISP, 1976). The phenomenon of gregariousness (COLE and KNIGHT-JONES, 1949), which will be discussed later, is another aggregating mechanism.

Observations on patchiness in newly settled spat are abundant (SAVAGE, 1956; HIDU and HASKIN, 1971; WAUGH, 1972; EAGLE, 1975; DARE, 1976; HIDU, 1978; READING, 1979; CAFFEY, 1982).

The bibliography available is highly biased towards epifaunal species, and particularly towards mussels and oysters. The only information coming from infaunal species is the existence of dominant age groups in quadrats which may be considered evidence of patchiness; but this is quite separated in time from the larval stage to provide any indication concerning its origin.

c) Differential survival seems a less likely source of patchiness in the case of the Manila clam in the area studied. Habitat heterogeneity such as that arising from the sedimentary characteristics studied does not correlate with location or density of patches. If predation were patchy, the tendency to circular patches, and the density gradients inside them would not be easily explained. Among the possible predators, the adult population deserved special consideration, and a simple experiment was available as a byproduct of the main census.

As a result of the sampling, a large area of the beach was almost completely defaunated; either by the collection process, by burial or by physical damage most of the adult population was eliminated from the plot. This fact was used to gather some information concerning the pattern of settlement and survival of spat in an area without adult interference of any type. The number of spat per core is shown in Table V.

Patchiness of the spat is evident from the table, the variance/mean ratio (ELLIOTT, 1977) yielding $d = 4.37$ $p < 0.001$ significantly departing from randomness. If further, the beach is divided into 4 sections, upper and lower, left and right, the densities in spat per square meter for each section are:

****

TABLE V: # of Manila clam spat per core

tidal level	Q	R	S	T	U	V	W	X	row
+7.84	0		0		0		0		0
+7.60		1		0		1		0	2
+7.36	-		0		0		0		0
+7.12		0		1		0		0	1
+6.87	0		0		0		1		1
+6.63		0		0		0		1	1
+6.38	0		0		0		1		1
+6.14		0		0		1		0	1
+5.89	2		0		1	0	0		3
+5.65		0		1		1		0	2
+5.41	2		4		1		0	0	7
+5.17		4		1		2		0	7
+4.93	4		4		2		1		11
+4.68		5		0		2		2	9
col	8	10	8	3	4	7	3	3	46

****

	LEFT	RIGHT
UPPER	53 (n=13)	99 (n=14)
LOWER	684 (n=14)	288 (n=16)

The setting is rather weak compared to other figures available for the Puget Sound (WILLIAMS, 1980b; ANDERSON, 1982), as could be expected if an adult population serves as an attractant to the spat. The results are not sufficient to conclude that the low density is caused by the absence of an adult population in the plot, but they show clearly that patchiness exists even in that case.

Regardless of the debate on the origins of patchiness, it will be assumed that the age-patches observed in the contour maps appear very early in the benthic life of the clam. Habitat selection, gregariousness, differential survival or settlement of patches of larvae would yield similar results, so it is not necessary to adopt one mechanism.

After settlement, the patches may experience changes in size and shape caused by:

a) Mortality at the edges of the patch should result in reductions in patch size and possibly in shape changes.

b) Internal breakdown caused by mortality within the patch should result in an increase in number of patches accompanied by a decrease in size.

c) Internal breakdown caused by invasion of the patch by new recruits should not alter the structure of the patch but it may mask its identity, limits, etc.

d) Apparent "fusion" of patches falling in adjacent areas, arising from our inability to discriminate their origins, may make identification difficult.

The preceding comments are made only to suggest the multiplicity of factors determining the fate of a patch. It is not possible within the frame of a descriptive study to identify the exact causes of the patterns observed. However, it is possible to try to deduce the basic facts through observation.

Going back to Figs. 15 to 21, the darker areas of the figures (those with relative frequencies higher than 80% of the maximum value observed) for all age groups do not show any overlap at all; the nuclei of the patches are clearly segregated. If all areas with relative frequencies higher than 60% were included, some overlapping sections could be found. This overlap is particularly visible for consecutive year classes (1-2,2-3, etc.) and for year classes separated by 5 or 6 years. When the age difference is intermediate (2 to 4 years) the overlap is minimal in most cases, the sole exception being those involving the weak 4 year old class. It is especially interesting to notice the extensive overlap between the youngest age group (1's) and the older ones (6's and 7's), which seems to indicate the cycling of patches.

As a more general remark, older year classes occur on lower portions of the beach, probably indicating better survival at lower tide levels.

2) <u>Trend surface analysis</u>

This technique, frequently used by earth scientists, is a powerful way to describe spatial processes but it has been overlooked by most biologists. It provides a very clear picture of the changes in the variables, and besides it can be used to eliminate the location in space as a source of variation. It consists of the fitting of a polynomial surface to the data set in order to assess the presence and direction of trends in it. If we have 2 axes labelled x and y in Cartesian coordinates, then a polynomial on x and y is fitted which includes terms of the following form:

$$Z = a + b_1X + b_2Y + b_3X^2 + b_4XY + b_5Y^2 + b_6X^3 + b_7X^2Y + + b_8XY^2 + b_9Y^3 + \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

In this particular case, the coordinate x corresponds to the axis parallel to the shoreline and the y to the axis perpendicular to it.

The degree of the polynomial has to be determined beforehand. In this case, a set of ANOVAs was performed testing for trends in x and y separately for several variables correlated with age (WINER, 1971; NIE et al., 1975). Table VI indicates the significance of the results obtained for the degrees tested (1 to 4). In most cases a poynomial of degree 4 seems adequate to represent the trends observed ; the tests were stopped at that degree because most of them yielded non significant values.

After determining the best surface by a least square method, a map of residuals can be prepared and correlated with other sources of variation knowing that the location effect has been taken care of. The technique has been described by several authors

****

TABLE VI :ANOVA tests for trends. Significance of polynomial terms.

Variable: Length

Y-component

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Age	Linear	Quadr.	Cubic	Quart.
1	***	***	*	**
2	***	***	***	
3	***	***	***	
4	***	***		*
5	***	***		**

X-Component

Age	Linear	Quadr.	Cubic	Quart.
1	***		***	***
2	***		***	
3	***	**	*	
4				
5			**	

Variable: Weight

Y-Component

Age	Linear	Quadr.	Cubic	Quadr.
1	***	**		**
2	***	***	***	
3	***	*	***	
4	***	***		
5	***	***	*	***

X-Component

Age	Linear	Quadr.	Cubic	Quart.
1	***		***	***
2	***		***	*
3	***	*	*	
4				
5			*	

* * *

(KRUMBEIN and GRAYBILL, 1965; MERRIAM and COCKE, 1967; OLMSTEAD, 1968; NORCLIFFE, 1969; TINKLER, 1969; UNWIN, 1975; TIPPER, 1979; KOCH and LINK, 1981).

The results obtained here (Figs. 22-27) coincide with the previous ones, but providing a better defined although less detailed view of the distributions. Again we perceive the basic tendency to circular or elliptic shapes in the patches and the concentric gradients around the nuclei. Comparing for instance the distribution of the 2's or 3's with that of the 4's, 5's and 6's we see quite clearly the segregation in space mentioned above.

GRAPHICAL MODEL OF SPATIAL STRUCTURE

As a first step towards understanding the processes underlying the observations, a graphic model is proposed, based on the idea that each animal "claims" a small area of the beach around its siphon. Within this area of influence, settlement is prevented, probably through the filtering activity of the resident. This area, which should be a function of the size of the resident, is not conceived as a result of physical space limitations, but as a consequence of biological interactions that arise from the need to reduce the extent of local competition for food, etc. This concept

FIG. 22 : Trend surface analysis of density for age 1.
Polynomial degree = 4.
Intervals have the following densities (unit area = 30x30 cm^2).

darkest	10.13 - 13.36
	6.89 - 10.13
	3.66 - 6.89
	0.42 - 3.66
lightest	-2.81 - 0,42

Note: Negative values arise because of interpolation.

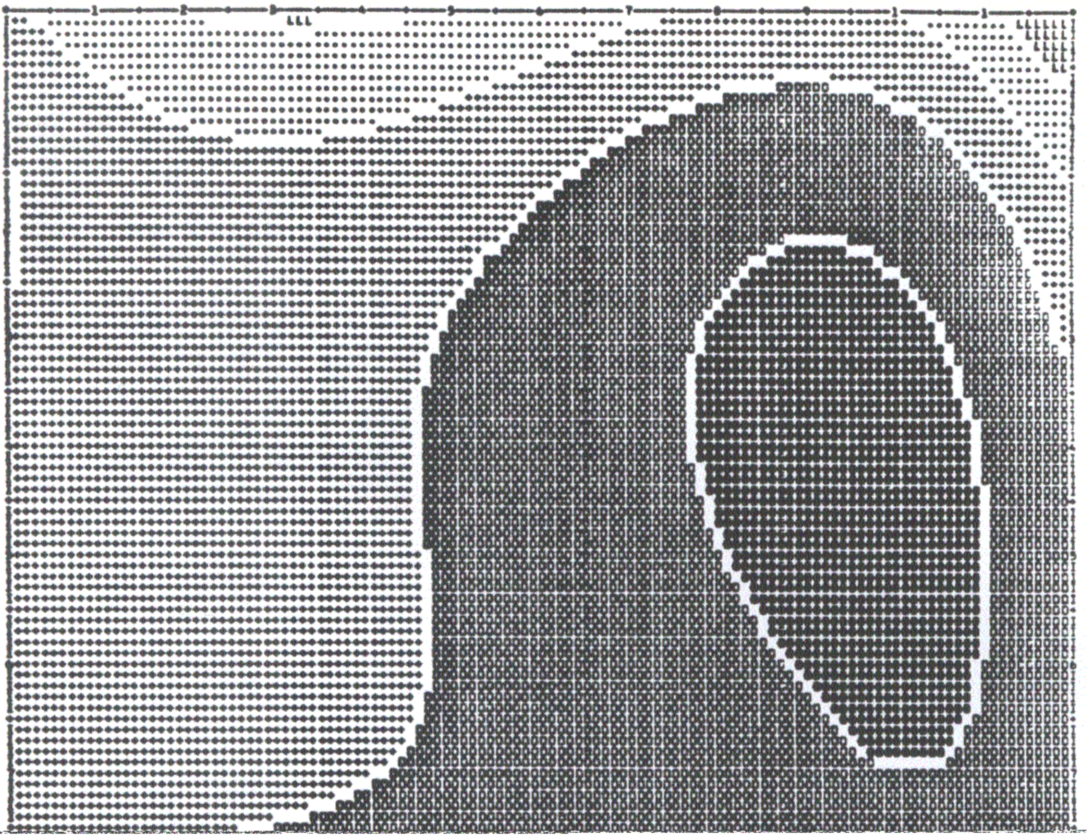


FIG. 23 : Trend surface analysis for age 2.
Polynomial degree = 4.
Intervals have the following densities (unit area = 30x30 cm^2):

darkest	4.99 - 6.32
	3.67 - 4.99
	2.34 - 3.67
	1.01 - 2.34
lightest	-0.32 - 1.01

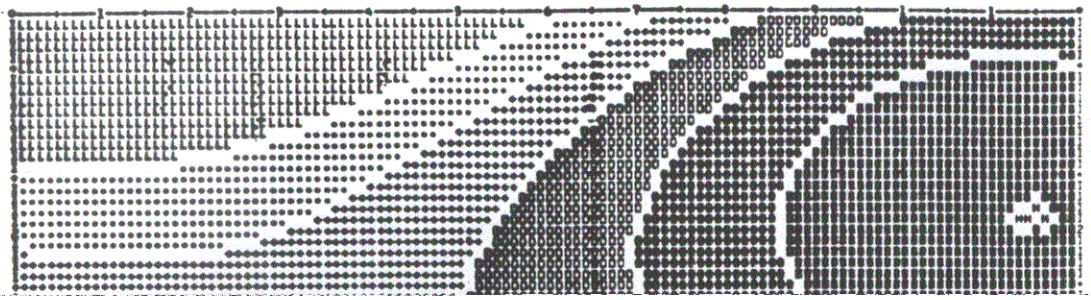


FIG. 24 : Trend surface analysis for age 3.
Polynomial degree = 4.
Intervals have the following densities (unit area=30x30 cm^2).

darkest	3.64 - 4.85
	2.42 - 3.64
	1.20 - 2.42
	-0.02 - 1.20
lightest	-1.23 - -0.02

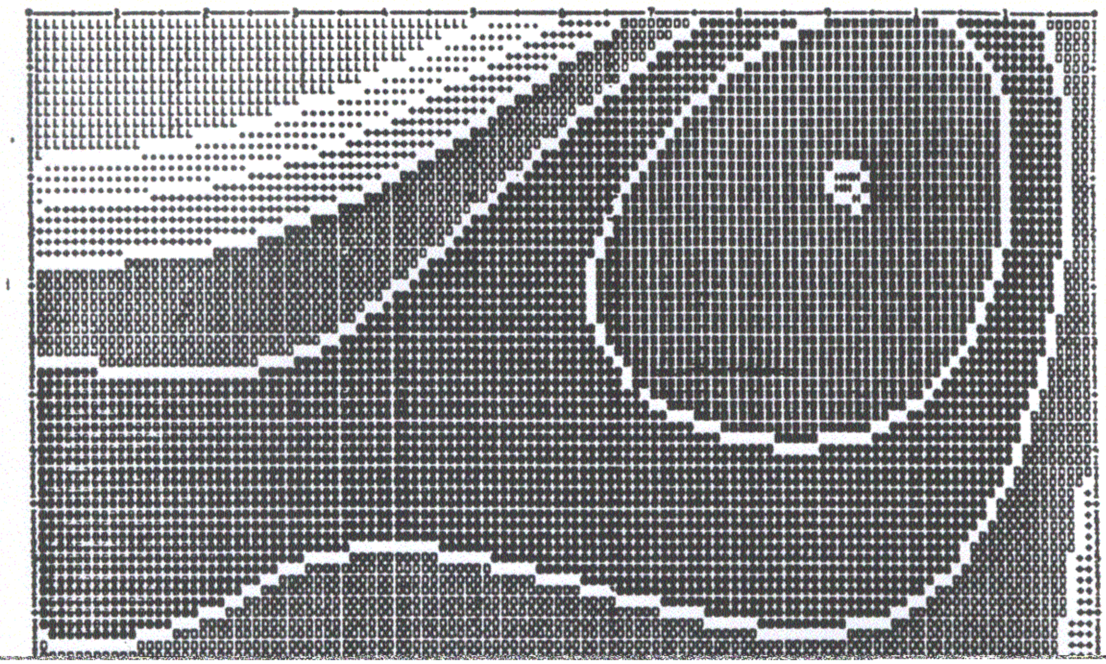
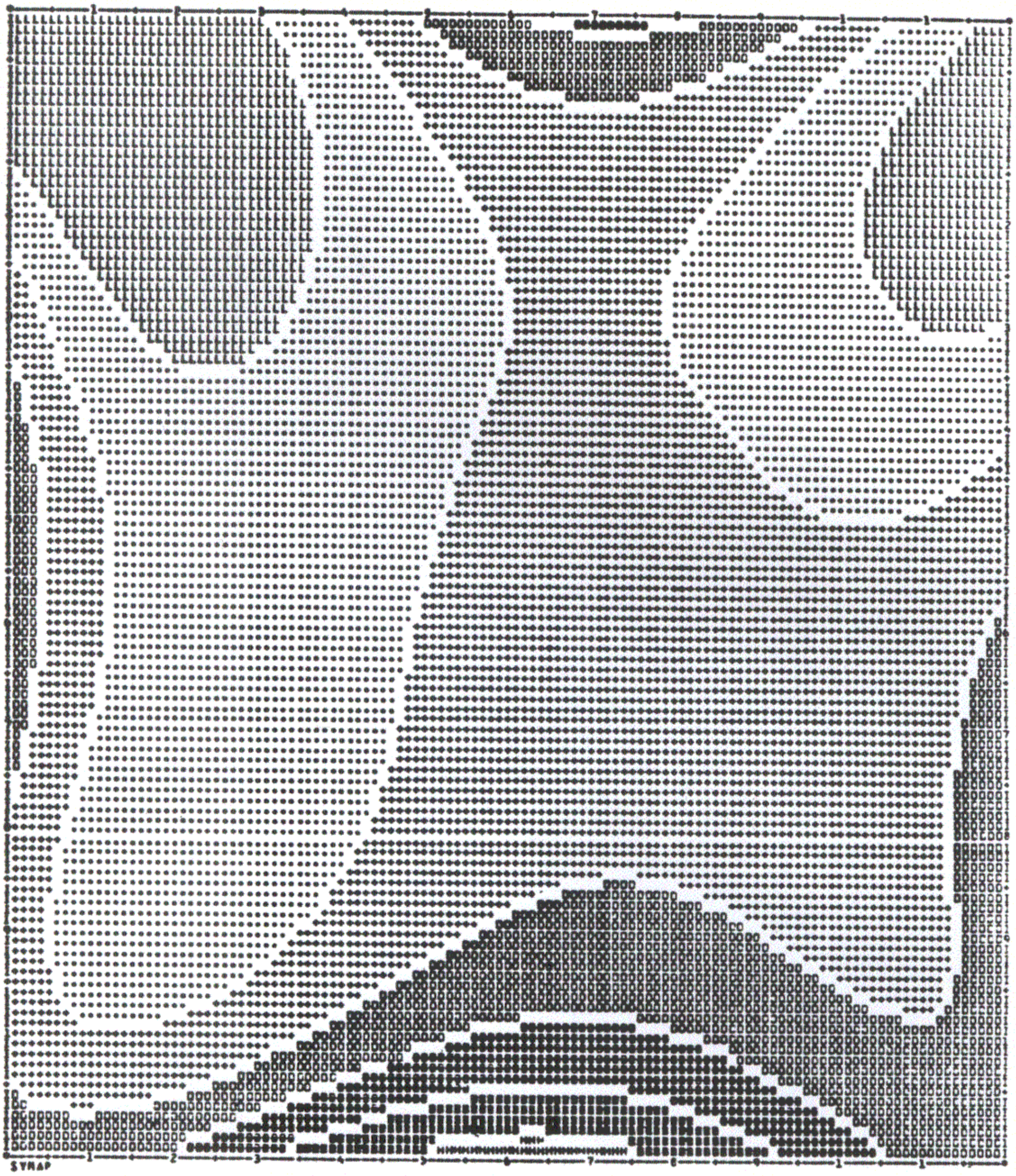


FIG. 26 : Trend surface analysis for age 5.
Polynomial degree = 4.
Intervals have the following densities (unit area = 30x30cm^2):

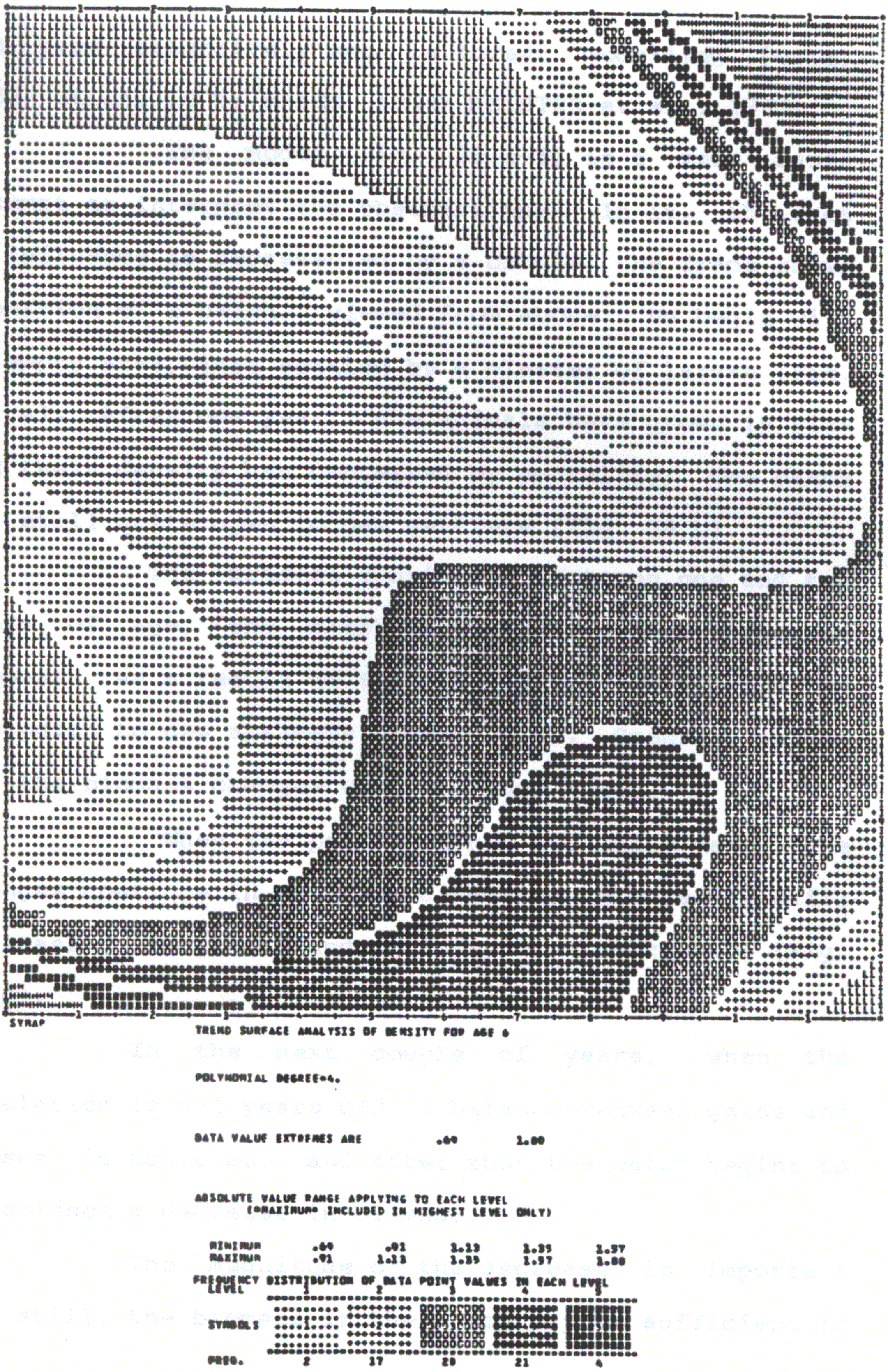
darkest	2.46 - 2.88
	2.05 - 2.46
	1.63 - 2.05
	1.22 - 1.63
lightest	0.80 - 1.22



```
TREND SURFACE ANALYSIS OF DENSITY FOR AGE 5.


POLYNOMIAL DEGREE=4.


DATA VALUE EXTREMES ARE          .80         2.88


ABSOLUTE VALUE RANGE APPLYING TO EACH LEVEL
       (*MAXIMUM* INCLUDED IN HIGHEST LEVEL ONLY)

  MINIMUM        .80        1.22        1.63        2.05        2.46
  MAXIMUM       1.22        1.63        2.05        2.46        2.88

FREQUENCY DISTRIBUTION OF DATA POINT VALUES IN EACH LEVEL
  LEVEL          1           2           3           4           5
          ***************************************************************
           .........  +++++++++  OOOOOOOOO  ØØØØØØØØØ  █████████
           .........  +++++++++  OOOOOOOOO  ØØØØØØØØØ  █████████
  SYMBOLS  ....1....  ++++2++++  OOOO3OOOO  ØØØØ4ØØØØ  ████5████
           .........  +++++++++  OOOOOOOOO  ØØØØØØØØØ  █████████
           .........  +++++++++  OOOOOOOOO  ØØØØØØØØØ  █████████
          ***************************************************************
  FREQ.         47          77          46          14          10
```

FIG. 27 : Trend surface analysis for age 6.
Polynomial degree = 4.
Intervals have the following densities (unit area 30x30 cm^2) :

darkest	1.57 - 1.80
	1.35 - 1.57
	1.13 - 1.35
	0.91 - 1.13
lightest	0.69 - 0.91

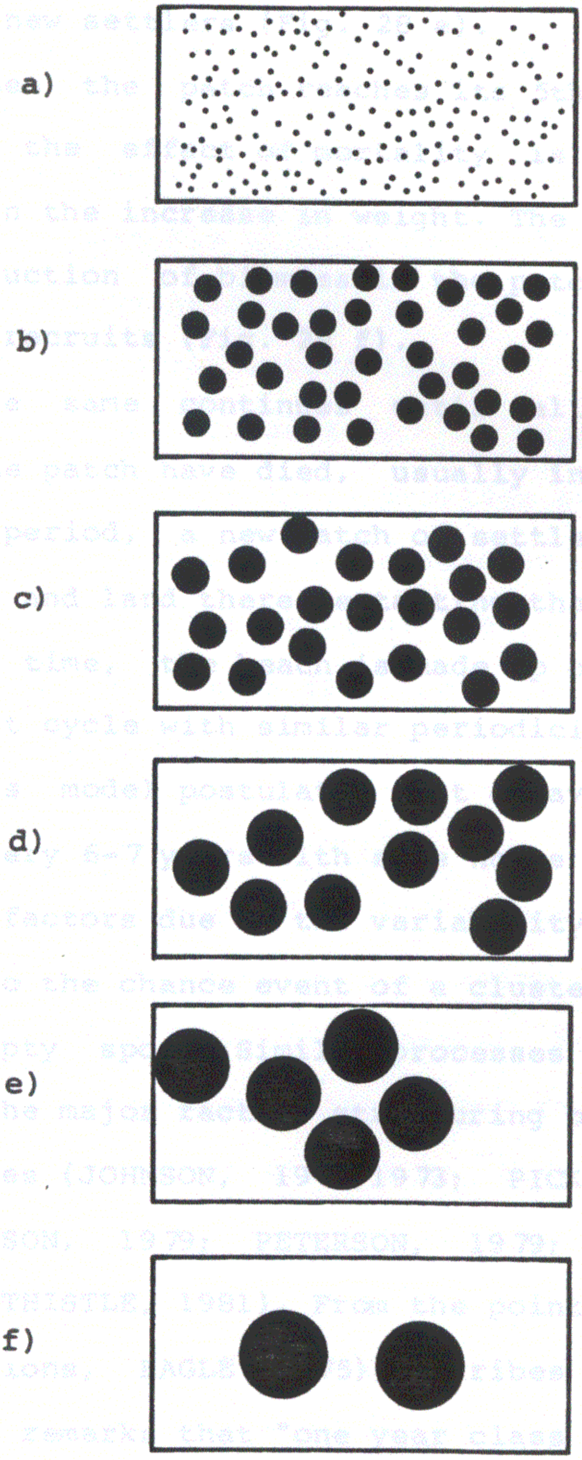


```
SYMAP
            TREND SURFACE ANALYSIS OF DENSITY FOR AGE 6

            POLYNOMIAL DEGREE=4.

            DATA VALUE EXTREMES ARE          .69       1.80

            ABSOLUTE VALUE RANGE APPLYING TO EACH LEVEL
                  (*MAXIMUM* INCLUDED IN HIGHEST LEVEL ONLY)

              MINIMUM        .69       .91      1.13      1.35      1.57
              MAXIMUM        .91      1.13      1.35      1.57      1.80
            FREQUENCY DISTRIBUTION OF DATA POINT VALUES IN EACH LEVEL
              LEVEL           1         2         3         4         5

              SYMBOLS         1         2         3         4         5

              FREQ.           2        17        28        21         4
```

has been extensively used in forest modelling (OPIE, 1968; BELLA, 1971; FRIES, 1974; KEISTER et al., 1975).

The model (Fig. 28 a-f) is a very basic attempt to interpret the observations. In it, the area of influence is represented by a circle; the frame

FIG. 28 : Graphical model of patch cycling.
Explanation in text.


a)
b)
c)
d)
e)
f)

prevent settlement. The idea is that there is a threshold in biomass, below which the patch is "permeable" to new settlers (Fig. 28 e).

When the patch reaches its 5th and 6th year of age, the effect of mortality is much more significant than the increase in weight. The result is a noticeable reduction of biomass in the patch and its opening to new recruits (Fig. 28 f).

The same continues until all original members of the patch have died, usually in their 7th year. In this period, a new batch of settlers may find the open space and land there restarting the cycle.

In time, the beach is made up of a mosaic of patches that cycle with similar periodicity but out of phase. This model postulates that on average each patch cycles every 6-7 years with some noise introduced by stochastic factors due to the variability in larval abundance and to the chance event of a cluster of larvae hitting an empty spot. Similar processes have been and may deter settlement of further generations of the same species; ... single year class populations must die, and replacement will be by the next spatfall". DAVIS (1923) provides one of the first descriptions of patchiness in infaunal bivalves and a very lucid analysis of its possible origins and maintenance. He also finds year class patches very well defined, and speculates on adult-larval interactions.

The model suggested, in spite of its simplicity (or because of it), provides a basis for elaboration and verification, because we can extract from it some hypotheses for testing. In the next pages, we derive a set of hypotheses from the model and proceed to test them statistically.

STATISTICAL VALIDATION OF THE MODEL

In order to validate the proposed model, a set of relatively simple hypotheses arising from it will be tested for statistical significance. Even if all these tests agreed with our expectations from the model we could not be certain that this is the only valid explanation of the observed facts. The uncertainty however, can be reduced in part by testing a reasonable number of hypotheses; in this way the possibility that some other alternative explanation were the valid one decreases with the increasing complexity and amount of evidence accumulated. At least, the model should be considered a parsimonious alternative; others will be discussed later.

(Because of their numbers, younger individuals will prevail in this measure).

VII) The average distance between nearest neighbors <u>of the same age</u> should increase with age (within a patch) because of the thinning process arising from the overlap of areas of influence. In this case younger individuals do not have a strong impact on the values.

It is easy to see that some of these hypotheses could arise from other processes (e.g. random mortality within the patch would increase interindividual distances, etc.). However, the alternatives that were considered failed to satisfy some of them (e.g. random mortality does not explain hypothesis I or V, to mention only two).

TESTS

Hypotheses I and II are verified using a test by PIELOU (1977) to detect spacing regularities in distributions of distances to the nearest neighbor. The common frequency distribution of distances, based on a straightforward arithmetic scale of distances fails to show any discrepancy between expected and observed values at the lower end of the scale of distances. The reason for this is the lumping of values in the first intervals which probably masks the underlying facts.

To avoid this problem, PIELOU suggests to use a different scale for the frequency distribution based on the Poisson model. First, the parameter λ is estimated from the data. Then, using this value, a set of intervals is prepared in such a way that each of them is equally likely under the assumed distribution. This uniform (rectangular) distribution is a much better way to analyze whether there are discrepancies at the lower end of the scale (usually a deficit in frequencies if there is a tendency towards regular spacing). As the endpoints of the intervals are calculated to satisfy the rectangular distribution, their spacing is not equal in the arithmetic scale, so the intervals are not equal in width.

The distribution is truncated to the right in an arbitrary way after making sure that the range of distances considered of interest is included. In this case, 10 cm were chosen as a distance long enough to exceed the possible limits of regularity.

In mathematical terms, the class boundaries are estimated as follows (PIELOU,op cit):

let r=distance to the nearest neighbor

$\omega = r^2$

c=truncation point squared

The untruncated distribution function is:

$$F(\omega) = 1 - e^{-\lambda\omega}$$

After truncation

$$F(\omega | 0 \leq \omega \leq c) = \frac{1 - e^{-\lambda\omega}}{1 - e^{-\lambda c}}$$

and its expectation

$$E(\omega) = \frac{1}{\lambda} - \frac{ce^{-\lambda c}}{1 - e^{-\lambda c}} \qquad (1)$$

To divide into i intervals (j=1,2,3......,i)

with ω_r being the upper limit of the rth interval

$$\frac{F(\omega_r) - F(0)}{} = \frac{1 - e^{-\lambda\omega_r}}{} = \frac{r}{}$$

degree of approximation when N is large by substituting the observed mean $\overline{\omega}$ for the theoretical expectation in (1) and solving for λ .

After this, the frequency in the first interval (f_1) is tested against its expected value (N/i)

$$\frac{\left(\frac{n}{i} - f_1\right)}{\sqrt{n\,\frac{1}{i}\,\left(1 - \frac{1}{i}\right)}} = \frac{n - if_1}{\sqrt{n(i-1)}}$$

and a one-tail test is performed

$H_0 \; : \; f_1 \geq \frac{n}{i}$

$H_1 \; : \; f_1 < \frac{n}{i}$

In order to detect not only the presence of regularity but to get an idea of the distances involved, a series of tests based on different numbers of intervals are used. The procedure allows a test for regularity at increasing distances. For instance, dividing the range into 60 intervals yields a class boundary for the first interval (ω_1) of 0.62 cm; the data in these classes are tested for significance. If H_0

is rejected, then the distribution is divided into 30 intervals with ω_1 =0.87 cm; the third step involves a division into 20 intervals with ω_1 =1.08 cm, and so on until there are only 2 intervals with ω_1 =3.94 cm. In this way, an approximate idea of the distance of interaction is found by observing the transition from significant to nonsignificant. As the values of ω_1 increase, a limit is reached beyond which the tests become not significant as a result of pooling together values from the area of influence with those from outside which dilute their effect.

Table VII shows the significance of the tests performed for different intervals for ages 1 to 5, and for all age groups combined. Age groups 6 and 7 were not tested separately because of their small sample sizes. The horizontal lines in Table VII indicate the maximum distance at which a significant result was detected. This distance increases with age as predicted. If those values are thought to represent twice the

* * *

TABLE VII:SIGNIFICANCE OF PIELOU'S TESTS FOR REGULARITY

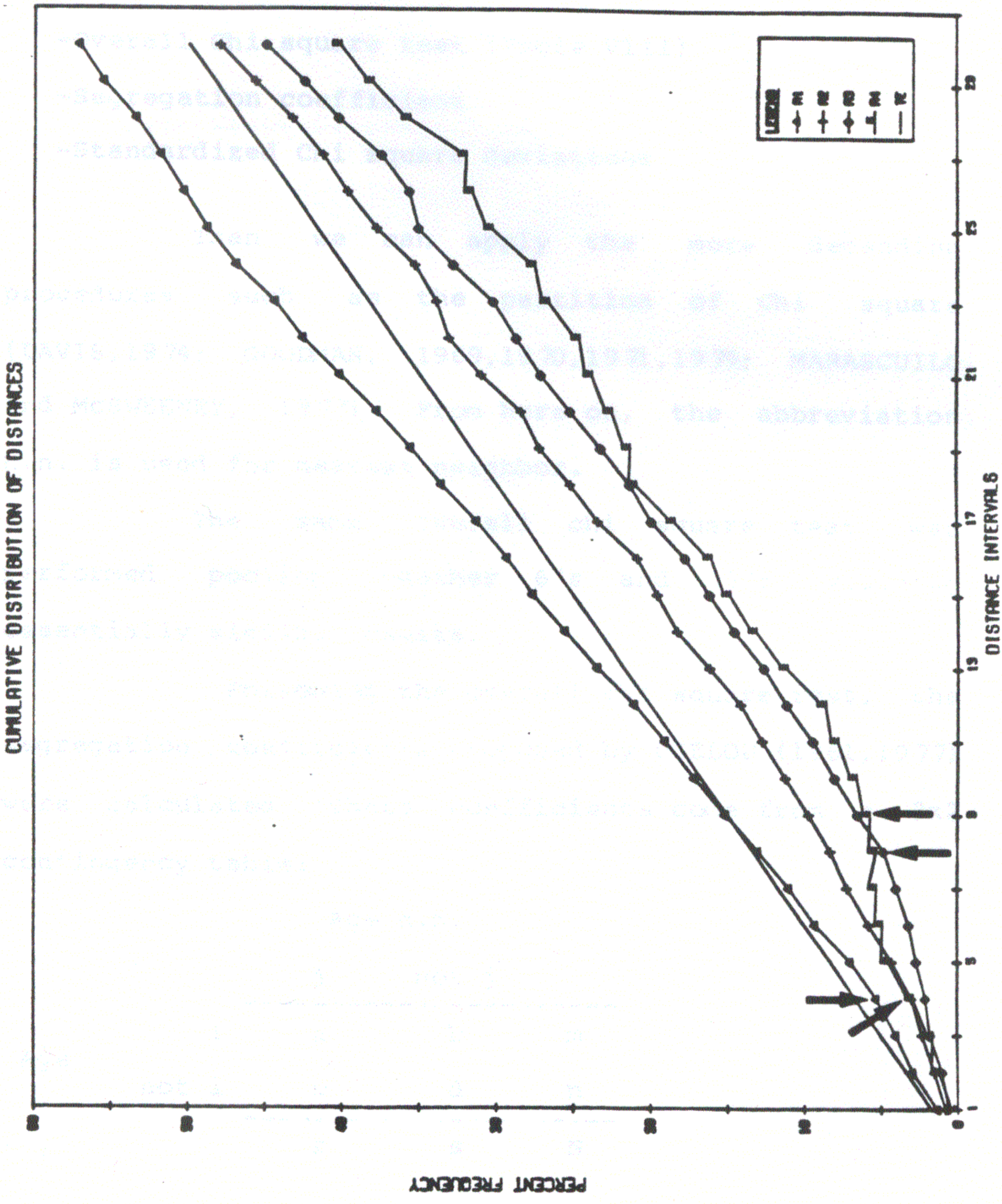
# INTERVALS	ω_1 (DISTANCE cm.)	ALL	AGE1	2	3	4	5
60	0.62	***	NS	***	**	**	NS
30	0.87	*	NS	***	***	NS	NS
20	1.08	***	*	***	*	*	*
15	1.25	***	*	***	***	NS	*
		----	----	----			
12	1.40	NS	NS	NS	**	NS	*
10	1.54	NS	NS	NS	***	*	NS
6	2.03	*	NS	NS	*	*	*
5	2.24	NS	NS	NS	*	**	NS

4	2.54	NS	NS	NS	NS	*	*

3	3.02	NS	NS	NS	NS	NS	*
2	3.94	NS	NS	NS	NS	NS	**

* * *

FIG. 29 : Cumulative distribution of distances to n.n. The distance intervals are those of Table VII. The frequency of individuals whose distances to the nearest neighbor are less than or equal to the distance considered are accumulated for increasing values of this variable. The arrows show approximately the point at which the lines become parallel or converge to the theoretical value (bisector TE). They correspond in position to the horizontal lines from Table VII. Symbols A1 to A4 refer to age groups 1 to 4.


CUMULATIVE DISTRIBUTION OF DISTANCES
PERCENT FREQUENCY
DISTANCE INTERVALS
0
1
5
9
13
17
21
25
29
LEGEND

The verification of hypotheses III to V requires a combination of techniques. First we look for an approach to present and describe the data:

- -Overall Chi square test (Table VIII)
- -Segregation coefficient
- -Standardized Chi square deviations

Then we can apply the more demanding procedures such as the partition of Chi square (DAVIS,1974; GOODMAN, 1969,1970,1971,1979; MARASCUILO and McSWEENEY, 1977). From here on, the abbreviation n.n. is used for nearest neighbor.

The same overall chi square test was performed pooling together 6's and 7's yielding essentially similar results.

Following the overall chi square test, the segregation coefficients proposed by PIELOU (1961,1977) were calculated. These coefficients come from a 2x2 contingency table:

		Age n.n.		
		j	not j	
Age	i	a	b	m
	not i	c	d	n
		r	s	N

****

TABLE VIII : Contingency table, age versus age of nearest neighbor.

Age n.n.	1	2	3	4	5	6	7
Age 1	1327	592	341	96	95	37	6
2	623	377	211	56	53	9	3
3	378	226	243	35	23	7	1
4	94	60	37	15	15	6	2
5	117	53	24	12	28	4	3
6	37	13	8	6	2	0	3
7	10	4	0	0	2	2	0

Chi square (D.F.=36) = 236.094 $p<0.0001$

****

From it we calculate for all possible pairs of age groups (including each group with itself) :

$$S=1-[N(b+c)/(ms+nr)]$$

The results are summarized in Table IX.

As we are more interested in the effect of differences in age, we can now average over the diagonals, eliminating or reducing the effect of the relative abundance of each cohort (Table X).

The maximum segregation is found between age groups separated by 2 or 3 years, high values are found for those separated by 1 or 4 years of age, and very low values for those of the same age or separated by 5-6 years.

A similar description may be obtained using the standardized Chi square deviations:

$$\frac{(\text{observed} - \text{expected})}{\sqrt{\text{expected}}}$$

The matrix of standardized deviations is shown in Table XI. If we average as before along the symmetric diagonals we obtain the results shown in Table XII. Again we find maximum association within the same year class, and maximum segregation when separated by 2, 3 or 4 years of age. In this case the results are clearer because the signs provide a good idea of the type of interaction present. The distribution of

****

TABLE IX: Matrix of segregation coefficients.

	Age n.n.	1	2	3	4	5	6-7
Age	1	8.3	6.9	19.0	7.0	13.6	6.7
	2		4.4	16.2	7.2	22.2	22.0
	3			12.7	16.5	45.5	35.3
	4				2.6	20.3	10.2
	5					8.2	31.6
	6-7						4.4

****

****

TABLE X : Mean values of segregation coefficients for differences in age.

Difference in age	0	1	2	3	4	5-6
Mean						

`*****************************************************`

TABLE XI: Standardized chi square deviations.

	Age n.n	1	2	3	4	5	6
Age	1	3.11	-1.31	-3.35	-0.79	-0.71	1.32
	2	-1.09	2.37	-0.49	0.06	-0.21	-1.73
	3	-3.25	-0.20	7.61	-0.51	-2.36	-1.19
	4	-1.63	0.40	-0.05	1.79	1.86	1.99
	5	0.04	-0.88	-2.41	0.65	5.83	0.68
	6	0.82	-0.88	-0.86	1.95	-0.43	-0.89

`*****************************************************`

`*****************************************************`

TABLE XII: Mean values of standardized deviations for differences in age.

Differences in age	0	1	2	3	4	5
Mean deviation	3.30	0.09	-0.87	-0.93	-0.82	1.07

`*****************************************************`

individuals separated by one year is almost perfectly independent. Those separated by 5 years show a strong positive association.

The partition of Chi square is performed using a combination of:

a) A simple contingency table (for each age group) in which the categories are as shown in the following example:

	Age n.n.	1	not 1	
Age	1	1327	1167	2494
	not 1	1259	1543	2802
		2586	2710	5296

Chi square= 36.167 D.F.= 1 $p<0.001$

b) Tests between all possible pairs of age groups following GOODMAN's procedures as described in MARASCUILO and McSWEENEY (1977). The matrix shown (Table XIII) indicates only the combinations yielding significant results.

Once the overall Chi square test has proved to be significant, then it is possible to analyze (partition) the results in such a way that the sources of deviation and their significance could be identified, when isolated from the rest of the table. In this manner, individual hypothesis can be tested. The test shows the same general pattern noticed previously

Table XIII: Partition of Chi square:Goodman's tests

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Age n.n.	1	2	3	4	5	6-7
Age 1	***		***			
2		**				
3			***		**	
4						
5					***	
6-7						**

although it yields fewer significant results. The relatively small sample sizes in some of the

****

TABLE XIV: Mean distance to the nearest neighbor (any age) for each age.

Age	Mean distance	S.E.
1	2.59	0.02
2	2.91	0.03
3	3.07	0.04
4	3.38	0.09
5	3.31	0.09
6	3.38	0.16
7	3.63	0.35

****

****

TABLE XV: Mean distance to the nearest neighbor of same age for each age.

AGE	Mean Distance	S.E.
1-1	2.46	0.03
2-2	2.99	0.07
3-3	3.30	0.07
4-4	4.39	0.37
5-5	3.34	0.38

Kendall's tau=0.8 $p<0.05$

****

DISCUSSION

Summarizing, the tests of hypotheses performed above provide support for the model proposed. The list of possible verifications goes much further, but the evidence obtained seems adequate. It is not possible to validate the graphical model completely on the basis of these results; there may be other ways to explain the facts observed. It is possible to examine some of the alternatives:

i) Recruitment to the beach is essentially a random or uniform process (non-aggregated); differential survival causes the patchiness we observe. This differential survival in turn may be a result of habitat heterogeneities or biological interactions such as aggregation of predators or competitors, etc. If this were the case, we should find neither the strong positive association within each age group nor the strong segregation of age groups separated by 2 to 4 years. Otherwise, we must be prepared to accept the fact that whatever is the source of differential mortality, it changes in location from year to year and that it also changes in space according to the age of neighboring individuals. These assumptions are considered much more demanding in credibility than those needed for the model proposed. The evidence from spat settlement in the absence of an adult population also argues against this alternative.

ii) Regardless of their settlement pattern, the individuals form patches as a result of passive transport (waves, tides, eddies, etc). Again here, it is necessary to assume that these causal factors change in time, otherwise they should result in simple accumulations of animals of all ages in a few preferred areas of the beach (TURNER, 1951; MATTHIESSEN, 1960). Without doubt, hydrodynamic factors do play a role in the distribution of larvae and early settlers (BAGGERMAN, 1953; SMITH, 1955; ANDERSON, 1982), but it does not seem possible that they may act on such a small scale. Year- to-year changes noticeable within a few meters seem a bit unlikely.

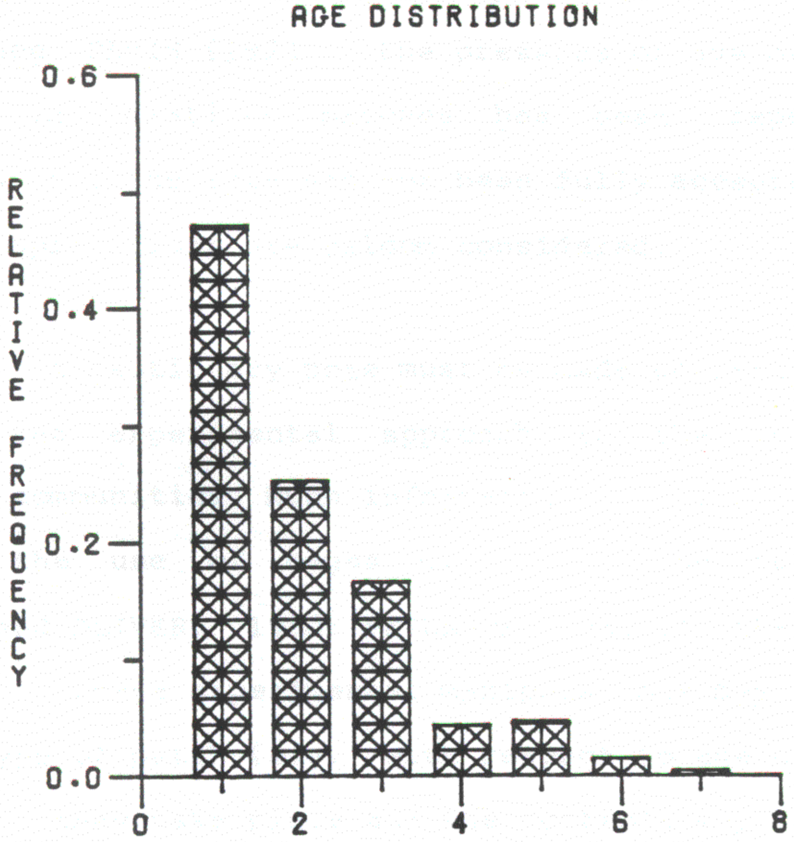
iii) Regardless of their settlement pattern, patches are formed by an active process which involves a good deal of mobility on the part of the individuals. This would require complex behavioral mechanisms (MEADOWS and CAMPBELL, 1972; CRISP, 1976) capable of assessing local density and responding to that with changes in the anchoring system (e.g. increasing growth of byssal tissues). But the complexity of a mechanism does not prevent its development if it has adaptive value, and it is quite likely this has a high one. The location of patches could be explained in a manner similar to the one proposed, the only difference being in the control mechanism. Instead of territorial control by the adults there is a very precise location control by the juveniles or maybe both mechanisms work simultaneously. The shape of the patches and the density gradients within them however, are not easily explained by this alternative.

Some of the tests presented here could also be considered as verifications of other hypotheses. For instance, the increase in distance between neighbors of the same age could also occur under any circumstances by mortality within the patch. The tests represent an attempt to provide independent pieces of evidence that originate in the model. The alternatives explored failed to explain all these observations as a whole in a better way.

Based on these observations, we should be very cautious about the validity of many assertions in the literature arising from small samples, usually quadrats, concerning for instance the existence of dominant age groups in bivalve populations. Most quadrats that could be sampled from the beach here studied would show a dominant cohort, but the cohort will vary from sample to sample. Bibliographic accounts of the presence of a dominant age group are very common (DAVIS, 1923; SEED, 1969; HUGHES, 1970; HANCOCK, 1973; JOHANNESSEN, 1973; EAGLE, 1975; HOSOMI, 1980; JOSEFSON, 1982; LUKANIN and OSHURKOV, 1982). Traditionally the dominance was attributed to extreme fluctuations in recruitment (KNIGHT-JONES, 1952; SAVAGE, 1956; HANCOCK, 1973), but more recently, WOODIN (1976) and TIMKO (1979) developed a new framework based on adult-larval interactions. Those two processes, of course, may act concurrently.

In the present study, only intensive sampling revealed that the age structure is quite close to what could be expected under constant recruitment and mortality (Fig. 30). There are fluctuations, but not of the order of magnitude usually considered. Without intending to deny the variability in year class strength, it may be pointed out that there is often a lack of solid evidence about this variability, its magnitude, and frequency of occurrence. OHBA (1959b) and SCHMIDT and WARME (1969) provide some examples of quite constant recruitment. On the other hand, authors such as HUGHES (1970) and LUKANIN and OSHURKOV (1982) devise very convoluted explanations for their finding of different age groups dominant in different locations, or

FIG. 30 : Age structure of the whole population. Frequency distribution by number of growth rings.



AGE DISTRIBUTION

at different levels of the same location. Recruitment fluctuations are used to justify any anomaly from preconceived patterns.

The evidence in the literature for year class patchiness is quite solid, and it would be even more so if non-parsimonious alternative explanations were weeded out. Since DAVIS (1923), the presence of age or size classes in distinct patches has been repeatedly mentioned, but the idea has not been fully accepted yet, and its implications are seldom considered.

A cautionary note must be made concerning the use of the experimental approach to the study of infaunal communities. Much information is being obtained through the use of cages or density manipulations (DAYTON and OLIVER, 1980; PETERSON, 1980,b); the impact of some of these experimental manipulations may depend on the type of patch (e.g. with respect to age or size) in which they take place and the controls may not be true controls. In a short distance (1-2 m.) it is possible to find patches with very different characteristics. If larvae also occur and settle in patches, then experiments reporting the effect of a treatment on recruitment (e.g. GOODBODY, 1961; WILLIAMS, 1978,1980a,1980b) are not valid unless the number of larvae attempting settlement is also manipulated, or at least subject to a careful scrutiny (e.g. with sediment traps). It seems therefore that some of the theories used to explain the dynamics of benthic populations and communities have extremely fragile experimental support.

From the management point of view, these results emphasize the need to redesign the sampling procedures used to estimate abundance and population parameters. Even though stratified or random quadrats may be adequate for abundance estimation, they do not seem adequate for other purposes such as determination of age structure for mortality studies, recruitment, etc. Some alternatives may be the use of many small sample units distributed randomly, or perhaps to replace the traditional quadrat shapes by longer, narrower trenches. In any case, it is necesary to have prior information concerning patch sizes and shapes.

STOCK-RECRUITMENT RELATIONSHIPS

MODEL AND RESULTS

It is possible now to develop a stock recruitment model based on the conclusions from the previous section.

A recruit is defined in this study as a clam growing past its first growth ring. This definition is arbitrary, but it reflects the fact that smaller individuals are not well represented in the samples as mentioned earlier. Another deficiency of the definition, and a more important one, is that it ignores all processes that take place between metamorphosis and an age of 3 to 6 months depending on the spawning date (review by MOTTET, 1980). During this period, many factors influence the newly settled individuals:

a) They are preyed on by meiofaunal and macrofaunal predators (THORSON, 1966; REYNOLDS, 1969;

1960; TEGELBERG and MAGOON, 1969; GLOCK, 1978).

c) They display a mobility that later disappears (HUGHES, 1970; JONES, 1974; MOTTET, 1980), although some species keep the ability to move (SCHMIDT and WARME, 1969).

The distribution of newly settled clams in the beach is a resultant of all these processes which have already taken place, and, in most cases have ceased to be of significance by the time they mark they first growth ring .

Successful recruitment in any portion of the beach depends on 3 components: i) the presence of larvae attempting to settle; ii) the characteristics of the site chosen (including the adult stock present on the beach) and iii) good conditions for survival.

The number of larvae attempting settlement on a beach is not likely to be related to the number of adults present there. Manila clam larvae spend between 2 and 4 weeks in the water column (YOSHIDA, 1953; QUAYLE and BOURNE, 1972; ANDERSON et al., 1982), so they are often transported over some distance and cannot be expected to settle in their place of origin. Larvae of benthic invertebrates remain close to their birthplace only under unusual hydrographic circumstances (SCHELTEMA, 1975). In a sense, the number of larvae may be a function of adult abundance over the whole region and of environmental conditions affecting their reproductive output (THOMPSON, 1979) and later, the survival of larvae in the plankton (THORSON, 1958). Each individual produces approximately 30000 eggs per spawning; if all of these survived through the larval stage, they could seed 1 to 1.5 square meters of the beach (OHBA, 1959b; WILLIAMS, 1978, 1980b). Considering some conservative figure for adult density, say 100-200 per square meter, it is difficult to imagine a limitation in the larval stock available.

In any case, for the site in question the number of potential settlers is not related to the local adult stock present. Recruitment to the beach (spatfall) however can be modified by the stock:

$$R = f(S)$$

where R = number of recruits per unit area

S = number of adults per unit area

It is now necessary to consider the ways in which these two segments of a population affect each other, and also the way in which they are modified by site effects. There seems to be 3 major components in this process:

a) A "congregating force", present in most species in which reproduction depends on a random encounter of small gametes in a vast medium. This force simply imposes a requirement of proximity for successful reproduction (ORTON, 1927; THORSON, 1950; KNIGHT-JONES and STEVENSON, 1950; CRISP, 1979). It has a wide range of options, from males that live attached to the female (PILGER, 1978; CALVO and MORRICONI, 1978) to looser relationships, but it is almost always present.

In marine invertebrates, gregarious settlement is very frequent and quite well known in epifaunal species (COLE and KNIGHT-JONES, 1949; KNIGHT-JONES and MOYSE, 1961; SEED, 1969; MEADOWS and CAMPBELL, 1972; SCHELTEMA, 1974; HIDU et al., 1978; HAMNER, 1978; CRISP, 1979). There is some confussion in the use of the term gregarious; some authors refer to the attraction of settling larvae for adults of the same species (e.g.KNIGHT-JONES and STEVENSON, 1950; SCHELTEMA et al., 1981), while others include the attraction among larvae (e.g.COLE and KNIGHT-JONES, 1949; HIDU, 1969; NELSON, 1979). SEED (1969) makes a distinction between them, and verifies the existence of both processes in mussels.

Several theories have been advanced to explain gregariousness (besides the proximity for reproduction), among them to reduce predation (HAMILTON, 1971; ELNER and HUGHES, 1978), to withstand wave action (SEED, 1969), etc. But experimental evidence is very limited; HIGHSMITH (1982) shows that larval sand dollars have better survival among adults of the same species because the adults exclude the most important predator of the settlers.

b) A "segregating force", which results in

i) the thinning of dense populations (CONNELL, 1961; KNIGHT-JONES and MOYSE, 1961; GREEN and HOBSON, 1970; HAMNER, 1978; JENG and TYAN, 1982). However, other authors do not observe density-dependent mortality (SHELDON, 1968; SUTHERLAND, 1970; BROCK, 1980; HOSOMI, 1980). PETERSON (1979) analyzing competition in soft bottom benthos concludes that the main effect of crowding is a significant depression of growth rates; mortality is not specially sensitive even to large increases in density.

ii) regularities in the settlement pattern that generate spacing between individuals (HOLME, 1950; KNIGHT-JONES, 1952; KNIGHT-JONES and MOYSE, 1961; CONNELL, 1963; HAMNER, 1978; CRISP, 1979; ANDERSON and KENDZIOREK, 1982). This is probably a result of competition for space or food.

iii) negative interactions between adults and larvae: besides the obvious example of larvae eaten or passed through filtering adults, many references point to a negative relationship without specifying the way in which it takes place. Heavy recruitment may follow a massive adult mortality (BAGGERMAN, 1953; SAVAGE, 1956; KRISTENSEN, 1957; HANCOCK, 1973; DARE, 1976). TIMKO (1979) believes that "cohorts of larviphagous species representing dominant year classes could settle only when adult mortality reduced population density to the by the inhibitory effects, but probably it still exists.

In most cases, the effects of a) and c) will be very difficult to separate, and they will have to be considered as a single process for modelling purposes.

In the graphical model presented before it is assumed that each animal claims a circular area of influence (SCHELTEMA et al., 1981) around its siphon which is a function of its weight:

$$\pi r_i^2 = f\ (w_i)$$

where r_i = radius of area of influence

w_i = weight

In the simplest case:

$$\pi r_i^2 = b\ w_i \qquad (1)$$

We now proceed to the description of a) and c), by assuming that recruitment will be a linear function of the adult biomass present in the area

$$R = k_1 \overline{w} S \qquad (2)$$

Solving for w_i in our definition of the area of influence (1) and replacing w_i and r_i by their expectations (E):

$$w_i = \frac{\pi r_i^2}{b} \qquad E(w_i) = \frac{\pi}{b} E(r_i^2) \qquad (3)$$

Now replacing w_i in (2) by $E(w_i)$ from (3)

$$R = k_1 \frac{\pi}{b} E(r_i^2) S = k_2 \pi E(r_i^2) S$$

where $\pi E(r_i^2) S$ is the total area "claimed" by adults per unit area which we will call A

therefore $R = k_2 A$

SEGREGATING EFFECTS

In the case of b), we can regard recruitment as proportional to the space available for settlement (not "claimed" by adults). For a unit area:

$$R \propto 1 - p(A)$$

where $p(A)$ = proportion of area "claimed" by adults

According to ROBBINS' bombing model (ROBBINS, 1945; CHAPMAN, 1973):

$$p(A) = 1 - e^{-\Sigma \pi r_i^2 n_i}$$

therefore

$$R \propto 1 - (1 - e^{-\pi\Sigma r_i^2 n_i})$$

simplifying

$$R = k_3 e^{-\pi\Sigma r_i^2 n_i}$$

However, the exponent is equal to A

$$\pi\Sigma r_i^2 n = \pi E(r_i^2) S = A$$

and replacing

$$R = k_3 e^{-A}$$

Rewriting

$$R = e^{-k_4 A}$$

The interactions between stock and recruitment reflect these antagonistic forces, a combination of processes balanced to satisfy independent adaptive requirements. After analyzing the two components separately, it is now possible to combine the results in a single model. As these processes probably interact with each other, a multiplicative model is used, resulting in:

$$R = k_1 A e^{-k_2 A}$$

This is Ricker's stock-recruitment model (RICKER, 1954; CHAPMAN, 1973) but based on the area covered by adults. [The notation of the constants has been slightly changed from the derivation]

What we need now is a quantification of

$$\pi\ r_i^2 = f\ (w_i)$$

To begin with, we know that the only way a clam can "claim" a territory is by its filtering activity. It is known that larvae of other species attempting to settle are sometimes eaten (KRISTENSEN, 1957; GREEN, 1957; MILEIKOVSKY, 1974; WILSON, 1980) or passed through the digestive system which often results in subsequent mortality, although there are some references that they may pass undamaged (WAUGH, 1972; HYLLEBERG and GALLUCCI, 1975)

Our observations on thinning out of patches seem to indicate that either mortality or emigration at early stages, are a result of interaction between neighbors. The distance at which these interactions may take place is assumed to be the maximum reach of the filtering activity, and this has to be related to the weight of the clam.

The simplest model is to assume that the area claimed by an individual is a linear function of its weight.

$$\pi\ r_i^2 = a + b\ w_i$$

In order to estimate a and b the following procedure was chosen:

a) Pairs of nearest neighbors with "similar" weights were selected, after defining "similar" as not differing in more than 15% either way.

b) For these animals, the distance to the nearest neighbor may be considered as twice the radius of influence because of their similar sizes. This distance is therefore halved from here on.

c) We obtain average distances after grouping in weight intervals (Table XVI).

****

TABLE XVI: Half distance to nearest neighbor for animals with similar weight.

mean w (g)	1/2 distance to n.n.
1.65	1.98
4.95	2.02
8.25	2.23
11.55	2.32
14.85	2.38
18.15	2.31
21.45	2.20
24.75	2.31
28.05	2.54
31.35	2.55
34.65	2.70

****

The differences in year class strength mentioned before show here again. To avoid the dangers of excessive extrapolation, we limit the validity of the linear function estimated to the range for which there is adequate coverage in the sample, and use the last value from that portion for all weights above:

$$0 \leqslant w \leqslant 36.7 \qquad r_i = 2.0503 + 0.0157\, w_i$$

95% C.I. intercept (1.8059,2.2969)

95% C.I. slope (0.0040,0.0274)

Correlation coefficient = 0.7105 $p<0.05$

$$\text{for} \quad w > 36.7 \qquad r_i = 2.5276 \quad \text{(constant)}$$

There are also biological reasons for this truncation, mainly that it seems unreasonable to expect the filtering activity to increase without bounds, and there is some experimental evidence for a stabilization or even decrease of filtration rates in larger animals (SRINIVASAN, 1968; FOSTER-SMITH, 1975).

Unfortunately, it is necessary to deal with the problem of the other bivalves present in the samples for whom there are not enough observations to develop an alternative function. Arbitrarily, the same function is imposed on all species present; this is probably wrong, but the small number and generally the small size of individuals from the other species reduces the significance of this problem. In any case, those samples in which more than 1/3 of the biomass consists of other species were eliminated.

With these functions, we now proceed to divide the beach into quadrats of 30x30 cm in order to generate a series of small areas on which stock and recruitment could be measured. Up to now, we have used weights measured in our sample; for these calculations however we need to back-calculate weights, to use values closer to the actual value at the time of settlement of the recruits considered. Using the weight-length relationship obtained from our data:

$$W = 0.000119\ L^{3.151908}$$

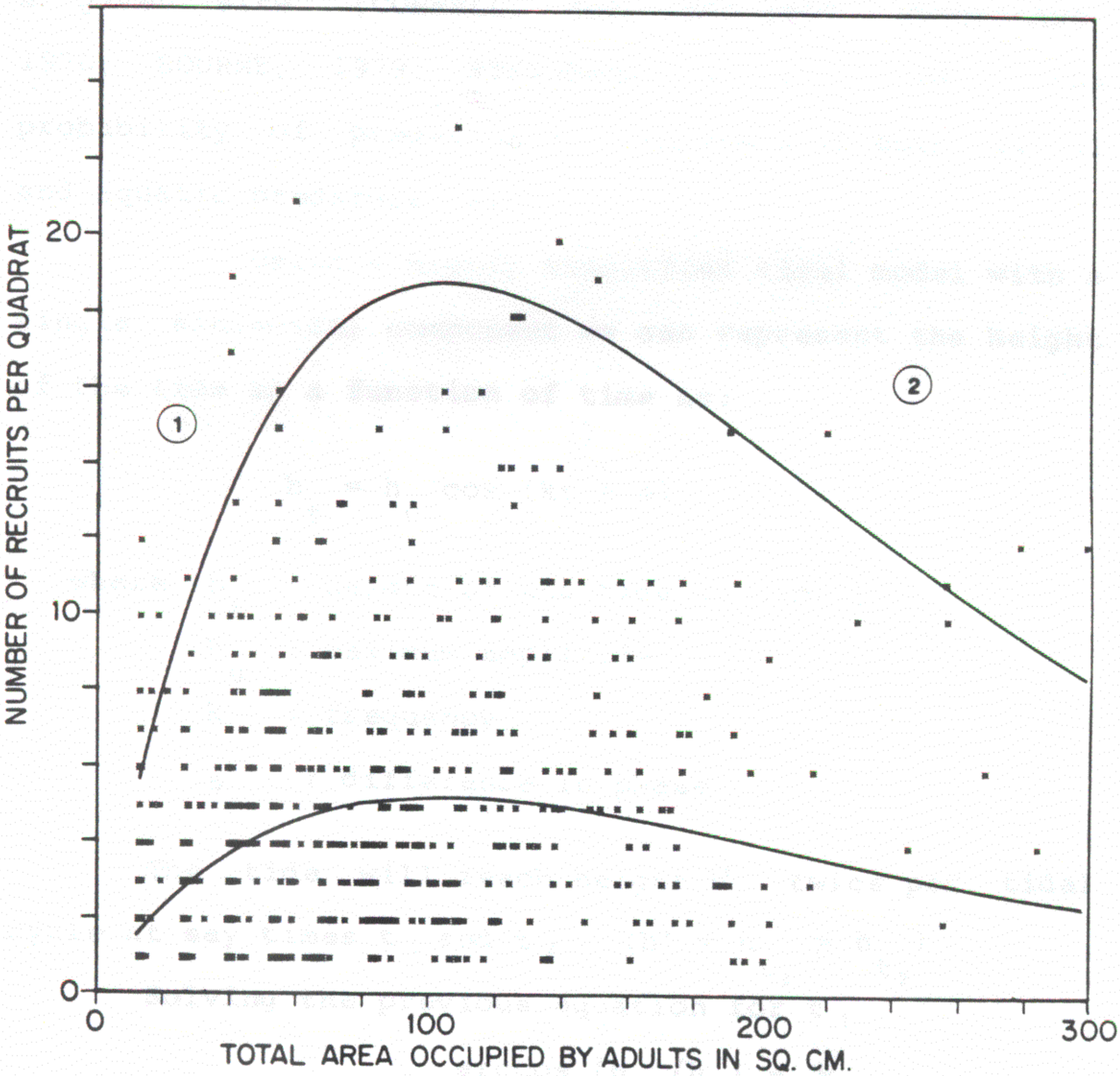
The exponent b compares well with the values mentioned for the same species by OHBA (1959b, 3.2-2.7) and JONES (1974, 3.11).

The weights one year ago were back-calculated using the size of the ring before last. This weight is then associated with an area, and summed over all individuals present in each quadrat. Again for other species it is necessary to use the present size because of the lack of measurements for previous rings. As a further simplification of the problem, it is assumed that the areas of influence do not overlap or overlap only slightly (this is supported by the results of Pielou's test for spacing); otherwise, halving distances to nearest neighbors and other steps would not be valid. The values obtained for areas occupied by adults are likely to overestimate the real values, but the approximation is good enough for the requirements of this study.

These areas can now be used to plot all

FIG. 31 : Number of recruits per unit area versus area occupied by adults in quadrats.

STOCK-RECRUITMENT MAIN AND BOUNDARY FUNCTION



exposed, depending on the choice of t and t)

$$t_2 - t_1 = \{\{(\arccos(h_{t_2}/h_0) - \phi)/k)\} - \{(\arccos(h_{t_1}/h_0) - \phi)/k)\}\}$$

This difference of arccos functions can be expressed as another arccos function because of the trigonometric properties of these inverse functions (ZUCKER, 1970). Therefore, we can postulate that the effect of the gradient may be modeled as an arccos function. This agrees fairly well with empirical studies on the relationship tidal level versus time of submergence (DOTY, 1946,1957; RICKETTS and CALVIN, 1952). It seems reasonable to expect that the recruitment function will be more responsive to the gradient (i.e.the tidal level) than the adults-area function because the adult population has had many other influences in shaping their spatial pattern and abundance.

Figures 32 and 33 show the plots for the two variables (Recruitment and Area "claimed" by adults) against tidal level in feet which confirm the model proposed for recruitment and indicate more complexity for the area of adults. However, even in this case, the arccos function seems to be a reasonable model.

Using non-linear regression, the best fit of the arccos function to the number of recruits per unit

FIG. 32 : Recruitment versus tidal level in feet.

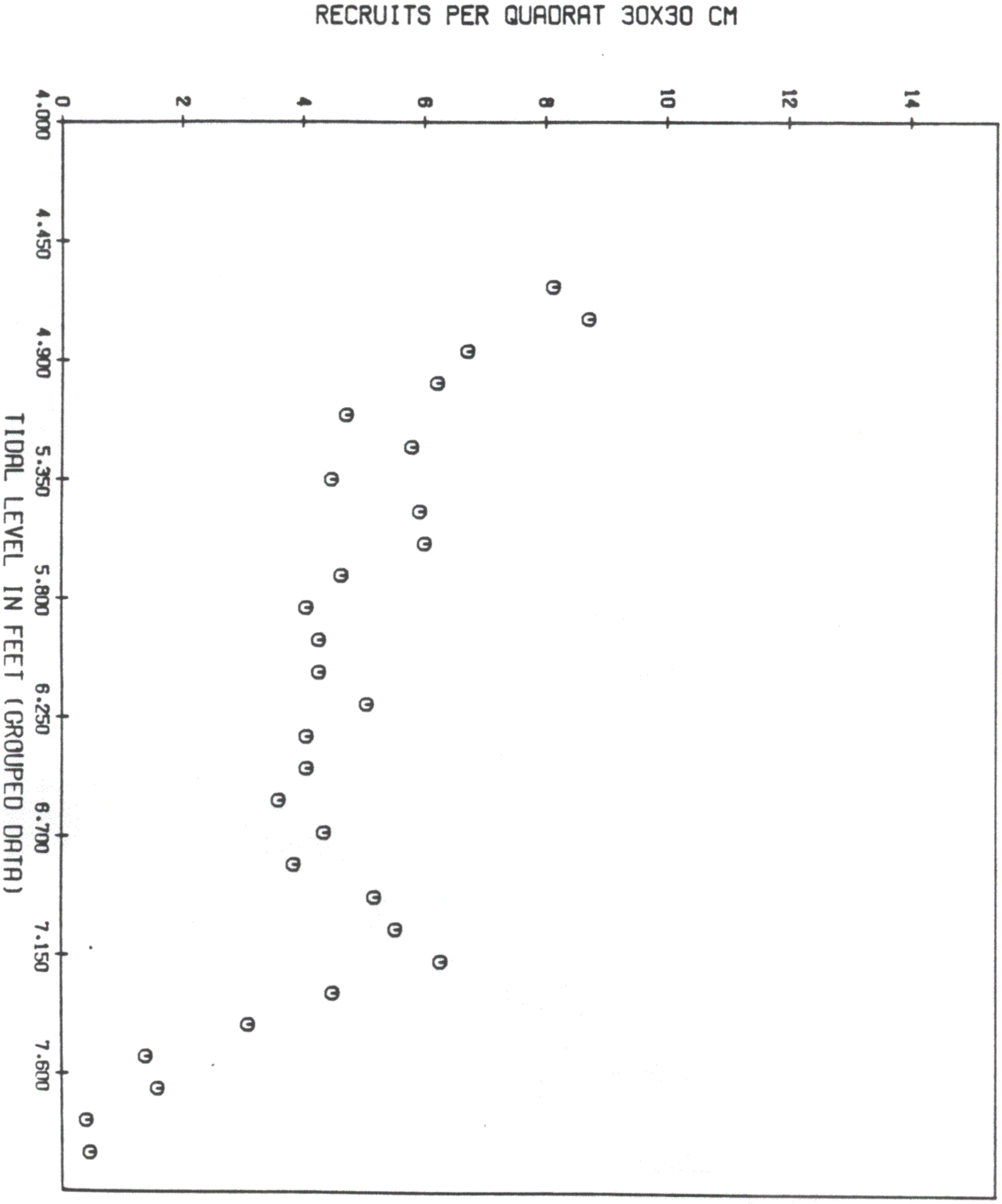
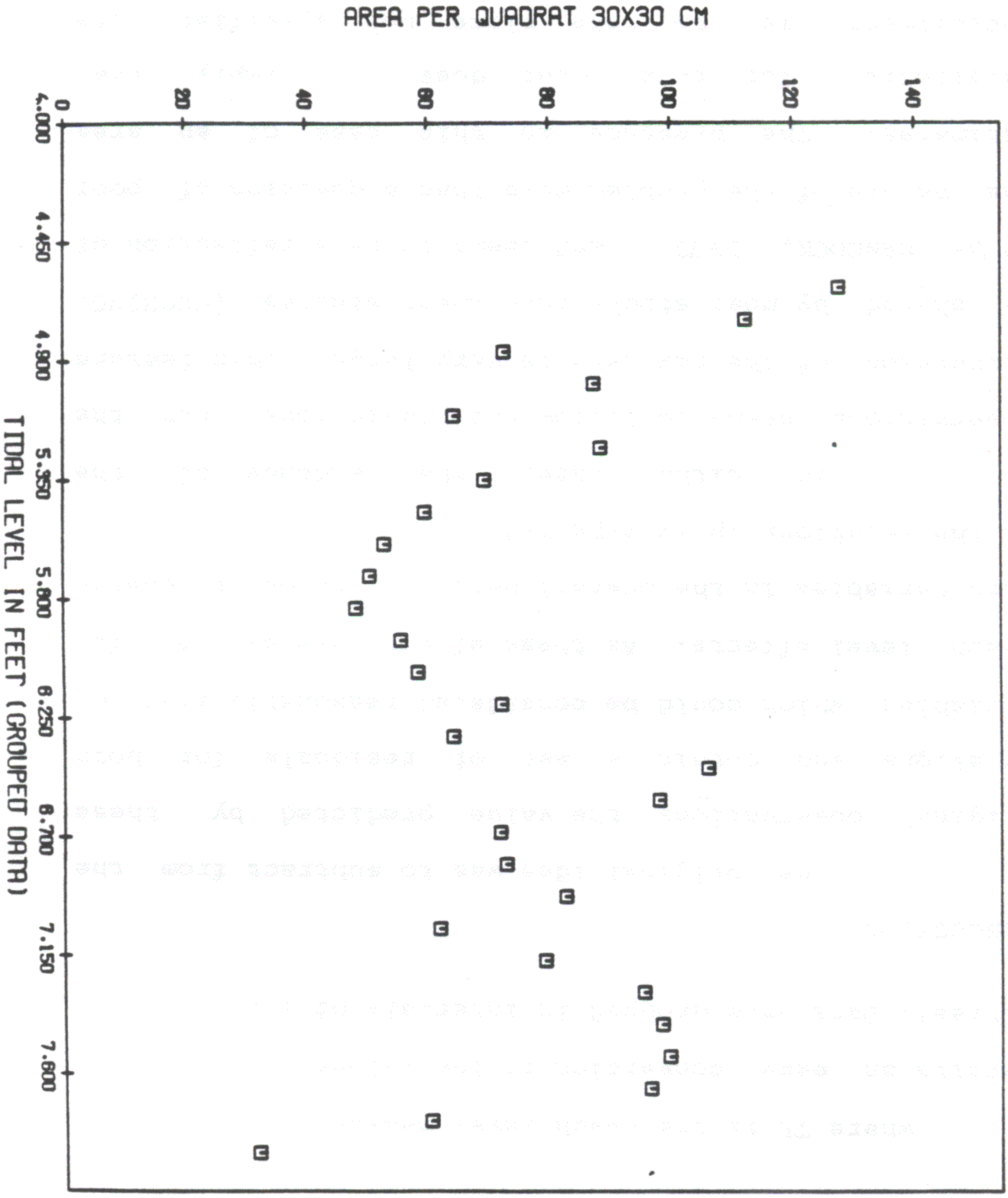

RECRUITS PER QUADRAT 30X30 CM
0
2
4
6
8
10
12
14
4.000
4.450
4.900
5.350
5.800
6.250
6.700
7.150
7.600
TIDAL LEVEL IN FEET (GROUPED DATA)

FIG. 33 : Area occupied by adults per 30x30 cm^2 quadrat versus tidal level in feet.


AREA PER QUADRAT 30X30 CM
0
20
40
60
80
100
120
140
4.000
4.450
4.800
5.350
5.800
6.250
6.700
7.150
7.600
TIDAL LEVEL IN FEET (GROUPED DATA)

area versus tidal level is (after reducing the number of parameters by transformation):

$$R = 7.0822 \arccos (0.1248\ TL)$$

where TL is the beach level measured in feet (this permits an easy conversion to the values in the Tide Tables). Data were grouped in intervals of TL.

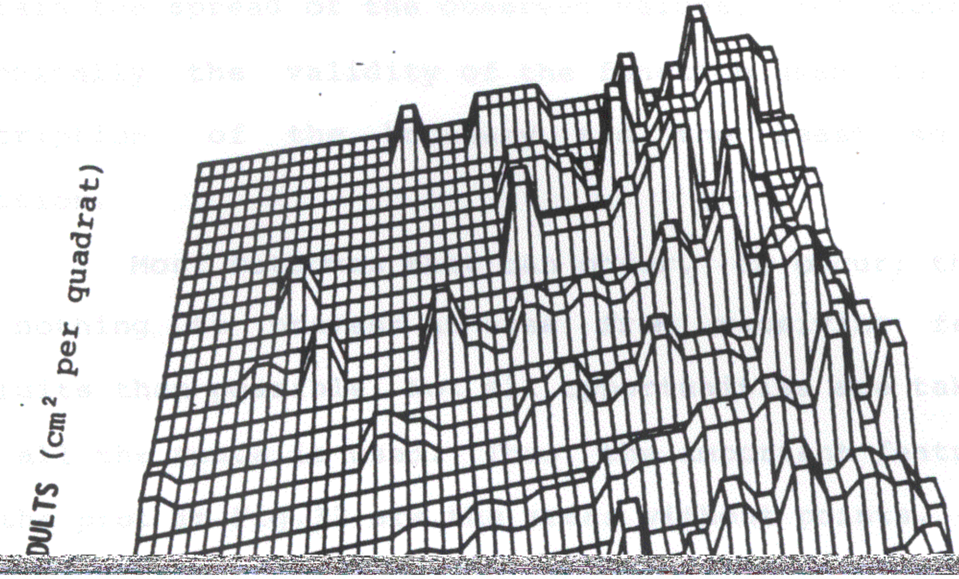
DISCUSSION

The original idea was to subtract from the original observations the value predicted by these equations and obtain a set of residuals for both variables which could be considered reasonably free of beach level effects. As these effects are similar for both variables in the overall pattern, no major change in the relationship is expected.

In either case, the tendency of the observations seems to follow the predictions, but the dispersion of the raw data is very large. This feature is shared by most stock-recruitment studies (CUSHING, 1973; HANCOCK, 1973), and seems to be a reflection of the nature of the problem more than a question of poor estimates. The presence in this case of an area "available" for recruitment does not imply that recruitment is to take place nor specifies its magnitude (KREGER, 1940; WAUGH, 1972). Even though space available is one of the conditions for successful recruitment (DARE, 1976; HAWKINS and HARTNOLL, 1982), it is by no means a sufficient one. There is a very important stochastic component in the fact that larvae must find the space to settle. The most information we can obtain from this type of model is a probabilistic statement separating permissible or likely combinations from those that aren't.

Essentially the plot (Fig.31) shows an upper boundary rarely surpassed. This boundary function was calculated using the linearized form of the Ricker function for which confidence intervals based on the standard error of the estimate can be obtained (Here, the one-tailed value of the t-distribution was utilized to define the parameters of the function that included approximately 95% of the observations).

Below this value there is only an average over space and probably over time also. Fig.34 shows the frequency distributions corresponding to different intervals of area occupied by adults. It can be seen that the location of modal values is higher for intermediate values of area occupied and that the general shape of the distributions is truncated for low values of area, and approximately normal towards the


DULTS (cm² per quadrat)

center of the range studied. These elements could be used in a stochastic recruitment model; they serve to explain the spread of the observed values, and confirm graphically the validity of the function used in the description of the boundary and the least square function.

Most outcomes that can occur, do occur; there is nothing to prevent an area from receiving fewer recruits than possible. Not all opportunities are taken, not all the space is used. Thus, the important features of the plot in Fig.33 are the areas without points. The first one, labelled (1) in the figure, shows the common response of adults and recruits to unfavorable environments (they are mostly samples taken high in the beach) and perhaps the attractive effect superimposed to this one.

The second region, called (2) in the same figure, shows the impact of the adult population in reducing the number of recruits in areas with large biomass. In between these 2 areas of the plot lies what we could call the optimum adult level for recruitment.

MORTALITY

MORTALITY COEFFICIENTS AND MODEL

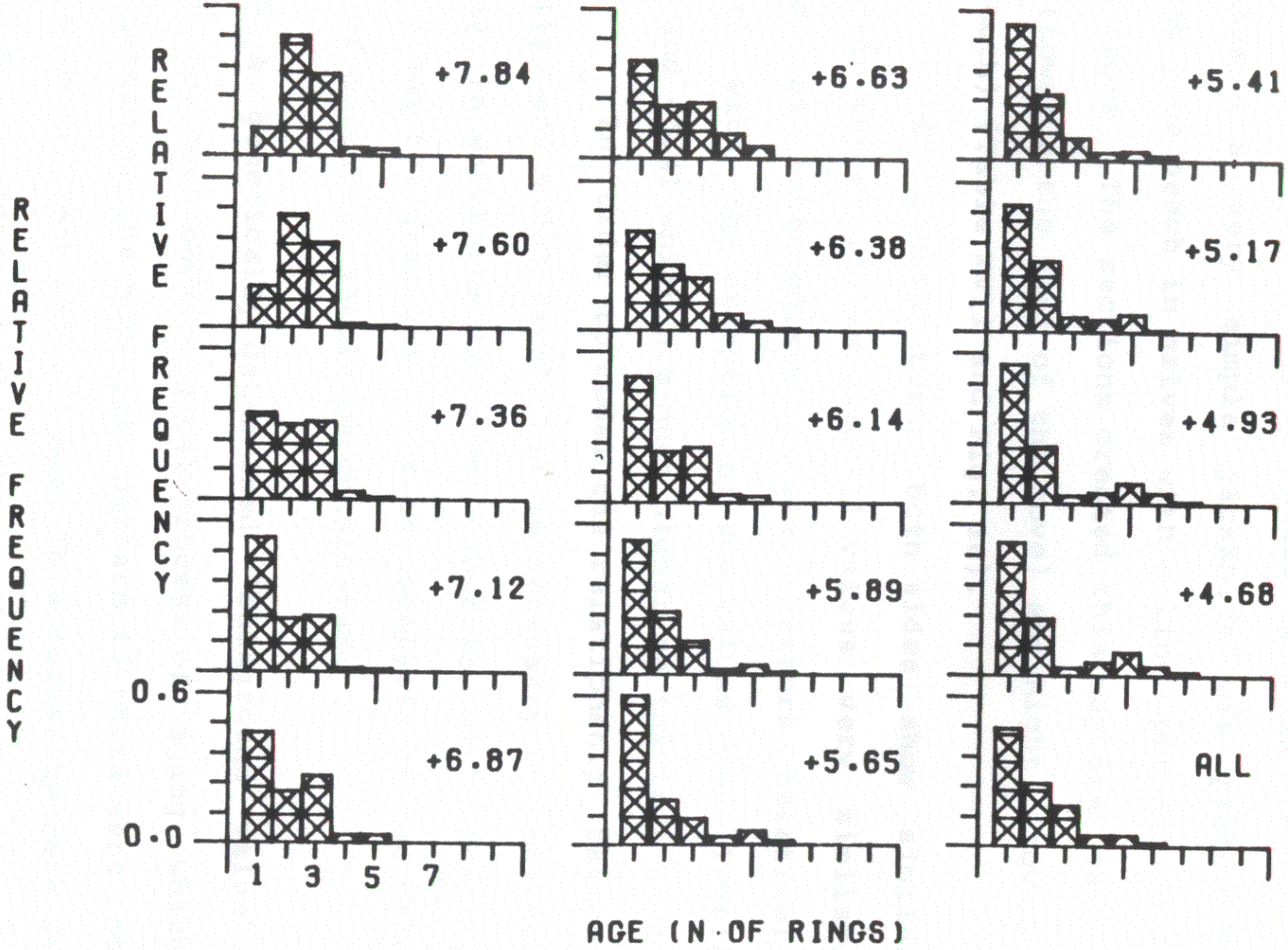
At the planning stages of this work, it was thought it would be posible to obtain mortality estimates for quadrats or for small areas in general. When the patchy age structure in space was recognized, this approach had to be discarded because it was not possible to get reasonable estimates under these conditions.

In order to avoid or reduce this problem, it was decided to pool together all quadrats in each one of the 14 rows in which the plot was divided (Fig.5). The age distribution for each row, and the one corresponding to the whole area censuses are shown in Fig. 35. The plot shows, among other features, the absence of 6's and 7's from the higher portions of the beach, indicating better survival in the lower levels.

The overall age distribution suggests a fairly constant recruitment (Fig.35 or larger plot in Fig.30). At least there are no changes of the order of magnitude expected for a highly fluctuating population. In any case, the presence of only 7 age groups in the sample does not allow us to carry these inferences to the long term.

With these data we can calculate mortality

AGE DISTRIBUTION BY TIDE LEVEL



rates using the Chapman-Robson estimate (CHAPMAN and ROBSON, 1960; ROBSON and CHAPMAN, 1961). In order to verify the effect of year class patches in those estimates, a very simple jackknife was performed, dividing the beach in halves with a line perpendicular to the shore. The sections created this way are called Left (towards the head of the cove) and Right (towards the mouth) (Table XVII and Fig. 36).

In general terms, both sides show similar trends in the estimates (overall values very similar, maximum at intermediate levels, errors relatively similar) with the exception of the values for levels +5.17 and +5.41 which are much higher on the left half.

In order to model the relationship between mortality and tidal level, it is necessary to consider the way in which the different sources of mortality change along the gradient. For the analysis, three main causes of mortality should be considered:

1) A genetically determined "background value", related to the physiological process of aging which would determine the mortality pattern if there were no other cause of death but old age. This mortality rate is assumed to be constant throughout the beach because there seems to be no reason to believe that there are genetic differences in this respect between segments of

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TABLE XVII: Mortality estimates for tidal levels (jackknife) for halves and overall rows. Instantaneous mortality rates and standard errors.

tidal	LEFT		RIGHT		ALL	
level	M	S.E.	M	S.E.	M	S.E.
+7.84	-	-	0.533	0.052	0.541	0.052
+7.60	-	-	0.594	0.036	0.590	0.034
+7.36	0.594	0.081	0.676	0.034	0.667	0.031
+7.12	0.714	0.066	0.884	0.047	0.838	0.038
+6.87	0.555	0.045	0.784	0.045	0.693	0.032
+6.63	0.501	0.035	0.712	0.044	0.603	0.028
+6.38	0.529	0.039	0.727	0.044	0.632	0.029
+6.14	0.626	0.047	0.889	0.058	0.755	0.037
+5.89	0.700	0.059	0.865	0.061	0.794	0.014
+5.65	0.825	0.067	0.791	0.050	0.809	0.013
+5.41	0.960	0.075	0.697	0.043	0.785	0.012
+5.17	1.012	0.072	0.585	0.036	0.724	0.011
+4.93	0.749	0.046	0.621	0.038	0.681	0.009
+4.68	0.681	0.033	0.533	0.033	0.626	0.007
all	0.682	0.014	0.700	0.011	0.693	0.009

****

FIG. 36 : Instantaneous mortality rates versus tidal level in feet; observed values and fitted model. Confidence intervals for each Chapman-Robson estimate indicated with dashes

the population living at different beach levels.

2) A stress component: individuals higher in the beach suffer more intense exposure to extreme temperatures, freshwater, ice, desiccation, etc. (RAPSON, 1952; CONNELL, 1961,1970; HUGHES, 1970; FOSTER, 1971; VERMEIJ, 1972); these factors may reduce their life span with increasing levels of the beach.

3) A predation component which in the case of intertidal organisms may be divided into the fraction arising from aquatic predators (such as fish, crabs; GLUDE, 1964; SEED, 1969; KELSO, 1979; VLAS, 1979; MILLER, 1982; ANDERSON et al., 1982) and the one arising from terrestrial or aerial predators (such as many birds, raccoons; DRINNAN, 1958; ANDERSON, 1982; SUTHERLAND, 1982). The impact of the different predators may be assumed to be proportional to the amount of time

stress component because both follow similar trends. Since only experimental evidence could distinguish between them, they will have to be modelled as a single process.

Expressing these concepts in a simple equation:

$$M_T = M_0 + M_{ap} + M_{ts}$$

where M_T = total mortality

M_0 = background value

M_{ap} = mortality attributed to aquatic predators

M_{ts} = mortality attributed to terrestrial or aerial predators and stress

To model a process for which only the direction of change is known but not the shape of the response function a very flexible function is needed. The power function qualifies as such because of the variety of shapes it can assume with a relatively small number of parameters.

If the different functions are expressed as

$$M_0 = a$$

$$M_{ap} = b_1 TL^{b_2}$$

$$M_{ts} = b_3 TL^{b_4}$$

and substituting in (3)

$$M_T = a + b_1TL^{b_2} + b_3TL^{b_4}$$

Using again non-linear regression to estimate the parameters, we obtain

$$M_T = 0.4332 + 0.8953\ TL^{3.3372} + 0.8900\ TL^{3.3400}$$

Fig.36 shows both observed and predicted values; the fitted function gives a reasonable approximation although there is a noticeable deviation at intermediate values. That may suggest that the impact of predation could be modelled as a sum of two normal (or similar) functions, with peaks corresponding to maxima of activity , but without more detailed evidence the simpler model will be retained.

This model is likely to be valid for many other intertidal populations or, in general, for populations inhabiting environmental gradients or ecological interfaces. A comparison of the intensity of the different factors in play could be obtained from the parameters for both power functions, although some of the effects are confounded. The more interesting fact is the existence of a maximum mortality in the area of overlap of the different factors for which there is no record in the literature.

Combining the data for the whole area censused we obtain an overall estimate of the instantaneous mortality rate M = 0.693 (Table XVII). Going back to Fig.36 and looking at the distribution of mortality values along the gradient one sees that the overall estimate gives a poor description of the real dynamics of the beach. The spatial changes are so important that the average value is an improbable one to find in a sample of the beach. In a parallel fashion, recruitment to the beach is quite constant if the whole area is considered, but practically any quadrat sampled from it would suggest otherwise.

DECLINE IN PATCH SIZE WITH AGE

Parallel to the concept of mortality, we must consider the decline in size of patches, the other "units" of population change (PAINE and LEVIN, 1981).

It is very difficult and quite arbitrary to define the limits of patches in the map of the population. To reduce this problem the concept of proximal map is used where every point in space is "assigned" to the individual nearest to it (DOUGENIK and SHEEHAN, 1977). Thus, a discrete set of points in space is transformed into a mosaic of areas that share some property and cover the entire plot. In this study, the points (clams) were identified by a property (age) which was extended in such a way as to generate patches associated with it. These areas are identified by a shading pattern in Fig. 37.

It is now possible to estimate the area for the each patch. The procedure is objective and reproducible, so it seems advantageous with respect to other alternatives. Its major drawback is that the package capable of performing this task (SYMAP) has a limited capacity for data handling so that sampling was required.

The 1's were omitted because of their very large patch sizes, which resulted in very laborious measurements. The 6's and 7's were pooled into a single class, and a sampling fraction of 20% was utilized. As a result the patch sizes are expected to be overestimates, because smaller patches will tend to dissappear during the sampling process. Areas with very low density were omitted because they generate falsely large patches. The mean values for patches of ages 2 to 6 in cm are shown in Table XVIII.

If the decrease in mean patch size with age is now plotted on the y-axis, the decrease in numbers (for the whole area) in the same axis, and age (=time) in the x-axis, it is possible to compare the decline of both functions which is very similar (Fig.38).

FIG. 37 : Proximal map of age distribution. Patches for ages 1 (lightest) to 6 (darkest) are shown as shaded areas. Ages 6 and 7 pooled. Sampling fraction 20% (see text).

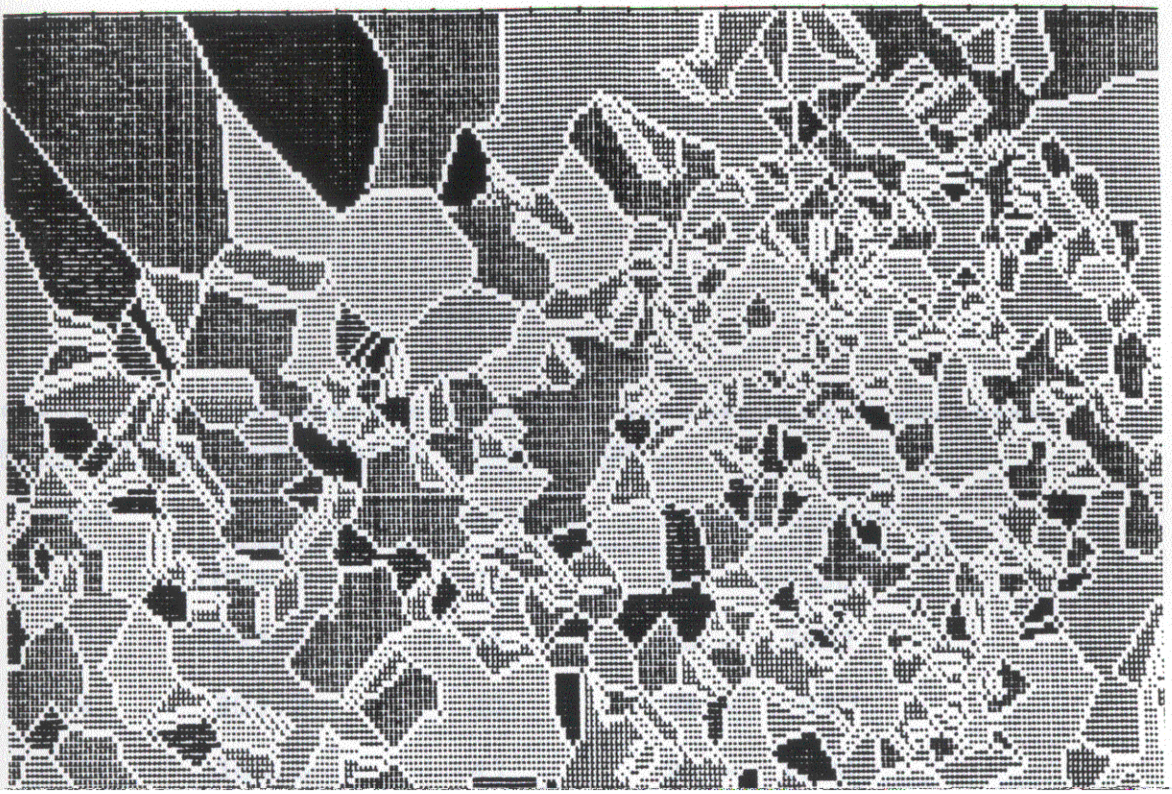

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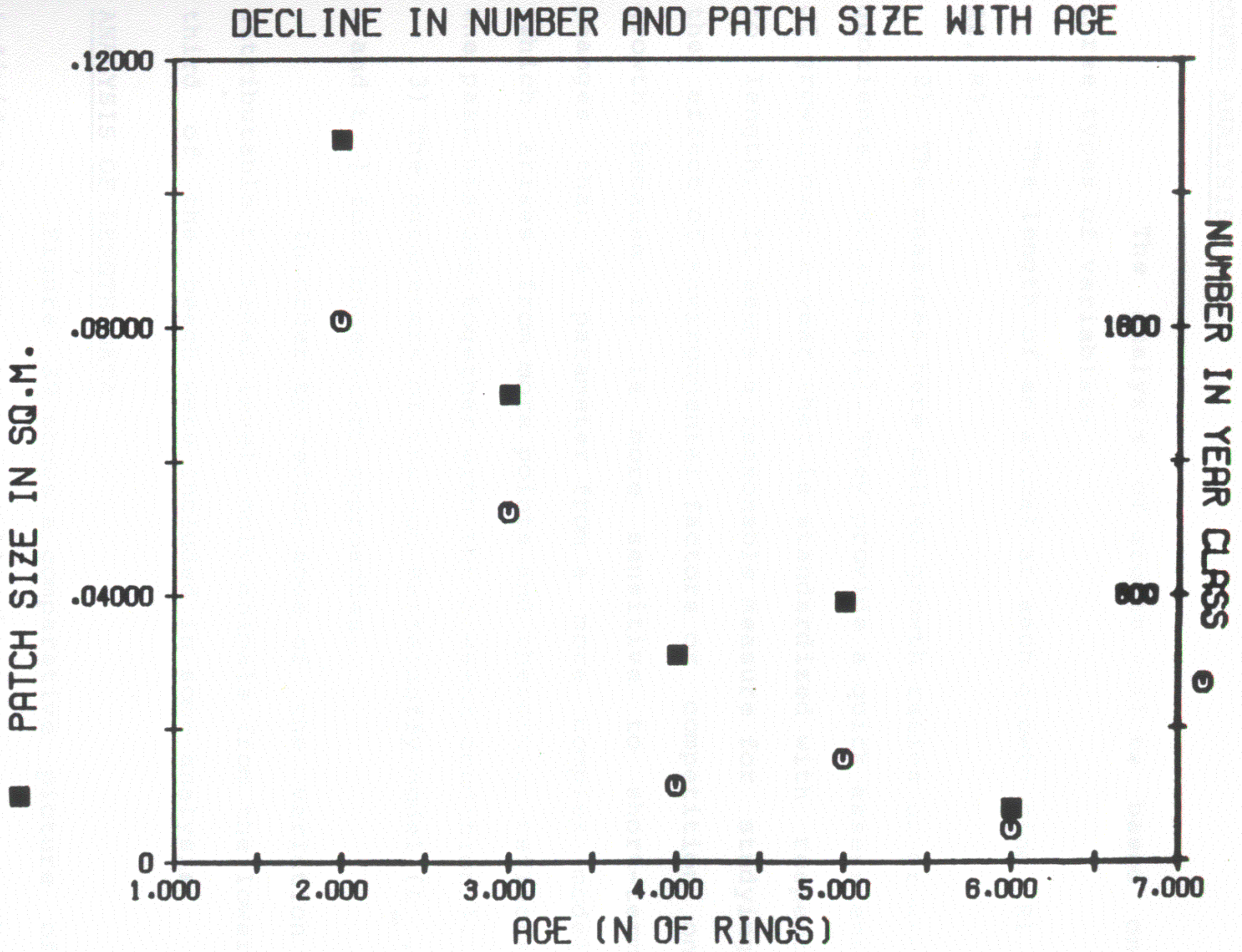
TABLE XVIII: Mean Patch Area in cm .

Age	Mean	#patches	Range(approx.)

FIG. 38 : Decline in numbers and in patch size with age.


DECLINE IN NUMBER AND PATCH SIZE WITH AGE
■ PATCH SIZE IN SQ.M.
NUMBER IN YEAR CLASS
.12000
.08000
.04000
0
1600
800
1.000
2.000
3.000
4.000
5.000
6.000
7.000
AGE (N OF RINGS)

GROWTH ANALYSIS

The analysis of growth will be based on three types of variables:

1) The length of an animal at each growth ring R1, R2, R3,....

2) The measures here called growth ratios or growth quotients, R(i+1)/R(i). They provide a quick assessment of growth over a year that is standardized with respect to length. It seems a reasonable measure for studying the effect of environmental factors or competition on growth because it is more sensitive to short-term changes than a parameter from a more complex model (which arises from more points and therefore reflects the past history together with the present conditions).

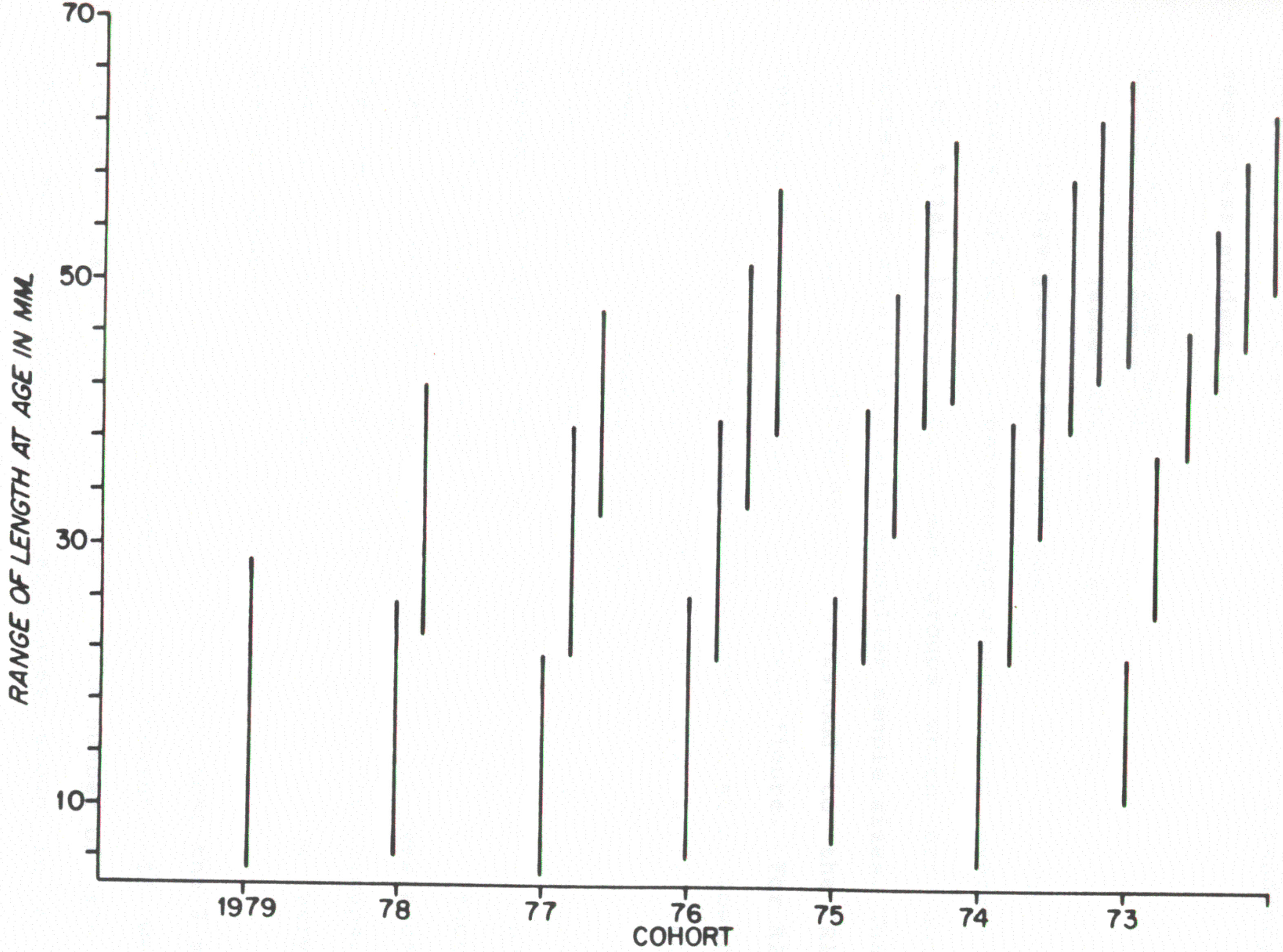
3) The parameters of the von Bertalanffy model (L_∞, k and t_0) for longer-term approaches.

In order to reduce some of the variation attributable to tidal level, only animals from the lower third of the beach were included in some analysis.

ANALYSIS OF LENGTH DATA

Figure 39 shows a comparative picture of individual length values for all cohorts present on the beach. The observations are reasonably similar for most age groups, with the exception of the 3's which show a

FIG. 39 : Ranges for length at age for cohorts on lower third of the beach. Length in mm, cohorts indicated by year of origin. For each cohort the range at each ring is shown as a vertical bar.


RANGE OF LENGTH AT AGE IN MM.
70
50
30
10
1979
78
77
76
75
74
73
COHORT

noticeable lower size at their first ring. This tendency seems less evident for later rings.

LENGTH AT AGE FOR COHORTS

Table XIX shows length at the different rings by age group. An ANOVA was carried on to compare lengths of the rings between age groups using averages over tidal levels. Some age groups which are not represented at all levels have smaller sample sizes. The more significant differences correspond to the R1 values, with the 3's showing the lowest figure. For R2 there are still significant differences but at a lower tidal level; the values for the 3's are still the lowest, but the margins are narrowing. All other sets show nonsignificant values. In almost all cases the two largest values for each row correspond to the 6's and 7's, but this is probably an artifact due to the fact that these age groups are limited to the lower levels of the beach, where growth is better. The other groups, scattered across a range of tide levels show very similar values.

It has already been mentioned that the 3's constitute the strongest year class present. If we projected backwards in time the present number of 3's, using some of the mortality estimates shown in the corresponding section, it is easy to reach the

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TABLE XIX : Length at age for cohorts and ANOVA (mm)

	AGE							
	1	2	3	4	5	6	7	ALL
R1	12.97	12.99	9.83	12.74	12.86	13.39	14.79	12.62
R2		28.71	25.72	26.77	26.99	27.81	30.69	27.51
R3			35.65	35.96	35.35	37.21	39.49	36.38
R4				41.46	41.48	43.35	45.07	42.47
R5					45.09	47.60	48.94	46.79
R6						50.48	52.49	51.26
R7							55.20	55.20
n	14	14	14	14	14	11	7	

F values and significance

	F	signif.
R1	6.29	$p < 0.001$
R2	2.64	$p < 0.05$
R3	1.58	N.S.
R4	1.47	N.S.
R5	2.00	N.S.
R6	1.29	N.S.

Pairwise comparisons using Scheffe's test (NIE et al., 1975) (performed after eliminating the 7's because of their absence in the higher levels of the beach), yield :

R1 $3\ \underline{1\ 2\ 4\ 5\ 6}$ $p < 0.05$

R2 No significant differences

conclusion that this year class probably originated in a much denser settlement than the other groups. If mortality were higher at higher densities as observed in some planting experiments (MILLER et al., 1978; ANDERSON et al., 1982), then the initial abundances would have been even higher. Further evidence of the dense settlement of 3's is provided by measures of interindividual distance within age groups (Table XV) and with respect to any nearest neighbor (Table XIV). In both cases the 3's are quite far from the pattern shown by the other groups.

As a result of their high density, their patches were overcrowded and competition arose, leading to a slower growth. It is not known how this combines with self-thinning, but both processes are probably caused by the crowding of settlers. PETERSON (1979) believes that competition in soft bottom benthos results in depressed growth rates but not in mortality increases, but he emphasizes (1977,1980) competition for space. For many years, it was believed that food could not be a limiting resource for filter feeders (e.g. LEVINTON, 1972); however an increasing body of evidence is accumulating pointing to the posibility of competition for food (RAPSON, 1952,1954; TEGELBERG and MAGOON, 1969; GLYNN, 1973; BUSS, 1979; BUSS and JACKSON, 1981). Of special interest are recent contributions by CLOERN (1982) and OFFICER et al. (1982) which show the impact of filter feeders on the water column. If that happens in a bay, it seems quite likely that shallower areas such as tidal flats, small coves, and in general all the intertidal may experience local depletion of food. In the case of the intertidal, and using as an example the beach studied, the mean height of the water column over a point in the beach (throughout the tidal cycle) will be roughly between 2-4 ft. The volume of water that could be associated with this figure is not very large when compared to filtration rates of the order of 7 m^3/m^2/day (MOHLENBERG and RIISGARD, 1979, for the Manila clam at a density of 360 adults/ m^2). Considering that water renewal is less than perfect, and that a relatively thin layer passes over a whole bed of filter feeders, then it seems possible that food resources within the water mass may be depleted locally. If this were the case, animals high in the beach (which are known to have smaller growth rates than those in lower levels) may be experiencing not only the obvious reduction in feeding time but also the results of a decrease in their food supply. These comments ignore the probably significant role of resuspension from the bottom.

The smaller size of the 3's could be explained in some other way. The possibility of a late settlement or the survival of only the late portion of a normal one can be considered, but the densities observed in themselves suggest a heavy settlement.

Another explanation would be the occurrence of an environmentally very "bad" year (low production, frequent stresses, etc.). Its effect however, should also be reflected in the growth of the other year classes present, likewise exposed to them, which was not observed.

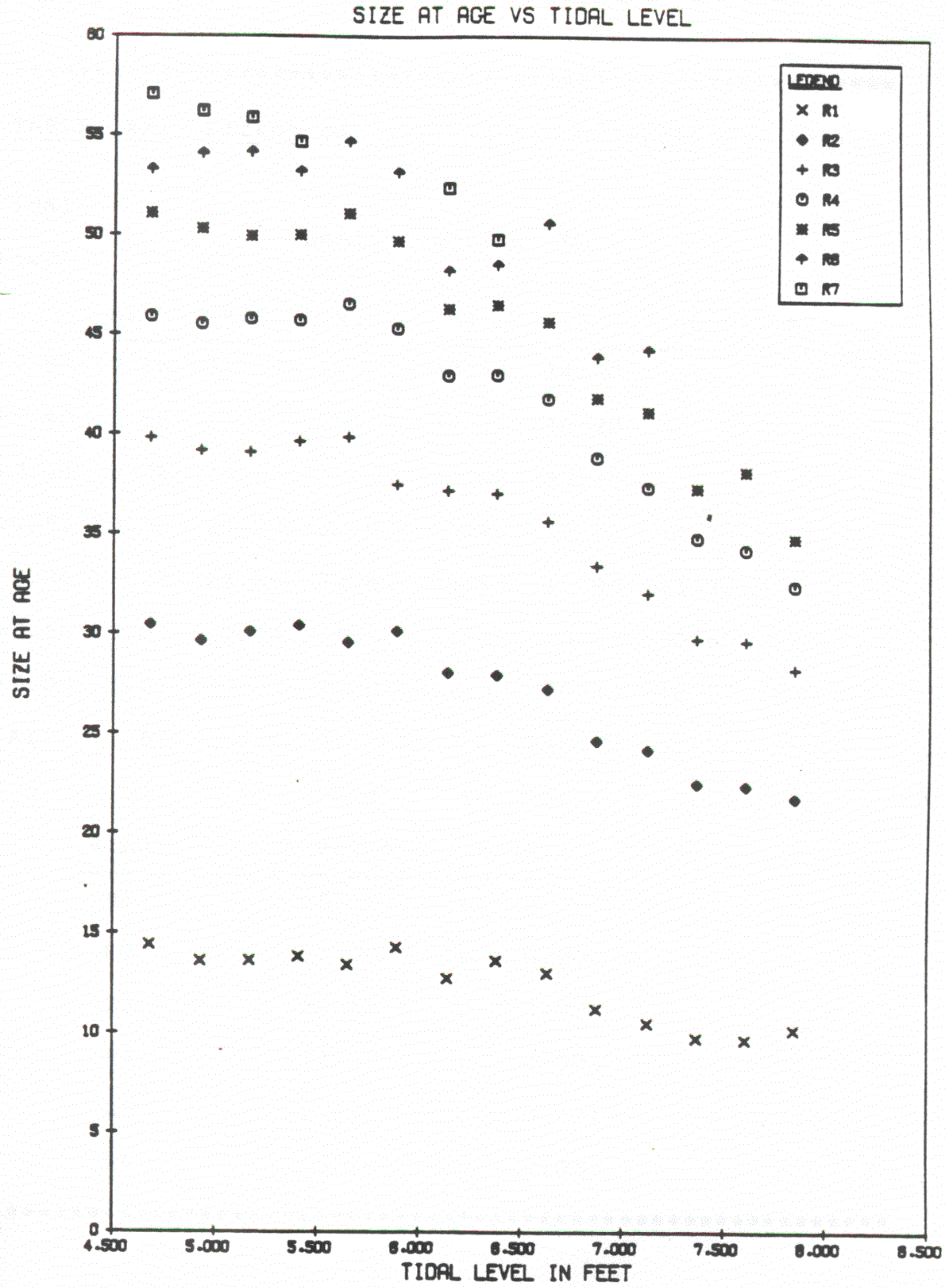
There are other possible explanations, such as changes in the pattern of mortality, especially in the selection against a given size range, etc., but they seem much less likely.

At the other end of the density scale, the 4's are the weakest year class present, and their patches show much less crowding (Tables XIV and XV). It is interesting to notice that in spite of the lower crowding, the 4's do not show an advantage in growth. This indicates that in most cases, the densities present in the beach are not high enough to result in intense competitive interactions. Only cohorts arising from heavy settlements experience the strong density dependent effects described for other species (SAVAGE, 1956; SEED, 1969; TEGELBERG and MAGOON, 1969) . The observations are limited to the range of sizes considered in this study; the interactions affecting larvae or spat are inferred from indirect evidence.

EFFECT OF TIDAL LEVEL ON LENGTH

The effect of tidal level is shown in Fig. 40 and Table XX. Significant differences were expected in this case, and it seemed more interesting to concentrate the analysis on the effects of tidal level. In Table XXI, the ratios between size at level i over size at the lowest level of the beach are shown as a measure of the proportion of realized growth. There is a remarkable homogeneity in the proportion of growth realized at the different rings. From approximately +6.0 ft down there is no noticeable change, as illustrated in the All column. Fig.41 shows these mean values plotted against tidal level. The level at which this asymptote is reached indicates for all practical purposes, the beginning of the subtidal area as far as growth is concerned. There are no differences between growth at this level or further down on the beach.

FIG. 40 : Length at age versus tidal level in feet.
Length in mm.


SIZE AT AGE VS TIDAL LEVEL
SIZE AT AGE
TIDAL LEVEL IN FEET
0
5
10
15
20
25
30
35
40
45
50
55
60
4.500
5.000
5.500
6.000
6.500
7.000
7.500
8.000
8.500
LEGEND
R1
R2
R3
R4
R5
R6
R7

****

TABLE XX: Effect of tidal level on length (7 levels)

Tidal level	Length at ring (mm)						
	R1	R2	R3	R4	R5	R6	R7
+7.84	10.16	21.77	28.27	32.45	34.80		
+7.48	9.68	22.37	29.63	34.25	38.20		
+7.00	9.74	22.50	29.77	34.80	37.30		
+6.52	10.50	24.20	32.05	37.40	41.15	44.30	
+6.04	11.22	24.66	33.42	38.87	41.85	43.90	
+5.56	13.02	27.24	35.67	41.80	45.65	50.60	
+5.08	13.63	27.97	37.04	42.97	46.30	48.50	49.80
All	12.62	27.51	36.29	42.47	[illegible]	[illegible]	[illegible]

****

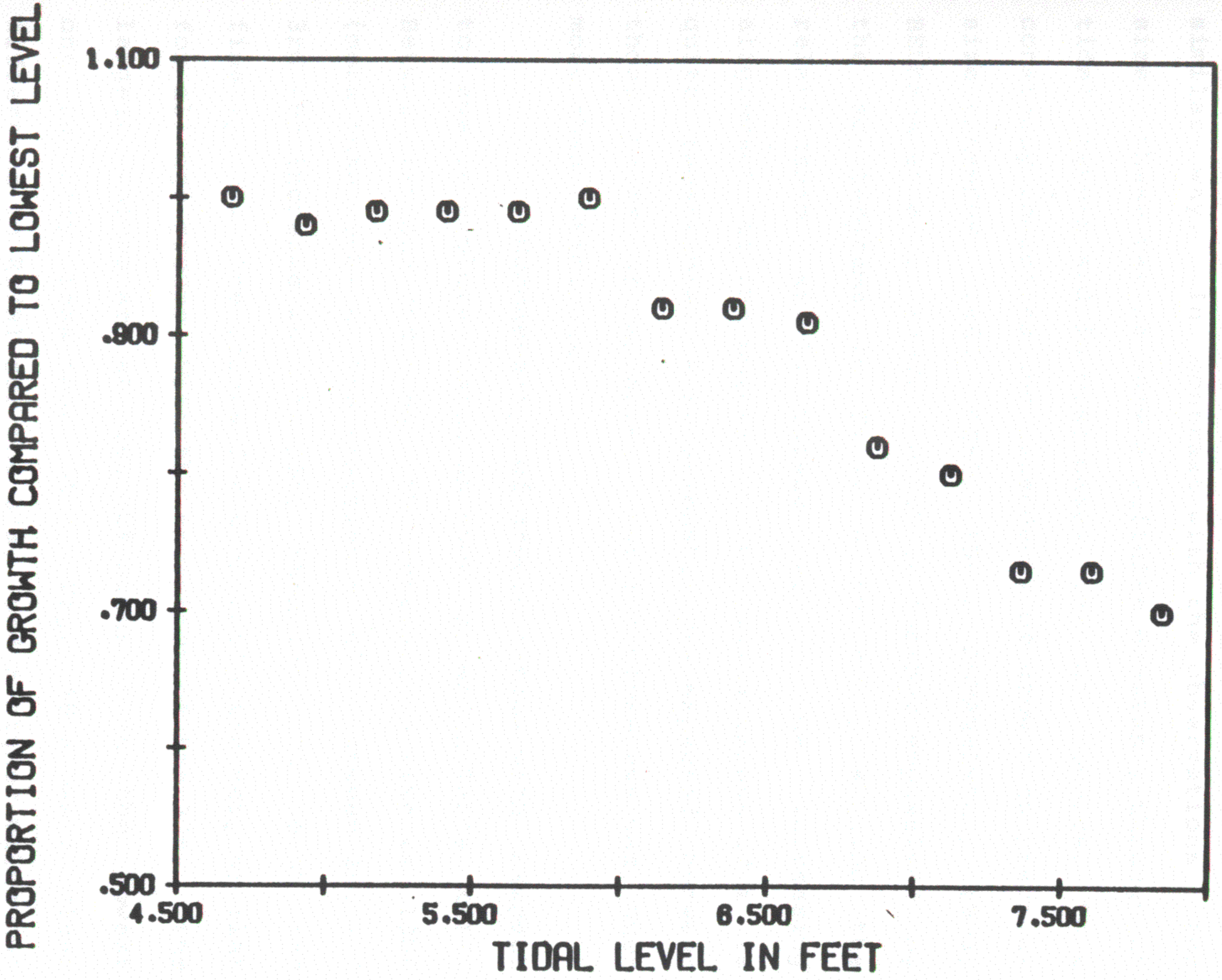
TABLE XXI: Proportion of growth realized at each level

R(level i)/R(lowest level)

k	R1	R2	R3	R4	R5	R6	R7	All
+7.84	0.70	0.71	0.71	0.71	0.69			0.70
+7.60	0.67	0.73	0.74	0.75	0.76			0.73
+7.36	0.68	0.74	0.75	0.76	0.74			0.73
+7.12	0.73	0.79	0.81	0.81	0.82	0.83		0.80
+6.87	0.78	0.81	0.84	0.85	0.84	0.82		0.82
+6.63	0.90	0.89	0.90	0.91	0.91	0.95		0.91
+6.38	0.95	0.92	0.93	0.94	0.92	0.91	0.87	0.92
+6.14	0.89	0.92	0.93	0.94	0.92	0.91	0.92	0.92
+5.89	0.99	0.99	0.99	0.99	0.99	1.00	1.06	1.00
+5.65	0.93	0.97	1.00	1.01	1.02	1.03	--	0.99
+5.41	0.96	1.00	1.00	1.00	1.00	1.00	0.96	0.99
+5.17	0.95	0.99	0.98	1.00	1.00	1.02	0.98	0.99
+4.93	0.94	0.97	0.99	0.99	1.00	1.01	0.98	0.98

****

FIG. 41 : Proportion of growth realized (compared to lowest level) versus tidal level in feet.

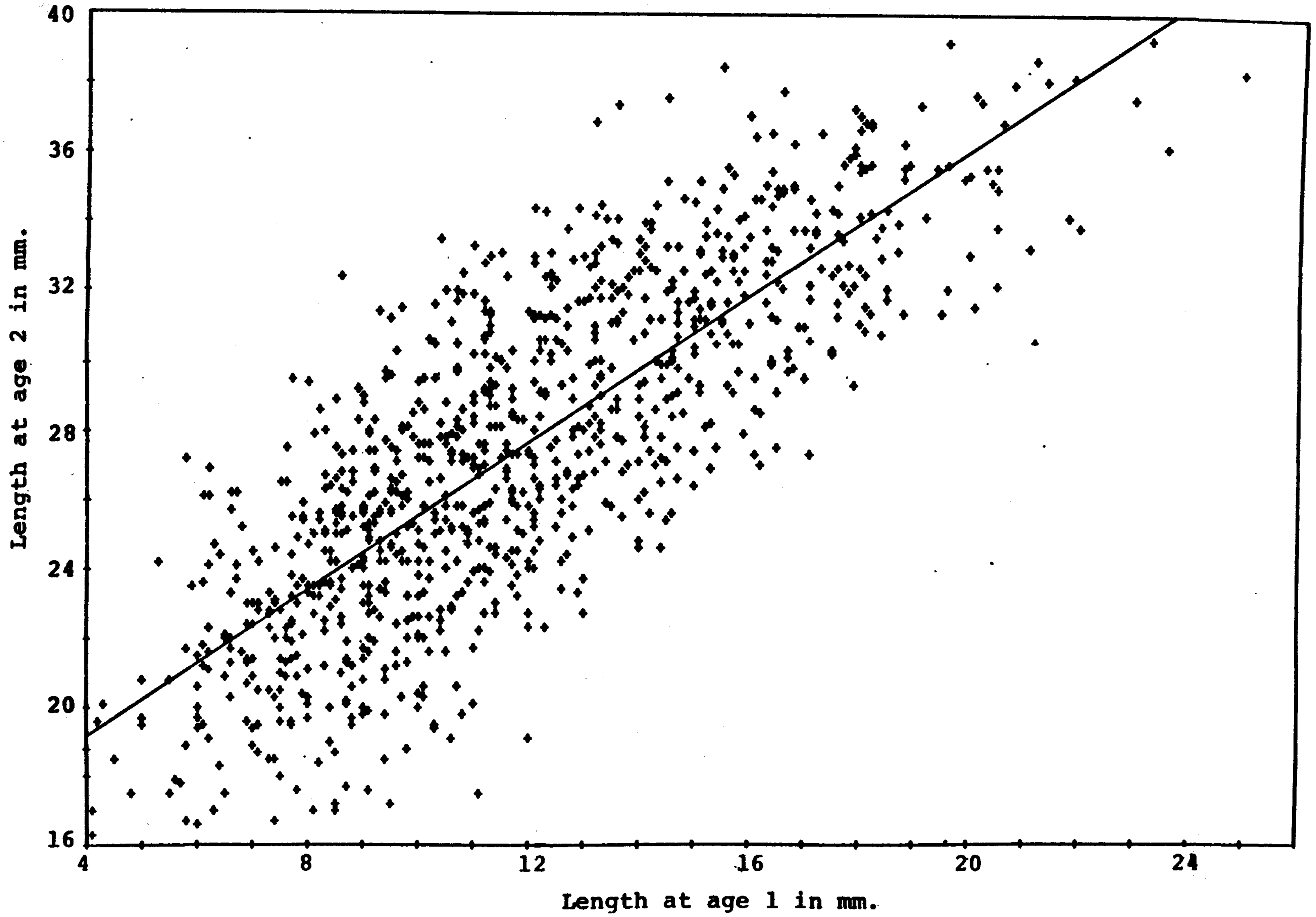

PROPORTION OF GROWTH COMPARED TO LOWEST LEVEL
1.100
.900
.700
.500
4.500
5.500
6.500
7.500
TIDAL LEVEL IN FEET

ANALYSIS OF GROWTH RATIOS

The growth ratios will be analyzed in a similar way. In contrast with the observations for size, these ratios show a definite constancy throughout tidal levels and in most cases through cohorts. This constancy indicates the dependency of growth on previous size (LAMMENS, 1967; SEED, 1969; JOHANNESSEN, 1973; BEUKEMA et al., 1977) which is further emphasized by the scattergrams in Figs. 42 to 47 , showing the relationship R(i+1) versus R(i). The increasing alignement of the points for increasing values of i is quite remarkable. A relationship was expected between those pairs of variables, but its closeness was much more than anticipated.

Homogeneity of growth ratios with respect to age is explored using an ANOVA shown in Table XXII. Between 1st and 2nd ring, the increase in size is 130% (more than doubling the starting size); between 2nd and 3rd the increase is only 35%, then 15%, 9%, 6.5% and finally 5%. The values for each ratio are very similar for all age groups. With the exception of the 3's, the largest values are at most 10% higher than the lowest one (usually less than 5%). Fig. 48 shows a clear difference in R2/R1 for the 3's, and a higher value but not remarkably so in the case of R3/R2.

FIG. 42 : Length at ring 2 versus length at ring 1.



40
36
32
28
24
20
16
Length at age 2 in mm.
4
8
12
16
20
24
Length at age 1 in mm.

FIG. 43 : Length at ring 3 versus length at ring 2.

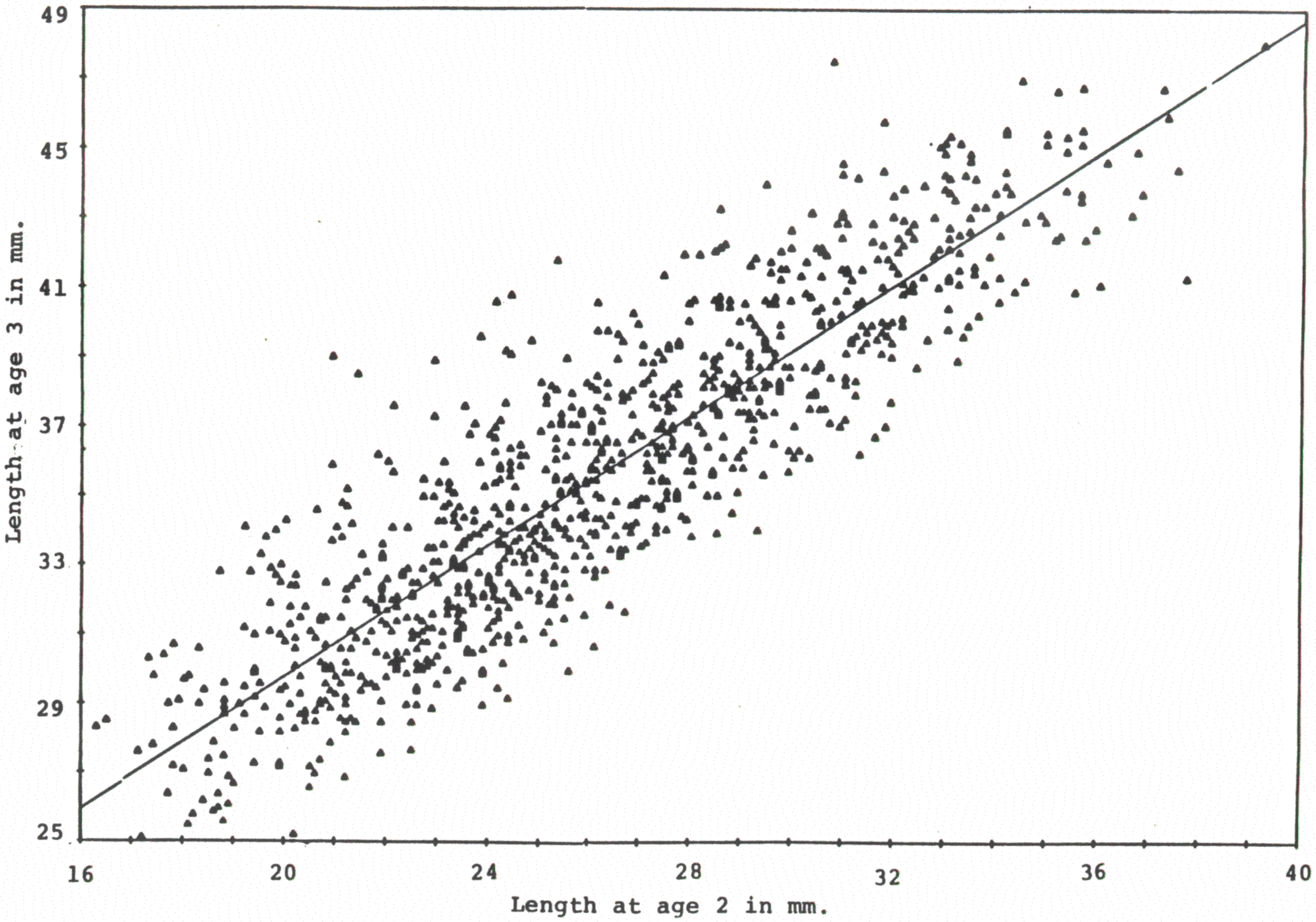

49
45
41
37
33
29
25
Length at age 3 in mm.
16
20
24
28
32
36
40
Length at age 2 in mm.

FIG. 44 : Length at ring 4 versus length at ring 3.

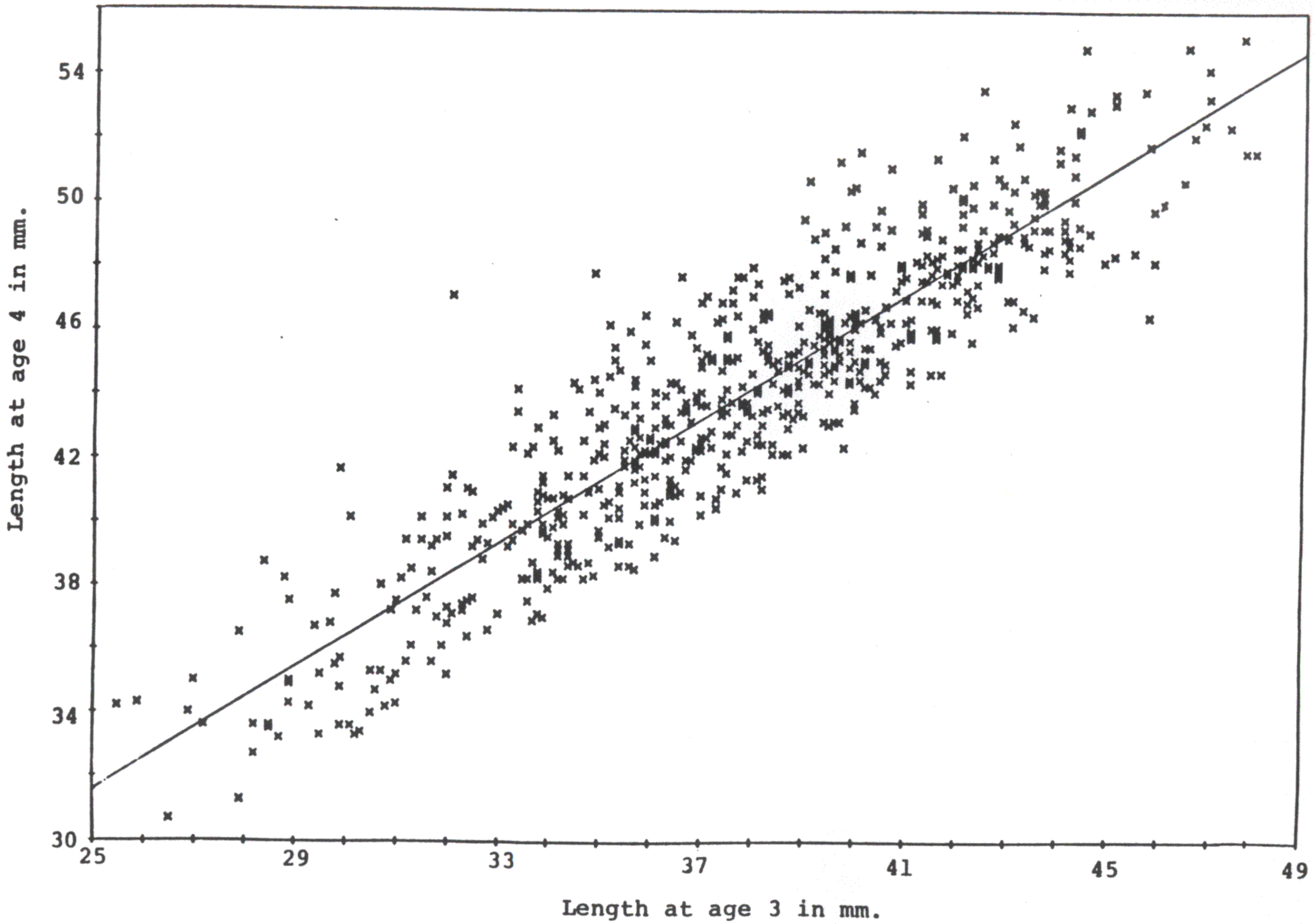

Length at age 4 in mm.
54
50
46
42
38
34
30
25
29
33
37
41
45
49
Length at age 3 in mm.

FIG. 45 : Length at ring 5 versus length at ring 4.

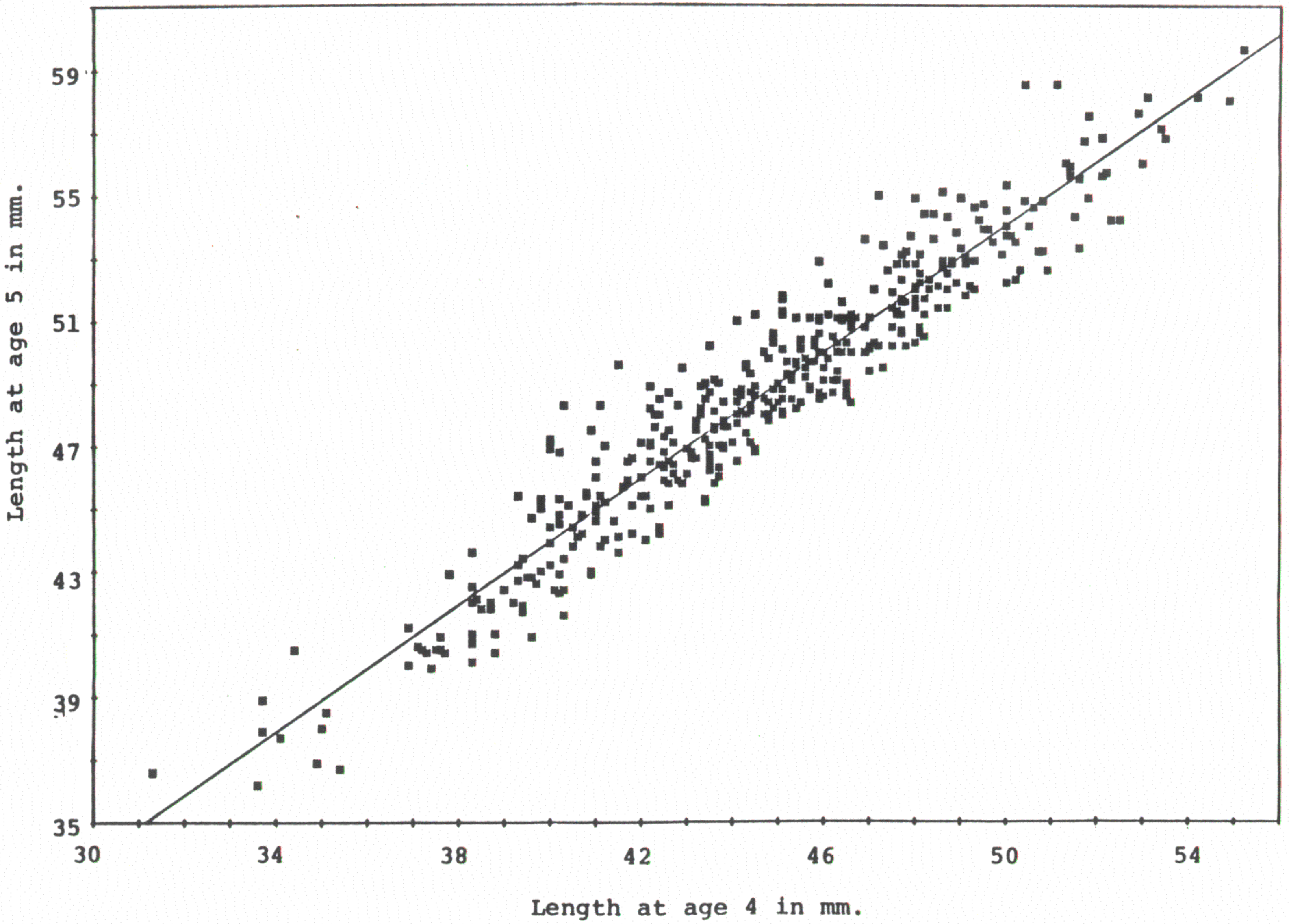

59
55
51
47
43
39
35
30
34
38
42
46
50
54
Length at age 5 in mm.
Length at age 4 in mm.

FIG. 46 : Length at ring 6 versus length at ring 5.

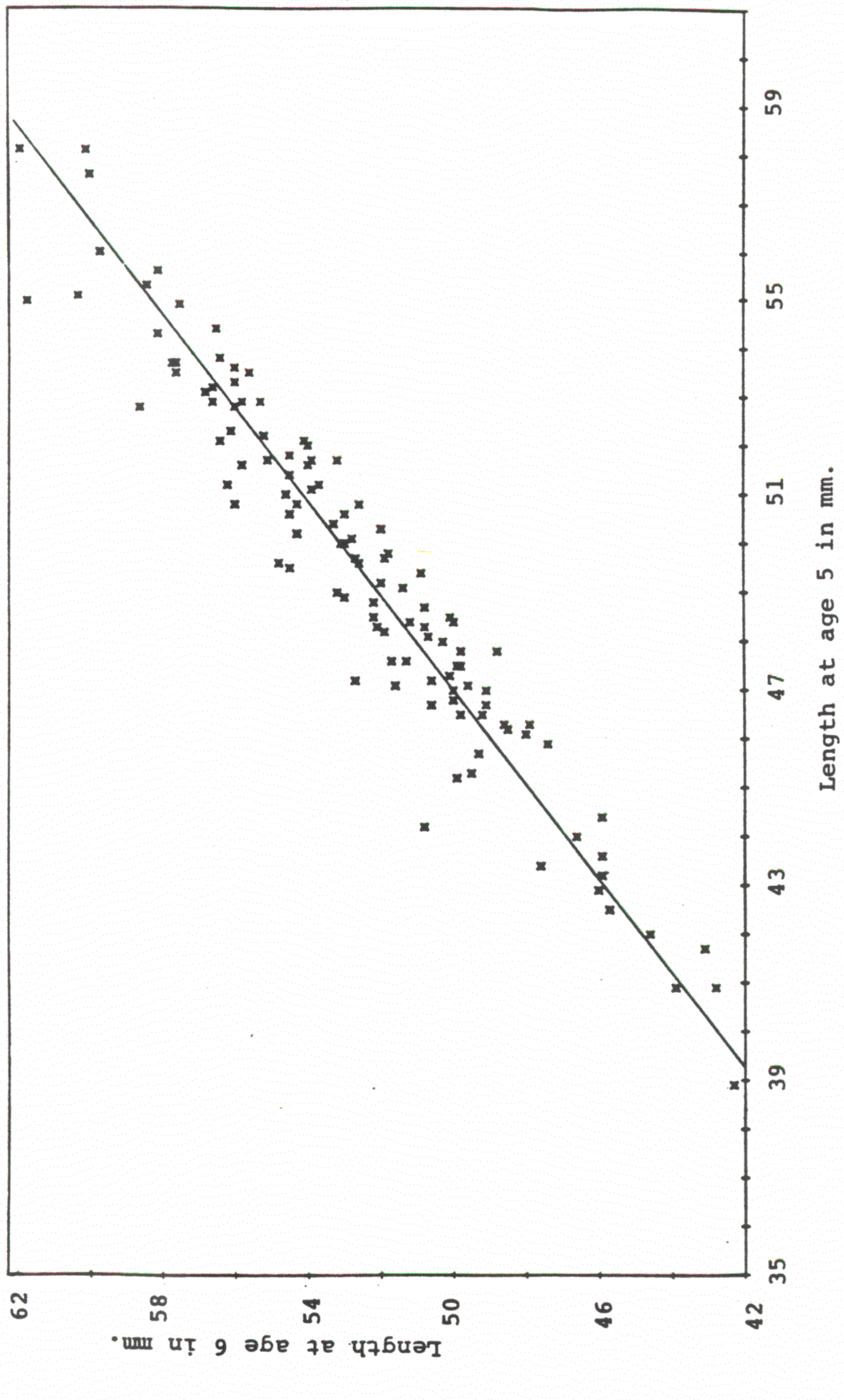

Length at age 6 in mm.
62
58
54
50
46
42
Length at age 5 in mm.
35
39
43
47
51
55
59

FIG. 47 : Length at ring 7 versus length at ring 6.

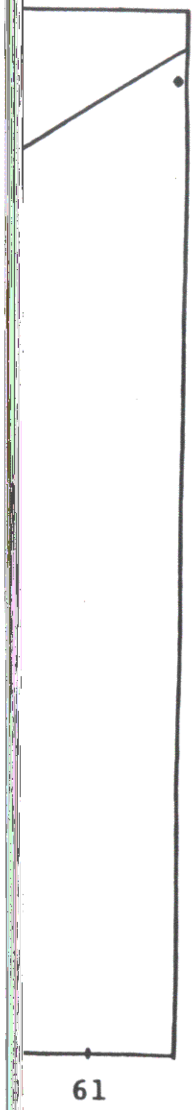
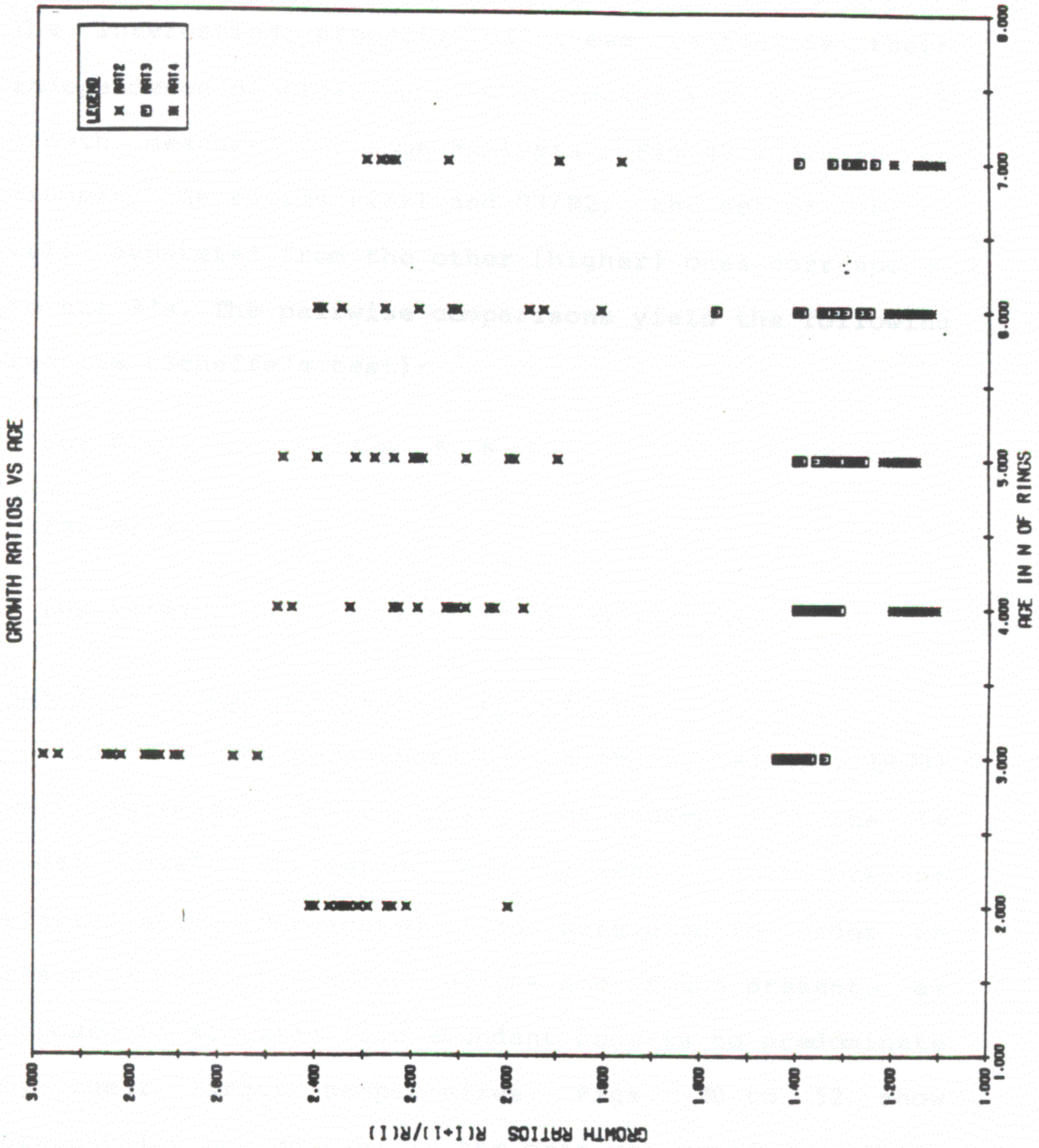

61

TABLE XXII: Growth ratios for each age (all cohorts) and ANOVA for homogeneity.

	AGE									
	2	3	4	5	6	7	ALL	N	F	Sign
R2/R1	2.30	2.77	2.18	2.19	2.16	2.12	2.31	74	32.5	***
R3/R2		1.40	1.35	1.32	1.35	1.29	1.35	60	6.7	***
R4/R3			1.15	1.18	1.17	1.14	1.15	46	3.5	*
R5/R4				1.09	1.10	1.08	1.09	32	2.7	NS
R6/R5					1.06	1.07	1.06	18	2.2	NS
R7/R6						1.05	1.05	7	-	-
n	14	14	14	14	11	7				

FIG. 48 : Growth ratios (R_{i+1}/R_i) versus age.

RAT2 = R2/R1
RAT3 = R3/R2
RAT4 = R4/R3


GROWTH RATIOS VS AGE
LEGEND
RAT2
RAT3
RAT4
GROWTH RATIOS R(I+1)/R(I)
3.000
2.800
2.600
2.400
2.200
2.000
1.800
1.600
1.400
1.200
1.000
AGE IN N OF RINGS
1.000
2.000
3.000
4.000
5.000
6.000
7.000
8.000

The next consideration is the relationship between growth ratios and tidal levels (Table XXIII). The interesting property of these ratios is their independence of tidal level which makes them a desirable growth measure for some analysis. Fig.49 shows as an example the ratios R2/R1 and R3/R2; the set of values well separated from the other (higher) ones corresponds to the 3's. The pairwise comparisons yield the following results (Scheffe's test):

for R2/R1 $\begin{array}{cccc} 3 & 4 & 5 & 6 \\ \cline{2-4} \end{array}$

for R3/R2 $\begin{array}{cccc} 3 & 6 & 4 & 5 \\ \cline{1-3} & & & \\[-2ex] \cline{2-4} \end{array}$

for R4/R3 no significant differences

ANALYSIS OF VON BERTALANFFY PARAMETERS

The parameters L_{∞}, k and t_0 (RICKER, 1979) were estimated by nonlinear least squares for the 14 tidal levels considered, and for each cohort present (Table A-5). Unweighted means were used in order to insure a more even effect of the age groups present, as opposed to allowing more abundant cohorts to predominate by their larger sample sizes. Figs. 50 to 52 show graphically the changes in the mean values of the three parameters versus tidal level.

The plot for L_{∞} (Fig.50) shows similar

TABLE XXIII: Growth ratios versus tidal level and ANOVA for homogeneity.

TIDAL LEVEL ft	R2/R1	R3/R2	R4/R3	R5/R4	R6/R5	R7/R6
+7.84	2.18	1.32	1.17	1.13		
+7.60	2.32	1.36	1.17	1.10		
+7.36	2.38	1.39	1.20	1.10		
+7.12	2.38	1.35	1.17	1.11	1.07	
+6.87	2.29	1.40	1.16	1.08	1.07	
+6.63	2.21	1.32	1.15	1.08	1.07	
+6.38	2.15	1.34	1.15	1.08	1.04	1.05
+6.14	2.30	1.36	1.16	1.09	1.07	1.10
+5.89	2.20	1.33	1.16	1.08	1.06	1.07
+5.65	2.40	1.37	1.17	1.09	1.06	
+5.41	2.38	1.33	1.16	1.09	1.05	1.03
+5.17	2.39	1.33	1.17	1.09	1.09	1.03
+4.93	2.37	1.36	1.16	1.10	1.07	1.04
+4.68	2.33	1.34	1.16	1.10	1.06	1.04
ALL	2.31	1.35	1.16	1.09	1.06	1.05
F	0.50	0.68	0.54	1.48	0.82	-
Sign	NS	NS	NS	NS	NS	

FIG. 49 : Growth ratios (R_{i+1}/R_i) versus tidal level.

RAT2 = R2/R1
RAT3 = R3/R2
RAT4 = R4/R3

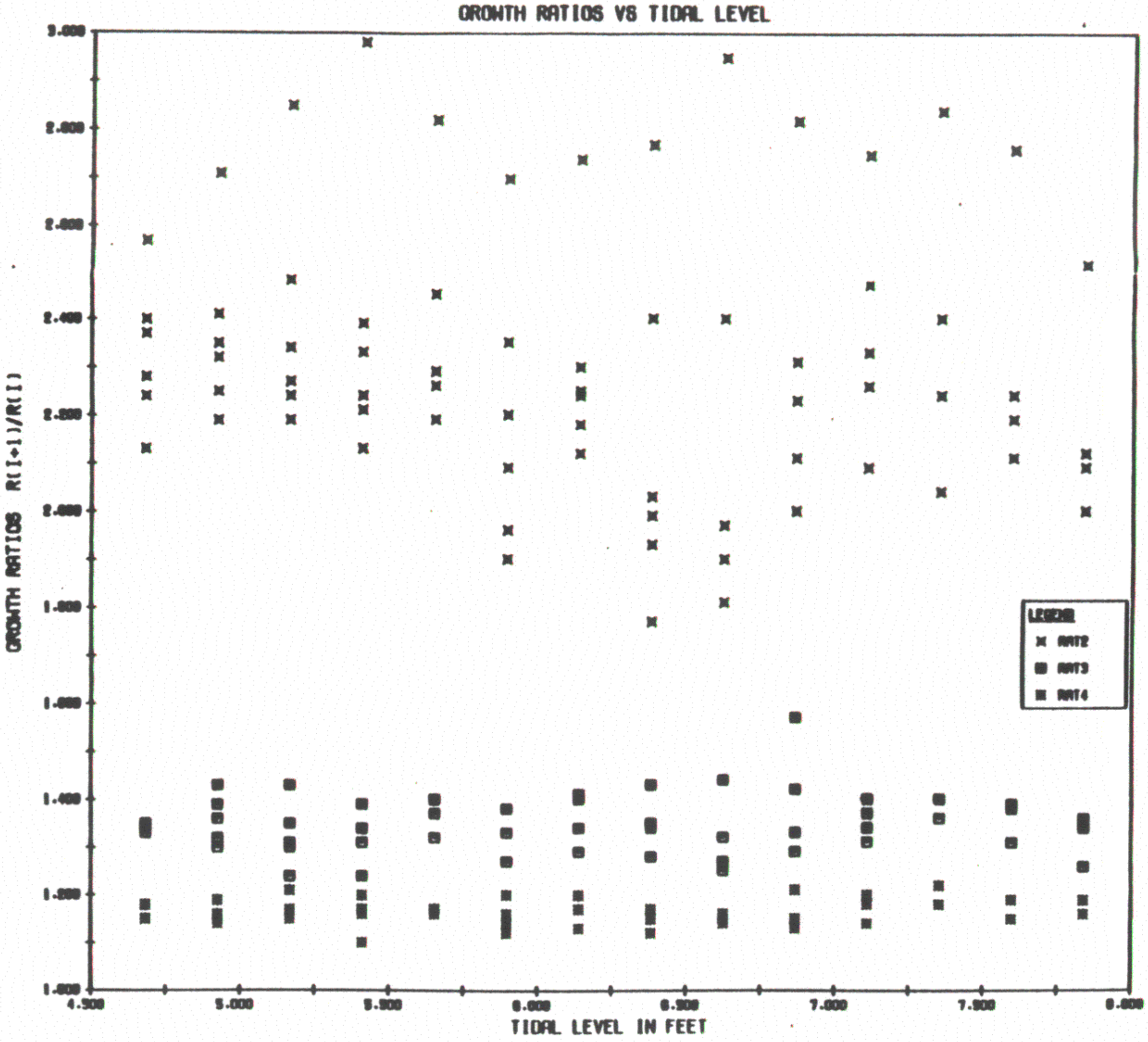

GROWTH RATIOS VS TIDAL LEVEL
GROWTH RATIOS R(I+1)/R(I)
TIDAL LEVEL IN FEET
3.000
2.800
2.600
2.400
2.200
2.000
1.800
1.600
1.400
1.200
1.000
4.500
5.000
5.500
6.000
6.500
7.000
7.500
8.000
LEGEND
RAT2
RAT3
RAT4

FIG. 50 : Asymptotic length (L_∞) versus tidal level in feet.

FIG. 51 : Parameter k versus tidal level in feet.

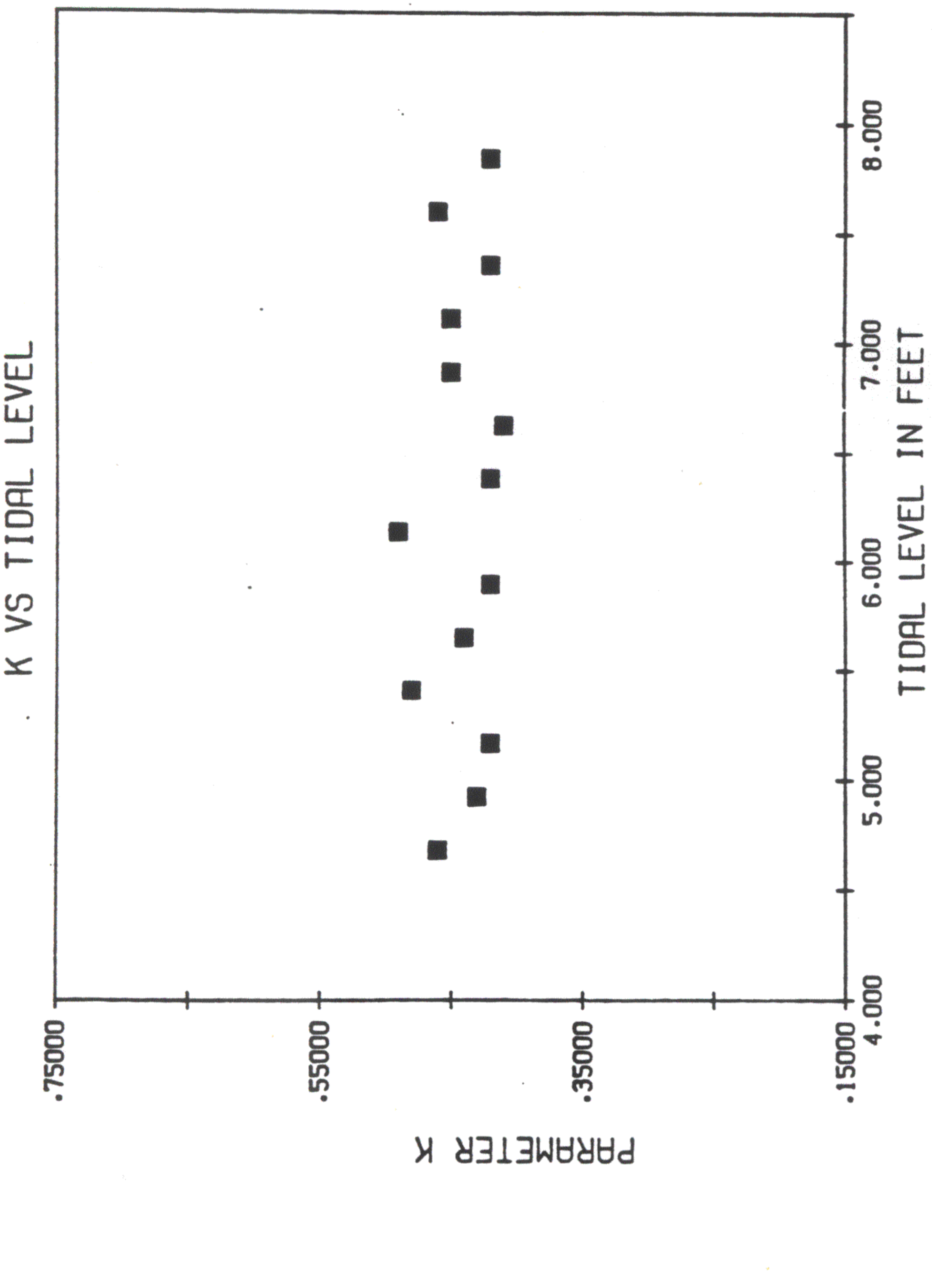
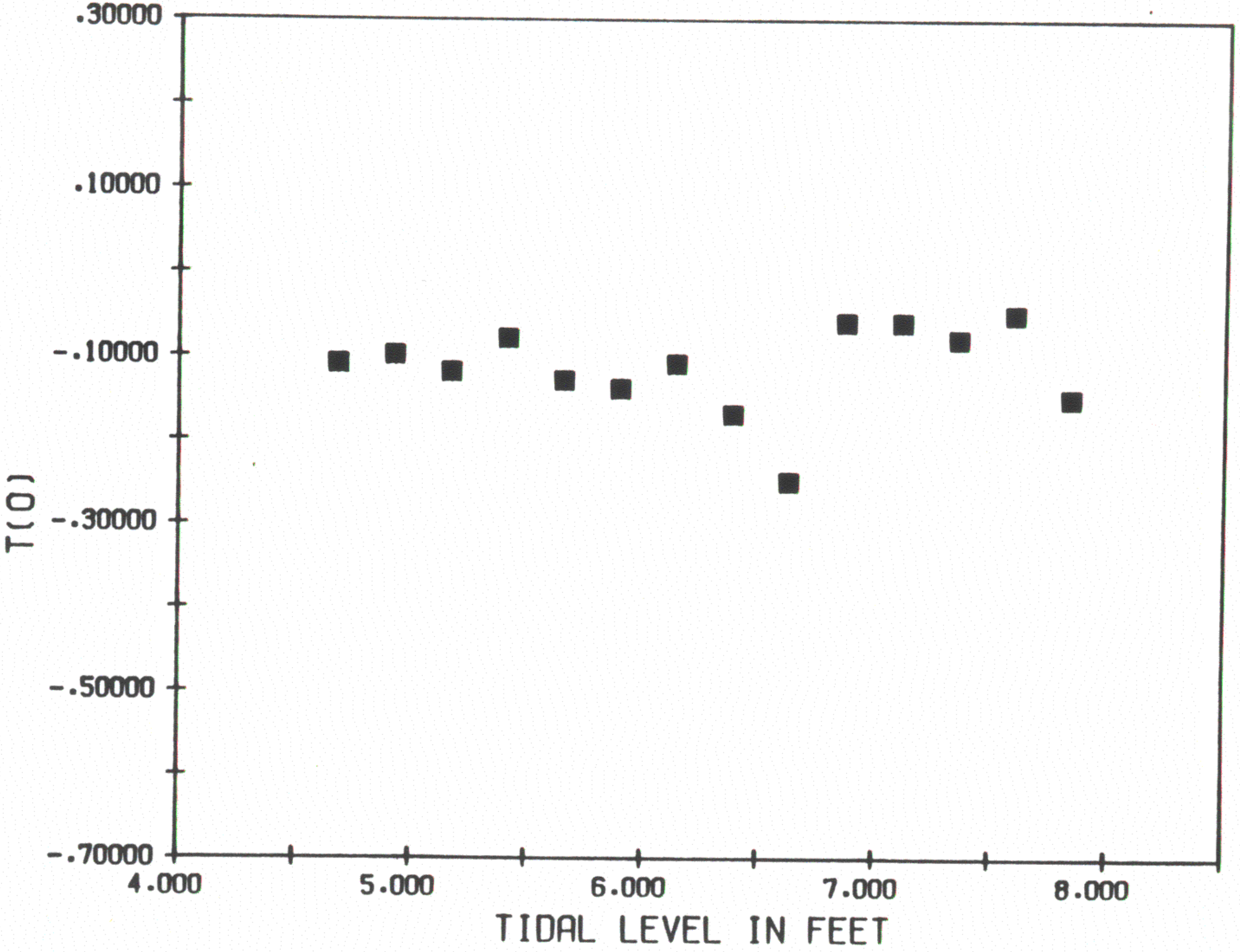

K VS TIDAL LEVEL
PARAMETER K
.75000
.55000
.35000
.15000
4.000
5.000
6.000
7.000
8.000
TIDAL LEVEL IN FEET

FIG. 52 : Parameter t_0 versus tidal level in feet.



T(O) VS TIDAL LEVEL

values in the lower portion of the beach, a decrease with increasing tidal level, and a hint of another stabilization high on the beach. The latter effect could perhaps be explained by the fact that beyond a certain level of stress, there is no sensitivity to any further increase until death occurs. With these ideas in mind, a logistic function was fitted to the data (Fig.50) yielding:

$$L_\infty = \frac{57.8013}{1 + 4.7172(10^{-5})) e^{1.1572\ TL}}$$

with SS = 39.7672 RMS(resid) = 1.9014 df = 11

An alternative would be to fit a linear function to part of the data, and assume a constant value thereafter, a simpler but discontinuos solution to the problem.

As the plots of k and t_0 showed a remarkable constancy at all tidal levels, a series of regressions were performed to test the significance of their slopes (Table XXIV). The results show non-significant values for these two variables and a highly significant negative correlation for L_∞.

The constancy of k and t_0, together with the constancy in growth ratios seems to indicate that growth throughout the life of the individual is only

TABLE XXIV: Regressions of von Bertalanfy parameters versus tidal level.

t vs tidal level (TL):

$t = -0.14 + 0.0044\ (TL)$ SE(b) = 0.0150

ANOVA

Source	df	SS	MS	F	
Regression	1	26	26	0.088	NS
Residual	12	36	3		

$r = 0.01$

k versus tidal level

$k = 0.46 - 0.0041\ (TL)$ S.E.(b) = 0.0070

ANOVA

Source	df	SS	MS	F
Regression	1	22	22	0.339
Residual	12	79	66	

$r = 0.03$

L versus tidal level

$L = 87.22 - 5.6123\ (TL)$ S.E.(b) = 0.7421

ANOVA

Source	df	SS	MS	F
Regression	1	442.14	442.14	57.19 ***
Residual	12	88.57	7.38	

$r = -0.83$

dependent on its previous size . Those animals settling higher in the beach grow less in their early stages, and from then on, this is reflected in their subsequent growth; they move along the same curve (length versus time) but with shorter steps. The dependence of growth on previous size emphasizes the importance of early growth on the rest of their lives and suggests some interesting possibilities for aquaculture and enhancement.

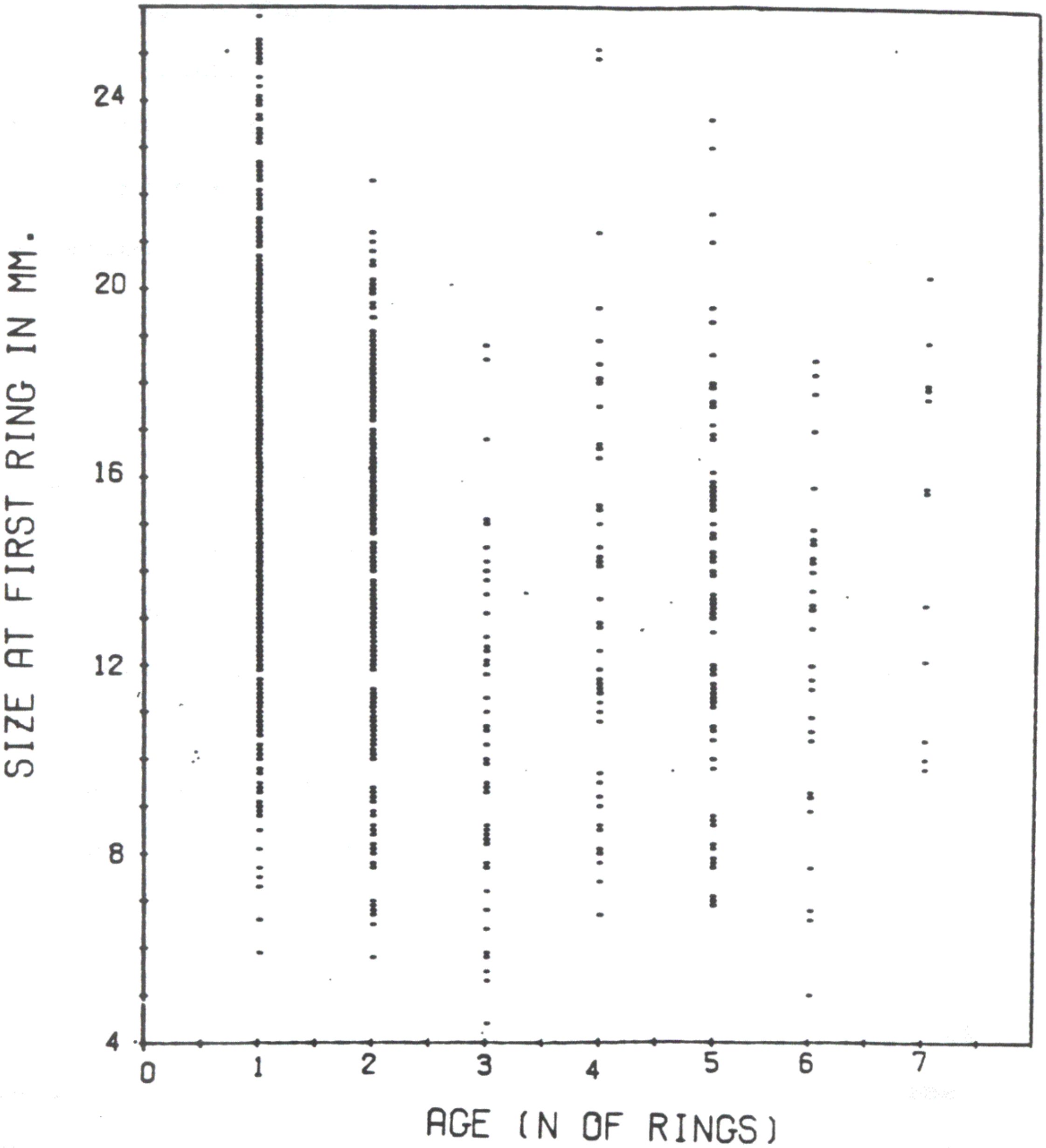
Combining all these results, a model predicting length L (mm) as a function of age t (years) and tidal level TL (ft) is:

$$L_{(t,TL)} = \frac{57.8013}{1+(4.7172(10^{-5}))e^{1.1572\ TL}}(1-e^{-0.4407(t-(-0.1150))})$$

GROWTH AND COMPETITION

It was mentioned before that the depression in size at first ring of the 3's is quite likely the result of intraspecific competition in a dense settlement (Fig. 53). The effect tends to vanish in the older animals, in the most part by a "catching up" process (LAMMENS, 1967) (Fig. 48) and perhaps also by size selective mortality. Either one or both processes are needed to explain why competition is reduced for

FIG. 53 : Length at first ring for all cohorts (mm).


SIZE AT FIRST RING IN MM.
24
20
16
12
8
4
0
1
2
3
4
5
6
7
AGE (N OF RINGS)

later ages, and why the depression does not continue to be present in later rings.

With the purpose of ascertaining the effect of crowding on the growth of the clams, the size of clams in their first year of life was studied. The problem is that the history of older clams is not known, and that our knowledge of the present situation only allows us to assume that these animals have grown throughout their lives under similar competitive pressures to those observed today.

To reduce the interference from other sources, the beach was divided into three vertical levels, and the analysis was performed in some cases for each of them. In other cases, only the lowest or the 2 lower levels of the beach were used in order to reduce the calculations while working in a relatively homogeneous set and with a relatively large sample size which it is located. The way in which the 2 components affect the process is defined as follows:

Some crowding indices (C_1, C_2 and C_3 below), taken or modified from those used in forest modelling (OPIE, 1968; GERRARD, 1969; BELLA, 1971; KEISTER, 1971,1972; KEISTER et al., 1975; MITCHELL, 1975; TAYLOR, 1975) are described in what follows.

Notation: W_j weight of jth neighbor (g)

D_j distance to jth neighbor (cm)

RI radius of influence (defined earlier, cm)

k,Q arbitrary constants

Only those neighbors whose distance to the individual in question is less than the radius of influence are included in the calculations. The summations are therefore performed over all neighbors within RI cm from the "center individual". The names chosen for the indices reflect the way in which the variable distance is introduced in the formulae.

I) Inverse-linear index (C_1)

$$C_1 = \Sigma \frac{W_j}{D_j}$$

This assumes that competition is directly (and linearly) related to weight and inversely (and linearly) related to the distance.

II) Exponential decline index (C_2)

$$C_2 = \Sigma W_j e^{-QD_j}$$

Here it is assumed that the effect of distance decreases exponentially. This seems correct if the interference is based in the overlap of circles of influence of neighboring animals. The overlap will decline much faster than the distance. The inconvenience of this formulation is that Q is arbitrary unless experimental information is available. A Q value of 0.46 was used, in order to reduce the effect of a competitor to 1% of its weight at a distance of 10 cm. The choice of distance is based on the belief that the vortex generated by the filtering activity of an animal is not likely to have a diameter of more than a few cm, so 10 cm is probably an overestimate of the area of influence.

III) Logistic decline index (C_3)

$$C_3 = \Sigma W_j\left(\left(\frac{k - 1}{k\left(1 - e^{-\ln(k)(D_j/RI)}\right)}\right) - 1\right)$$

The logistic term goes to zero when D_j = RI. It emphasizes the importance of closer neighbors. Again, we have an arbitrary constant (k) which is set to 2 in order to have boundaries of 0 and 1 for this term.

As the only other assumption for all three approaches was that size or growth ratios would be negatively correlated with crowding as measured by the indices, simple linear regressions were used to test for significance of the slopes. The results obtained for size of 1's in the lower 1/3 of the beach are shown in Table XXV. The values of r are quite low, but they are consistent in spite of the arbitrariness introduced in the calculation of the indices. A negative trend is present although it is not a very relevant factor. It must be remembered that these results arise from a single cohort which does not seem to be especially dense; quite likely, if the same process had been applied to the 3's in their first year, during the highest crowding, the results would have been much more significant.

For the other age groups, after eliminating the 6's and 7's because of their small sample sizes, and dividing the beach into 3 vertical levels we obtain the regressions shown in Table XXVI for the growth ratios.

As a first observation, the only age groups showing some effects of crowding on growth are the 3's and the 5's, which both were stronger age groups than

TABLE XXV: Length and weight l's vs crowding indices.

a) length (mm) versus crowding indices n = 192

		S.E.(b)	Sig.	r
C_1	$l = 24.55 - (0.0563)C_1$	.0334	*	-0.12
C_2	$l = 24.45 - (0.1022)C_2$	.0590	*	-0.12
C_3	$l = 24.63 - (0.0195)C_3$	.0074	**	-0.18

b) weight (g) versus crowding indices n = 192

		S.E.(b)	Sig	r
C_1	$w = 2.845 - (0.0135)C_1$	.0109	NS	-0.09
C_2	$w = 2.850 - (0.0308)C_2$	.0192	*	-0.12
C_3	$w = 2.893 - (0.0055)C_3$	.0024	*	-0.16

TABLE XXVI: Growth ratios (ages 2-6) vs crowding indices.

	b	S.E.(b)	Sig	r^2		
a) Lower third of the beach						
R5/R4	-0.0056	0.0022	**	.2834	n=167	(Index C_1)
R5/R4	-0.0081	0.0037	*	.2141	"	(Index C_2)
R5/R4	-0.0012	0.0005	*	.2088	"	(Index C_3)
b) Middle third of the beach						
R5/R4	-0.0010	0.0006	*	.0360	n= 81	(Index C_1)
R5/R4	-0.0018	0.0018	*	.0393	"	(Index C_2)
R5/R4	-0.0003	0.0001	*	.0447	"	(Index C_3)
R3/R2	-0.0060	0.0028	*	.0314	n=147	(Index C_1)
R3/R2	-0.0102	0.0051	*	.0271	"	(Index C_2)
R3/R2	-0.0014	0.0007	*	.0284	"	(Index C_3)
c) Higher third of the beach						
R5/R4	+0.0004	0.0002	**	.0321	n= 19	(Index C_1)
R5/R4	+0.0008	0.0005	*	.0192	"	(Index C_2)
R5/R4	+0.0001	0.0001	*	.0313	"	(Index C_3)

All other regressions were not significant.

the average. This would indicate that cohorts with a dense settlement experience throughout their lives the consequences of the original crowding, but cannot be taken as evidence that there is no crowding-dependent mortality in the population; it only shows that mortality from any source was not sufficient to reduce the population to a level where the interferences noticed disappeared completely. Recruits settling in dense patches may experience a retardation of growth which may last throughout their lives (if growth depends on size); and, in addition to that, if the process of thinning out does not take place or is not sufficient to reduce densities enough to eliminate competition, then competitive pressures would add their effect to that arising from initial slow growth. The Manila clam seems to be one of those species in which density-dependent mortality is absent or insufficient to eliminate competition. The results are not conclusive; the values of r^2 , even in the significant cases, are very low . On the other hand, the indices have some deficiencies in their formulation and it is not known whether they accurately represent the phenomenon they are supposed to measure. In spite of that, the 3's seemed to show a decline in size or weight at high values of the indices. In several scattergrams that were prepared, it was noticeable that for lower values of the indices the dependent variables showed no correlation with them, but at higher values a clear negative trend became apparent. The response described seemed to indicate that the effect of crowding was overestimated in the formulae or in the parameters chosen, or perhaps that there is a threshold in the process that has not been considered.

To avoid those difficulties, the age group experiencing the more visible decline at higher values was analyzed more carefully. The dependent variables chosen were weight, length at rings 1, 2 and 3, and growth ratios R3/R2 and R2/R1. It was assumed that the radius of influence had been overestimated, and the data sets were truncated to eliminate the lower third of the range of the indices. Most of the [illegible] correlation with the dependent variables used. The other two, however, show a very significant effect of crowding on size and weight (Table XXVII). At the same time, and in spite of the deficiencies noted, it seems that the indices used may be an adequate starting point for the study of competitive processes at the individual level.

In conclusion, it is quite clear in view of the densities observed, that the limiting resource on this beach is not space for growth. It seems that the depression in growth rates is caused by competition for food; this competition is only visible in a segment of some cohorts, which makes detection and measurement of its effects more difficult.

YIELD AND EXPLOITATION

Combining the models for growth and mortality, it is possible to build a model for the change in biomass in a patch of age t, at tidal level TL.

$$B_{(t,TL)} = N_{(t,TL)} \; W_{(t,TL)}$$

where N is a density (number/unit area). It is possible now to replace the two functions on the right hand side for the expressions derived earlier:

TABLE XXVII: Regressions weight, length versus crowding indices for 3's.

C_2 vs weight $w = 24.37 - 0.69\ C_2$ $r^2 = .4135$

$SE(b) = 0.22$ $n = 16$

C_2 vs R2 $R2 = 30.78 - 0.31\ C_2$ $r^2 = .3310$

$SE(b) = 0.12$ $n = 16$

C_2 vs R3 $R3 = 45.15 - 0.60\ C_2$ $r^2 = .5340$

$SE(b) = 0.15$ $n = 16$

C_3 vs weight $w = 21.64 - 0.08\ C_3$ $r^2 = .2411$

$SE(b) = 0.03$ $n = 23$

C_3 vs R3 $R3 = 42.81 - 0.06\ C_3$ $r^2 = .4093$

$SE(b) = 0.02$ $n = 23$

$$N_{(t,TL)} = N_{0(t,TL)} e^{-(b_1+b_2 TL^{b_3}+b_4 TL^{b_5})t}$$

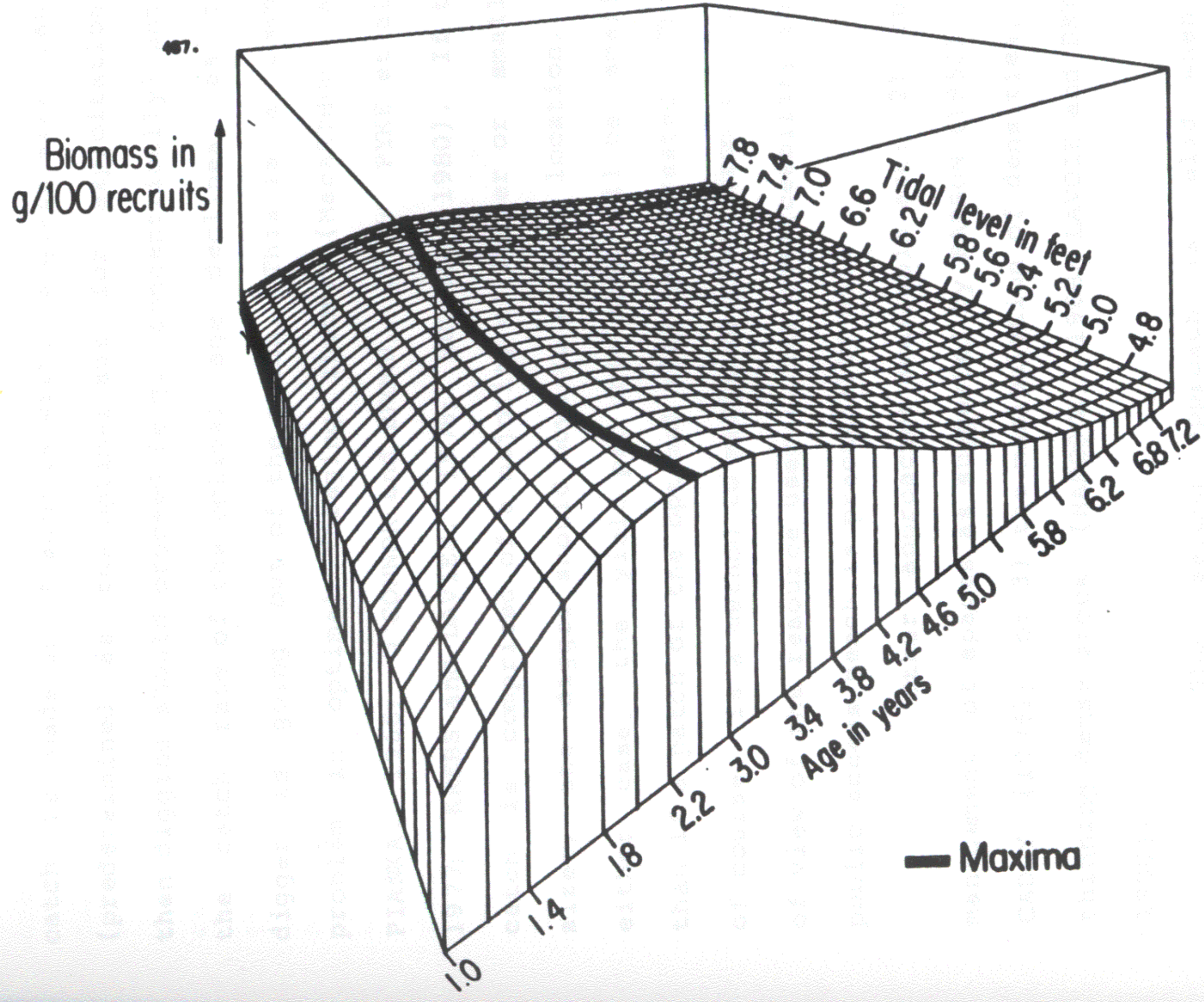
$$B_{(t,TL)} = b_6\left[\left(\frac{b_7}{1+b_8 e^{b_9 TL}}\right)\left(1-e^{-b_{10}(t-b_{11})}\right)\right]^{b_{12}}$$

A plot of the product of these two functions is presented in Fig.54 for a set of values of t and TL. The maximum value of biomass is reached at 2.4 years of age at the +4.5 ft level, earlier at the +6.0 level (2.2 years) and then again later at the +7.0 level (2.4 years) and at the +8.0 level (2.8 years). These values would be important in deciding a management strategy for the resource.

Assuming that a beach contains a random distribution of age groups in space, then one management objective would be to find an exploitation period that optimizes the combination of age groups. However, the knowledge of the existence of age-patches and the uncertainty about their location prior to exploitation (contrary to e.g. trees), force a reconsideration of the problem.

One possibility is the use of an adaptive strategy: a digger begins anywhere in the beach, and decides whether to continue digging there or move to a new site according to the catch. If the majority of the

FIG. 54 : Biomass as a function of age and tidal level.


487.
Biomass in g/100 recruits
Tidal level in feet
7.8
7.4
7.0
6.6
6.2
5.8
5.6
5.4
5.2
5.0
4.8
Age in years
1.0
1.4
1.8
2.2
3.0
3.4
3.8
4.2
4.6
5.0
5.8
6.2
6.8
7.2
Maxima

area by a natural disturbance (e.g. a mass mortality caused by freezing) or by exploitation.

Regardless of the origin, we have in this case basically a single-aged population as a target. The problem is thus very simple , and it is possible to maximize the biomass function to determine the time at which the maximum biomass can be harvested from a given cohort. Once this is established, exploitation follows with that periodicity. In order to spread harvests over time, a beach may be divided into subareas to be exploited as separate units (CADDY, 1975), with the same periodicity but different starting times. It is also possible to subdivide the beach vertically, and harvest different tidal levels according to their specific optimal periods.

OPTIMAL ROTATION: A BIOECONOMIC EXAMPLE.

Up to now, the objective has been to maximize short-term yield in biomass, usually from a single cohort; no attention has been paid to the long-term yield. In what follows the optimal dynamics of the system will be considered; the approach is essentially similar for the maximization of yield in biomass or in economic units.

The idea of optimal rotation has a long

tradition in forestry and some of the basic formulae were derived more than a century ago (PEARSE, 1967; KILKKI and VAISANEN, 1969; NASLUND, 1969; CLARK , 1976). In fisheries the idea has been discussed more recently for the Beverton-Holt model (CLARK et al., 1973). The basic point is that the optimal rotation period for a series of harvests differs from the optimal period for a single cohort . As the bioeconomic approach is the better known, it will be used to show the development of the problem.

The formula developed by Faustmann allows the interplay of market fluctuations of interest rates with the periodicity of the rotation. A short derivation of the solution is presented here; a full treatment of the subject, from which these formulae were extracted, is given by CLARK (1976).

If a payment P due some time in the future, say t years from now, with a discount rate of δ (instantaneous annual rate of interest compounded continuously), had to be cashed today, we would not receive the complete amount estimated (called "future value"), but a lower one because we have not allowed the investment to complete its term. The value that could be cashed today of that future obligation is called the "present value" of the investment (PV):

$$PV = P\ e^{-\delta t}$$

It is necessary to find an expression for the net value of a unit of the resource, and how it changes with age. The value per unit will most likely be a function of its size, but age will be used to keep consistent dimensions (V(t)). Costs are considered fixed, so the net value can be expressed as:

$$V(t)-c = \text{net value}$$

The function V(t) could include constraints such as the minimum market size or legal size below which the value is zero, and also complications such as changes in the manner of use (e.g. small animals used for canning, large for fresh consumption, etc) that could result in value changes.

The objective is to maximize the present value of the net value per animal, i.e. maximize

$$PV = (V(t) - c)\ e^{-\delta t} \quad \text{with respect to } t$$

To find the time t_* that maximizes PV, differentiate and obtain

$$(V'(t)\ e^{-\delta t}) + (V(t) - c)(-\delta)\ e^{-\delta t}$$

Collecting the exponential terms and setting the expression equal to zero yields:

$$e^{-\delta t}(V'(t) + (V(t) - c)(-\delta) = 0$$

Of these two terms, only the second can be equal to zero, therefore

$$(V'(t) + (V(t) - c)(-\delta) = 0$$

or

$$\frac{V'(t)}{V(t) - c} = \delta$$

With this equality we can solve for the value of t that satisfies it, which is t_*.

The solution however, does not take into account the rotational aspect of the harvest. The longer the time a resource is left in the site, the more it takes for a new cycle to begin. The comparison between alternatives is usually performed in forestry using yield tables (MOSER and HALL, 1969); Table A-6 shows the yield of clams in g per 100 recruits at several tidal levels. It is possible to see the difference between some simple options, say harvest once every 5 years or twice every 2.5 years, or between closer alternatives e.g. twice every 3 years or three times every 2 years. Obviously, the table is only valid for the site in question: better knowledge of the quality of different sites would allow the preparation of tables applicable for many areas with similar characteristics.

To solve the problem of optimal rotation analytically, it is necessary to consider the value of a sequence of harvests spanning an infinite horizon; if the period is assumed constant (i.e. the solution does not change over time), the present value of the sequence is

$$PV = e^{-\delta t}(V(t) - c) + e^{-2t\delta}(V(t) - c) + \ldots.$$
$$\ldots\ldots\ldots\ldots + e^{-nt\delta}(V(t) - c)$$

a series that can be represented by

$$PV = \sum_{1}^{\infty} e^{-k\delta t}(V(t) - c)$$

which converges to

$$PV = \frac{V(t) - c}{e^{\delta t} - 1}$$

Differentiating this expression with respect to t and rewriting

$$V'(t) = \delta(V(t) - c) + \delta\left(\frac{V(t) - c}{e^{\delta t} - 1}\right)$$

V'(t) is the change in the net value of the resource per unit time.

The first term of the right hand side is the interest to be earned by investing the value of the harvest (V(t) - c) at a rate δ. The second term of that side introduces the rotational aspect, being the present value of all future revenues from the site (the "site value" of the foresters). The solutions to this equation under different discount rates are usually presented in graphic form. The main virtue of the formula is that it shows clearly that there are two resources of value to be considered: the population <u>and</u> the site.

SOME MANAGEMENT CONSIDERATIONS

The optimal rotation defined here must be modified to accomodate several additional considerations:

a) access to the beach may be restricted to some seasons of the year because of the tidal regime.

b) the spawning process must be respected as a basic constraint for the harvesting dates.

c) the settlement period should be respected, and perhaps facilitated by previous harvest of the adult population present if the attractive effect is found to be less important than the inhibitory one.

d) economic considerations may dictate the options to follow when alternative rotation periods do not differ in yield by an amount that justifies the increase in costs of a more frequent harvest.

The management of clams and many other

sessile resources has several peculiarities when compared to the more traditional pelagic fisheries. As the stock harvested in an area usually does not coincide with the reproductive stock that provides new recruits for the area, the benefits of a prudent exploitation are not apparent to the beach owner. Further, the easy access to the resource, the mixture in many cases of recreational and commercial fisheries, and the lack of concentration centers for the exploitation (such as fishing ports) make the enforcement of regulations either very costly or very ineffective. With all these difficulties in mind, it may be more convenient that resource managers devote their efforts to try to achieve sustained recruitment, rather than attempting to control the harvest based on untested principles.

The problem of mantaining an acceptable recruitment level to the population must be dealt with in some of the several possible ways:

a) to replace natural recruitment with planting of spat or any other input of settlers. This has genetic implications that have to be considered.

b) to enhance and protect the settlement with a combination of habitat modification and predator protection measures.

c) to implement a regional management policy, utilizing some public beaches in an area as preserves of reproductive stocks, managed to optimize reproduction and to maintain genetic variability. For this purpose, intensive investigations are needed in the dispersal of larvae within the region, in order to define the location of these preserves. An aggressive policy should be pursued to insure that most habitat types and most areas of the region are represented in this network or preserves.

SOME BIOLOGICAL SPECULATIONS

The spatial structure of the population in a mosaic of "age-patches" may have some interesting implications in the biology of those species which have such characteristic.

If larvae about to settle occur in patches, and newly settled spat also show patchiness, it does not seem unreasonable to think that maybe there is continuity in the spatial structure, that is to say that the patch in the plankton becomes the patch in the benthos. The planktonic patch may experience reduction in numbers and size by predation, or be split in smaller units by turbulence, but what is dispersed as a unit is a patch of larvae. These would be patches of sibling larvae whose adaptive value has been discussed by STRATHMANN (1974).

If individuals with relatively similar genetic background, experience similar selective pressures during their pelagic life, and then settle together, it is quite likely that their growth and development would be quite homogeneous. In particular, size at sexual maturity, and consequently the timing of spawning could be expected to be synchronous. The two factors mentioned could explain the deficit of heterozygotes which characterizes many benthic invertebrates (GOSLING and WILKINS, 1977; PUDOVKIN and ZHIVOTOVSKII , 1981). The age-patch would coincide with the reproductive groups described by TRACEY et al.(1975), and the deficit of heterozygotes could originate from inbreeding or from the Wahlund effect (when a mixture of populations is sampled the results show a deficit of heterozygotes). The genetic structure of such a population in space would possibly resemble the "chaotic genetic patchiness" described by JOHNSON and BLACK (1982). In a sense, the population present in a beach may be a mosaic of populations with some degree of mixing. Individuals within a patch should usually be genetically more similar to each other than to members of other patches. In these circumstances, the adaptive value of negative interactions between adults and larvae is very clear; because of the long planktonic period, the probability of an adult destroying its own progeny is very low, and the incoming larvae are most likely invaders which must be prevented from settling.

If the interactions between larvae and adults in some species were so intense as it is believed (WOODIN, 1976), then it is possible that the timing of settlement is in part determined by this interaction (THORSON, 1958). It is known that many species experience heavy mortalities associated with spawning and other reproductive activities. Part of that mortality arises directly from stress, another part may come from indirect sources, such as increases in activity or visibility that may increase the risk of predation, etc. In either case, during the period following spawning the adult population is likely to suffer heavy losses. The seasonal patterns of mortality in invertebrates are also a requirement. For the Manila clam the peak of settlement coincides exactly with the seasonal period of minimum population biomass (OHBA, 1959b). It seems possible that the timing of settlement is governed by stock-recruitment interactions.

If this were the case, then why is the spawning date so long ahead of the right time for settlement that Manila clam larvae are "forced" to spend up to 4 weeks in the plankton?. The answer probably lies in the needs of adults to store reserves for the Winter; after the release of gametes, all the effort shifts to recovering condition. If spawning were to take place later in the season, lower productivity in the water column and a shortened period of recovery would reduce the probability of survival for the adults.

Some authors (THORSON, 1946) believe that the release of gametes is timed with the production cycle in order to insure supply of food to the larvae. In the case of filter feeders that share (in broad terms) the type of food with their larval forms, the timing also benefits the adults, allowing them to take full advantage of the more productive periods.

These speculations are mostly suggested as areas of further exploration. The acknowledgement of the existence of a spatial structure in a population will force a review of concepts in many aspects of the biology of sessile and sedentary organisms.

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APPENDIX A

TABLE A-1

Particle size analysis (%)

#	Phi size								
	-3	-2	-1	0	1	2	3	4	4
Q-1	58.56	12.13	6.41	3.67	2.54	5.32	7.78	2.77	0.83
Q-3	71.15	5.21	1.76	1.57	2.65	7.45	6.90	2.50	0.81
Q-5	68.16	5.35	1.95	1.93	3.75	8.36	7.44	2.31	0.75
Q-7	53.01	10.14	5.38	3.13	5.30	11.55	8.27	2.29	0.92
Q-9	46.46	9.35	5.74	4.80	8.10	13.18	9.28	2.26	0.83
Q-11	24.57	12.93	9.30	8.60	12.15	15.65	12.49	3.20	1.11
Q-13	32.22	13.63	11.17	9.72	8.24	10.04	10.58	3.08	1.31
Q-14	34.43	14.73	12.03	7.97	6.89	9.51	9.99	3.10	1.34
R-2	69.71	8.64	2.98	1.76	2.14	5.10	6.58	2.34	0.76
R-4	70.23	3.84	1.87	1.84	3.21	8.52	7.23	2.46	0.78
R-8	62.81	7.69	4.33	2.51	5.24	9.46	6.17	1.33	0.46
R-12	20.48	16.10	12.89	12.35	10.12	11.63	11.90	3.39	1.13
R-14	22.35	19.39	13.41	9.05	6.22	10.41	12.96	4.64	1.57
S-1	72.54	7.68	3.64	1.95	1.78	4.00	5.50	2.13	0.77
S-3	79.35	3.05	1.07	0.88	2.03	5.38	5.66	1.98	0.58
S-5	65.88	5.48	2.48	1.80	3.78	9.61	7.81	2.41	0.76
S-7	55.22	7.60	3.93	3.06	6.63	11.85	8.74	2.22	0.74
S-9	46.72	11.18	9.30	6.65	8.90	8.93	6.37	1.39	0.56
S-11	42.50	13.69	12.17	8.98	6.95	6.53	6.67	1.80	0.72
S-13	25.26	17.13	13.24	9.03	7.24	10.72	12.31	3.71	1.35

continues _

TABLE A-1 continued

Particle size analysis

#	Phi size								
	-3	-2	-1	0	1	2	3	4	4
T-2	70.87	6.28	2.16	1.70	2.18	6.69	7.07	2.40	0.66
T-4	64.14	6.11	2.78	2.46	4.60	9.60	7.40	2.20	0.71
T-6	61.23	5.93	3.44	2.89	6.18	11.07	6.97	1.67	0.63
T-8	31.12	8.28	6.04	6.05	11.95	18.15	14.38	3.04	0.99
T-10	38.09	19.51	14.63	8.80	6.27	5.40	5.22	1.42	0.64
T-12	34.08	17.42	15.46	8.65	4.90	7.28	8.30	2.78	1.13
T-13	38.85	17.09	9.71	5.86	4.55	8.41	10.99	3.37	1.18
T-14	29.53	17.94	9.64	6.81	5.27	10.28	13.72	4.73	2.07
U-1	63.89	7.87	4.01	2.35	2.83	6.71	8.30	3.16	0.88
U-2	63.12	6.89	2.87	2.23	3.15	8.30	9.05	3.42	0.97
U-3	64.34	7.15	2.29	2.03	3.61	9.56	7.61	2.61	0.80
U-4	68.91	5.16	2.46	2.04	4.04	8.84	5.98	1.96	0.61
U-5	58.99	7.95	3.08	2.85	5.70	11.65	7.11	1.94	0.73
U-7	48.46	9.34	5.12	4.95	8.87	11.90	8.54	2.02	0.78
U-9	39.49	12.55	10.39	8.15	7.34	9.41	9.18	2.40	1.08
U-11	34.23	19.79	15.48	9.27	4.63	6.29	7.26	2.31	o.73
U-12	29.31	17.59	11.59	7.88	5.28	9.24	13.20	4.30	1.62
U-13	41.87	15.41	7.81	4.73	3.78	9.74	11.32	3.91	1.43
V-2	67.19	6.36	2.69	1.88	3.21	7.95	7.26	2.63	0.83
V-3	44.15	9.40	4.40	3.21	7.88	15.64	10.82	3.33	1.17

continues

TABLE A-1 continued

Particle size analysis

#	Phi size								
	-3	-2	-1	0	1	2	3	4	4
V-4	51.97	7.51	3.43	3.15	7.53	13.66	9.13	2.70	0.92
V-6	51.71	8.37	3.86	4.33	8.67	12.42	7.94	1.93	0.77
V-7	38.17	10.72	7.70	6.93	9.31	12.73	10.17	2.94	1.32
V-8	33.03	15.88	9.14	7.24	8.61	12.46	9.88	2.64	1.11
V-10	29.49	21.69	16.02	9.07	5.04	7.02	8.22	2.43	1.01
V-12	31.40	19.05	11.26	5.61	4.15	9.93	12.67	4.31	1.62
V-14	34.34	15.47	10.36	5.08	4.21	10.61	13.10	4.78	2.06
W-1	61.39	8.27	4.09	3.08	3.28	6.98	8.55	3.49	0.86
W-3	51.58	9.67	4.31	3.14	6.58	12.57	8.58	2.64	0.92
W-5	49.83	7.70	4.83	4.71	8.67	13.96	7.57	1.96	0.76
W-7	50.27	7.39	6.27	5.45	8.28	10.87	8.39	2.18	0.90
W-9	24.86	18.20	12.71	9.24	6.29	11.13	11.47	3.88	2.22
W-11	27.43	17.38	9.37	6.26	4.57	11.01	15.66	6.20	2.12
W-13	34.93	15.83	8.03	4.91	4.63	12.36	13.28	4.25	1.79
W-14	29.65	12.57	8.35	5.60	6.06	14.97	14.55	6.11	2.14
X-2	67.58	7.50	4.10	2.27	3.08	6.60	5.94	2.28	0.66
X-4	50.68	10.95	5.84	3.66	7.41	12.12	6.56	2.04	0.72
X-6	36.90	7.50	7.04	6.55	11.78	16.34	10.49	2.54	0.86
X-8	31.14	14.94	8.99	8.15	7.65	13.44	11.39	3.03	1.28
X-10	27.78	20.31	9.62	6.59	5.82	11.56	12.87	4.05	1.39
X-14	28.17	13.21	9.36	7.63	8.57	14.45	12.28	4.41	1.91

TABLE A-2

Sediment statistics

#	Percentages			Sand/Mud	FOLK & WARD Values			
	Gravel	Sand	Silt	Ratio	Mean	Dev.	Skew.	Kurt.
Q-1	77.10	22.07	0.83	119.39	-1.89	2.26	0.77	1.28
Q-3	78.12	21.07	0.81	122.84	-1.96	2.25	0.81	1.98
Q-5	75.46	23.79	0.75	131.68	-1.91	2.27	0.80	1.13
Q-7	68.54	30.55	0.92	108.16	-1.73	2.31	0.75	0.64
Q-9	61.55	37.62	0.83	119.22	-1.53	2.36	0.65	0.60
Q-11	46.80	52.09	1.11	88.90	-0.69	2.41	0.00	0.62
Q-13	57.03	41.66	1.31	75.18	-1.16	2.46	0.29	0.64
Q-14	61.19	37.47	1.34	73.45	-1.28	2.45	0.38	0.66
R-2	81.32	17.91	0.76	130.29	-2.20	2.07	0.79	2.47
R-4	75.95	23.27	0.78	126.71	-1.92	2.27	0.81	1.28
R-8	74.83	24.70	0.46	216.16	-1.91	2.19	0.78	0.97
R-12	49.48	49.39	1.13	87.25	-0.72	2.34	0.15	0.68
R-14	55.15	43.28	1.57	62.71	-0.83	2.44	0.32	0.64
S-1	83.86	15.37	0.77	128.22	-2.67	1.71	0.74	2.78
S-3	83.48	15.94	0.58	172.13	-2.52	1.83	0.79	4.22
S-5	73.83	25.40	0.76	130.54	-1.86	2.30	0.80	0.83
S-7	66.75	32.51	0.74	133.26	-1.69	2.36	0.76	0.61
S-9	67.21	32.24	0.56	178.95	-1.74	2.15	0.61	0.71
S-11	68.35	30.93	0.72	138.65	-1.71	2.12	0.52	0.85
S-13	55.63	43.02	1.35	73.13	-0.93	2.42	0.30	0.64
T-2	79.30	20.04	0.66	150.42	-1.93	2.27	0.81	2.10

continues

TABLE A-2 continued

Sediment statistics

#	Percentages			Sand/Mud	FOLK & WARD Values			
	Gravel	Sand	Silt	Ratio	Mean	Dev.	Skew.	Kurt.
T-4	73.03	26.26	0.71	139.06	-1.87	2.27	0.79	0.79
T-6	70.59	28.78	0.63	158.46	-1.81	2.28	0.78	0.66
T-8	45.44	53.57	0.99	100.04	-0.53	2.42	-0.12	0.56
T-10	72.24	27.12	0.64	154.69	-1.90	2.00	0.44	0.94
T-12	66.96	31.91	1.13	87.39	-1.41	2.34	0.42	0.84
T-13	65.66	33.17	1.18	84.08	-1.41	2.49	0.53	0.66
T-14	57.12	40.82	2.06	47.41	-1.00	2.55	0.40	0.59
U-1	75.78	23.35	0.88	113.19	-1.85	2.32	0.79	1.18
U-2	72.88	26.15	0.97	102.53	-1.77	2.39	0.80	0.79
U-3	73.78	25.42	0.80	123.84	-1.85	2.30	0.79	0.85
U-4	76.54	22.85	0.61	161.65	-1.93	2.23	0.80	1.33
U-5	70.03	29.24	0.73	136.12	-1.83	2.26	0.77	0.65
U-7	62.93	36.29	0.78	127.22	-1.66	2.32	0.72	0.61
U-9	62.43	36.48	1.08	91.34	-1.36	2.32	0.47	0.69
U-11	69.50	29.77	0.73	135.44	-1.58	2.19	0.44	0.95
U-12	58.49	39.90	1.62	60.86	-1.02	2.51	0.39	0.61
U-13	65.08	33.49	1.43	68.74	-1.36	2.47	0.62	0.61
V-2	76.24	22.93	0.83	119.13	-1.91	2.27	0.80	1.30
V-3	57.95	40.88	1.17	84.18	-1.40	2.44	0.61	0.56
V-4	62.91	36.17	0.92	107.71	-1.63	2.39	0.75	0.59
V-6	63.94	35.28	0.77	128.40	-1.70	2.31	0.74	0.61

continues

TABLE A-2 continued

Sediment Statistics

#	Percentages			Sand/Mud	FOLK & WARD Values			
	Gravel	Sand	Silt	Ratio	Mean	Dev.	Skew.	Kurt.
V-7	56.59	42.08	1.32	74.64	-1.19	2.39	0.39	0.61
V-8	58.05	40.84	1.11	89.16	-1.25	2.41	0.37	0.62
V-10	67.20	31.78	1.01	97.64	-1.38	2.24	0.43	0.91
V-12	61.71	36.68	1.62	60.86	-1.13	2.51	0.46	0.62
V-14	60.16	37.77	2.06	47.48	-1.14	2.60	0.44	0.60
W-1	73.75	25.39	0.86	115.21	-1.80	2.35	0.79	0.94
W-3	65.57	33.51	0.92	107.78	-1.64	2.38	0.75	0.61
W-5	62.37	36.88	0.76	131.07	-1.67	2.31	0.73	0.60
W-7	63.93	35.17	0.90	109.73	-1.69	2.32	0.74	0.64
W-9	55.77	42.00	2.22	43.96	-0.93	2.44	0.32	0.65
W-11	54.18	43.69	2.12	46.06	-0.82	2.60	0.34	0.58
W-13	58.79	39.42	1.79	54.81	-1.19	2.57	0.45	0.59
W-14	50.57	47.30	2.14	45.81	-0.78	2.64	0.18	0.57
X-2	79.18	20.16	0.66	151.18	-2.06	2.15	0.79	1.66
X-4	67.48	31.80	0.72	137.60	-1.72	2.28	0.73	0.63
X-6	51.44	47.70	0.86	115.60	-0.97	2.36	0.17	0.58
X-8	55.06	43.65	1.28	76.90	-1.09	2.45	0.29	0.59
X-10	57.71	40.90	1.39	71.01	-1.05	2.46	0.42	0.60
X-14	50.74	47.34	1.91	51.22	-0.84	2.53	0.16	0.60

TABLE A-3

FORMULAS TO CALCULATE FOLK AND WARD VALUES

Let ϕ_p be the particle size measured in the ϕ scale that, in the cumulative frequency function leaves to its left a proportion p of the total distribution (p percentile).

$$\text{Mean size} = \frac{\phi_{16} + \phi_{50} + \phi_{84}}{3}$$

$$\text{Deviation} = \frac{\phi_{84} - \phi_{16}}{4} + \frac{\phi_{95} - \phi_{5}}{6.6}$$

The scale used in the traditional classification is:

Deviation $\leq$ 0.35	very well sorted
0.35 - 0.50	well sorted
0.50 - 1.00	moderately sorted
1.00 - 2.00	poorly sorted
2.00 - 4.00	very poorly sorted
> 4.00	extremely poorly sorted

$$\text{Skewness} = \frac{\phi_{16} + \phi_{84} - 2\phi_{50}}{2(\phi_{84} - \phi_{16})} + \frac{\phi_{5} + \phi_{95} - 2\phi_{50}}{2(\phi_{84} - \phi_{16})}$$

Scale:

-1.00 - -0.30	very negative-skewed
-0.30 - -0.10	negative-skewed
-0.10 - +0.10	nearly symmetrical
+0.10 - +0.30	positive-skewed
+0.30 - +1.00	very positive skewed

Kurtosis

$$K = \frac{\phi_{95} - \phi_5}{2.44\ (\phi_{75} - \phi_{25})}$$

Scale:

0.67 - 0.90	platykurtic
0.90 - 1.11	mesokurtic
1.11 - 1.50	leptokurtic
1.50 - 3.00	very leptokurtic
> 3.00	extremely leptokurtic

TABLE A-4 I

PERCENTAGE ORGANIC MATTER IN QUADRAT

	Q	R	S	T	U	V	W	X
1	1.42		1.36		1.29		1.34	
2		1.29		1.14	1.32	1.53		1.10
3	1.09		1.06		1.16	1.22	1.18	
4		1.33		1.08	1.04	1.10		1.05
5	1.11		1.03		1.11		1.38	
6				1.62		1.19		1.04
7	1.41		1.35		1.03	1.06	1.18	
8		1.37		1.20		1.49		1.22
9	1.15		1.07		1.48		1.33	
10				1.27		1.27		1.54
11	1.55		1.32		1.16		1.43	
12		1.22		1.27	1.40	1.30		1.30
13	1.29		1.22	1.16	1.52		1.62	
14	1.41	1.66		1.62		1.40	1.43	1.20

TABLE A-4 II

MEAN PHI VALUE IN QUADRATS

	Q	R	S	T	U	V	W	X
1	-1.89		-2.67		-1.85		-1.80	
2		-2.20		-1.93	-1.77	-1.91		-2.06
3	-1.96		-2.52		-1.85	-1.40	-1.64	
4		-1.92		-1.87	-1.93	-1.63		-1.72
5	-1.91		-1.86		-1.83		-1.67	
6				-1.81		-1.70		-0.97
7	-1.73		-1.69		-1.66	-1.19	-1.69	
8		-1.91		-0.53		-1.25		-1.09
9	-1.53		-1.74		-1.36		-0.93	
10				-1.90		-1.38		-1.05
11	-0.69		-1.71		-1.58		-0.82	
12		-0.72		-1.41	-1.02	-1.13		
13	-1.16		-0.93	-1.41	-1.36		-1.19	
14	-1.28	-0.83		-1.00		-1.14	-0.78	-0.84

TABLE A-4 III

DEVIATION IN PARTICLE SIZE DISTRIBUTION

(Used by FOLK & WARD, op cit, as a measure of sorting)

	Q	R	S	T	U	V	W	X
1	2.26		1.71		2.32		2.35	
2		2.07		2.27	2.39	2.27		2.15
3	2.25		1.83		2.30	2.44	2.38	
4		2.27		2.27	2.23	2.39		2.28
5	2.27		2.30		2.26		2.31	
6				2.28		2.31		2.36
7	2.31		2.36		2.32	2.39	2.32	
8		2.19		2.42		2.41		2.45
9	2.36		2.15		2.32		2.44	
10				2.00		2.24		2.46
11	2.41		2.12		2.19		2.60	
12		2.34		2.34	2.51	2.51		
13	2.46		2.42	2.49	2.47		2.57	
14	2.45	2.44		2.55		2.60	2.64	2.53

TABLE A-4 IV

SKEWNESS IN PARTICLE SIZE DISTRIBUTION

	Q	R	S	T	U	V	W	X
1	0.77		0.74		0.79		0.79	
2		0.79		0.81	0.80	0.80		0.79
3	0.81		0.79		0.79	0.61	0.75	
4		0.81		0.79	0.80	0.75		0.73
5	0.80		0.80		0.77		0.73	
6				0.78		0.74		0.17
7	0.75		0.76		0.72	0.39	0.74	
8		0.78		-0.12		0.37		0.29
9	0.65		0.61		0.47		0.32	
10				0.44		0.43		0.42
11	0.01		0.52		0.44		0.34	
12		0.15		0.42	0.39	0.46		
13	0.29		0.30	0.53	0.62		0.45	
14	0.38	0.32		0.40		0.44	0.18	0.16

TABLE A-4 V

KURTOSIS IN PARTICLE SIZE DISTRIBUTION

	Q	R	S	T	U	V	W	X
1	1.28		2.78		1.18		0.94	
2		2.47		2.10	0.79	1.30		1.66
3	1.98		4.22		0.85	0.56	0.61	
4		1.28		0.79	1.33	0.59		0.63
5	1.13		0.83		0.65		0.60	
6				0.66		0.74		0.58
7	0.64		0.61		0.61	0.61	0.64	
8		0.97		0.56		0.62		0.59
9	0.60		0.71		0.69		0.65	
10				0.94		0.91		0.60
11	0.62		0.85		0.95		0.58	
12		0.68		0.84	0.61	0.62		
13	0.64		0.64	0.66	0.61		0.59	
14	0.66	0.64		0.59		0.60	0.57	0.60

TABLE A-4 VI

PERCENTAGE OF GRAVEL IN QUADRATS

	Q	R	S	T	U	V	W	X
1	77.10		83.86		75.78		73.75	
2		81.32		79.30	72.88	76.24		79.18
3	78.12		83.48		73.78	57.95	65.57	
4		75.95		73.03	76.54	62.91		67.48
5	75.46		73.83		70.03		62.37	
6				70.59		63.94		51.44
7	68.54		66.75		62.93	56.59	63.93	
8		74.83		45.44		58.05		55.06
9	61.55		67.21		62.43		55.77	
10				72.24		67.20		57.71
11	46.80		68.35		69.50		54.18	
12		49.48		66.96	58.49	61.71		
13	57.03		55.63	65.66	65.08		58.79	
14	61.19	55.15		57.12		60.16	50.57	50.74

TABLE A-5: Von Bertalanffy parameters by cohort and level.

ASYMPTOTIC LENGTH

TIDAL LEVEL ft	AGE 3	4	5	6	7	MEAN
+7.84	40	43	48			43.6
+7.60	42	42	45			43.0
+7.36	44	48	46			46.0
+7.12	44	45	50	49		47.0
+6.87	49	47	47	52		49.7
+6.63	52	52	50	57		52.7
+6.38	55	57	51	55		54.5
+6.14	53	52	54	52	52	52.6
+5.89	53	58	56	53	63	56.6
+5.65	55	57	58	61	66	59.4
+5.41	54	55	56	60	56	56.2
+5.17	61	55	57	63	59	59.0
+4.93	58	54	59	60	60	58.2
+4.68	54	57	57	58	61	57.4

(Table A-5 continues)

TABLE A-5 (continuation)

parameter k

TIDAL LEVEL ft	AGE					
	3	4	5	6	7	all
+7.84	0.55	0.43	0.28			0.42
+7.60	0.52	0.45	0.41			0.46
+7.36	0.52	0.37	0.37			0.42
+7.12	0.55	0.49	0.38	0.40		0.45
+6.87	0.46	0.50	0.49	0.34		0.45
+6.63	0.42	0.41	0.46	0.37		0.41
+6.38	0.41	0.38	0.49	0.42		0.42
+6.14	0.50	0.54	0.48	0.49	0.45	0.49
+5.89	0.54	0.37	0.46	0.48	0.26	0.42
+5.65	0.52	0.47	0.45	0.41	0.34	0.44
+5.41	0.55	0.49	0.45	0.41	0.50	0.48
+5.17	0.40	0.50	0.45	0.34	0.41	0.42
+4.93	0.44	0.48	0.41	0.42	0.40	0.43
+4.68	0.57	0.47	0.45	0.39	0.43	0.46

(Table A-5 continues)

TABLE A-5 (continuation)

parameter t_0

TIDAL LEVEL ft	AGE 3	4	5	6	7	ALL
+7.84	0.04	-0.12	-0.38			-0.15
+7.60	0.09	-0.10	-0.14			-0.05
+7.36	0.10	-0.19	-0.14			-0.08
+7.12	0.09	-0.14	-0.06	-0.12		-0.06
+6.87	0.08	-0.11	-0.19	-0.04		-0.06
+6.63	0.06	-0.27	-0.32	-0.47		-0.25
+6.38	0.04	-0.23	-0.20	-0.29		-0.17
+6.14	0.07	-0.05	-0.12	-0.10	-0.37	-0.11
+5.89	0.07	-0.20	-0.12	-0.24	-0.21	-0.14
+5.65	0.09	-0.04	-0.15	-0.09	-0.47	-0.13
+5.41	0.12	-0.06	-0.14	-0.11	-0.19	-0.08
+5.17	0.05	-0.05	-0.15	-0.21	-0.23	-0.12
+4.93	0.01	-0.11	-0.08	-0.12	-0.18	-0.10
+4.68	0.01	-0.16	-0.11	-0.14	-0.16	-0.11

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TABLE A-6

Yield table in g per 100 recruits

Age	Tidal level (ft)											
	4.6	4.8	5.0	5.2	5.4	5.6	5.8	6.0	6.2	6.4	6.6	6.8
0.6	45	44	43	42	41	40	39	38	36	35	33	31
0.8	75	73	72	70	68	66	64	62	60	57	54	51
1.0	107	104	102	99	97	94	91	88	85	81	77	73
1.2	139	135	131	128	124	120	116	112	108	104	99	93
1.4	167	162	157	153	148	143	138	133	128	123	118	111
1.6	191	185	179	173	167	161	156	150	145	139	133	126
1.8	210	202	195	188	181	175	169	162	156	150	144	137
2.0	223	214	206	198	190	183	177	170	164	157	151	144
2.2	231	221	212	203	195	187	180	173	167	160	154	148
2.4	234	223	213	204	195	187	180	173	166	160	154	148
2.6	232	221	210	201	192	184	176	169	163	157	151	146
2.8	228	216	205	195	186	177	170	163	157	152	146	141
3.0	220	208	197	187	177	169	162	155	150	144	140	135
3.2	210	198	187	177	168	160	153	146	141	136	132	128
3.4	199	187	176	166	157	149	142	136	131	127	123	120
3.6	187	175	164	154	146	138	132	126	121	117	115	111
3.8	174	162	152	143	134	127	121	116	111	108	105	103
4.0	161	150	140	131	123	116	110	106	102	98	96	94
4.2	148	138	128	119	112	106	100	96	92	89	87	86

4.4	136	126	116	108	101	95	90	86	83	81	79	78
4.6	124	114	106	98	91	86	81	78	75	73	71	70
4.8	113	103	95	88	82	77	73	69	67	65	64	63

TABLE A-6 (continuation)

Yield in g per 100 recruits at different tidal levels

AGE	TIDAL LEVEL					
	7.0	7.2	7.4	7.6	7.8	8.0
0.6	29	26	23	20	17	14
0.8	48	44	39	34	30	25
1.0	68	62	56	50	43	37
1.2	87	81	73	66	57	49
1.4	105	97	89	80	71	61
1.6	119	111	102	93	83	72
1.8	130	122	113	103	93	82
2.0	137	129	120	111	101	90
2.2	141	133	125	116	106	96
2.4	142	135	127	119	110	100
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2.6	140	134	127	120	112	103

2.8	136	131	125	119	112	104
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3.0	131	126	122	117	111	104
3.2	124	121	117	113	108	103
3.4	117	114	111	108	105	101
3.6	109	107	105	103	100	98
3.8	101	100	98	97	96	94
4.0	93	92	91	91	90	90
4.2	85	85	85	85	85	85
4.4	77	77	78	79	80	81

4.6	70	71	71	73	74	76
4.8	63	64	65	67	69	71
5.0	57	58	59	61	64	67
5.2	51	52	54	56	59	62
5.4	46	47	49	51	54	58
5.6	41	42	44	46	50	54
5.8	36	37	39	42	45	50
6.0	32	33	35	38	41	46
6.2	28	30	32	34	38	42
6.4	25	26	28	31	34	39
6.6	22	23	25	28	31	36
6.8	20	21	23	25	28	33
7.0	17	18	20	22	26	30

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