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THE EFFECT OF CONSPECIFIC ASSOCIATION ON GROWTH AND DISPERSION OF THE GEODUCK CLAM, *PANOPE GENEROSA*

by

David A. Fyfe

B.Sc., McGill University, 1979

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
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The Effect of Conspecific Association on Growth and Dispersion

of the Geoduck Clam, (*Panope generosa*)

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ABSTRACT

The settlement and survival of planktonic marine invertebrate larvae is often greatly influenced by the presence of conspecific adults. To date, field observations on the influence of adult geoducks on conspecific settlement and survival have yielded conflicting results. The main purpose of this research was to assess the growth and dispersion of geoducks which were associated with conspecifics to varying degrees. All research was conducted at a depth of 13m, using SCUBA. Selection of the study site was based on relative homogeneity of environmental parameters which may influence an organism's growth and dispersion. Sediment composition was analysed for particle size and organic content. Fine sand containing little organic matter, dominated the area.

The detectability of geoducks throughout the year, was monitored for a 22-month period. An inactive period when approximately half of the population had their siphons retracted, occurred between November and mid-February. More than 90% of the population was active during the rest of the year. These values are considerably greater than has been previously reported and indicate that a sample of geoducks taken during the active period, would be representative of the whole population. The onset of inactivity coincided with decreasing water temperature and decreasing food availability, but siphon re-extention occurred in mid-winter, when both temperature and food abundance were low.

Geoduck shell size was not correlated with observed population density (4.0-7.7 geoducks/m^2). Geoducks from an intermediate density plot had the smallest shells. This was even apparent in the youngest age class (4 years), by comparison with the mean shell size of 4 year olds from other plots. An index of shell thickness was positively correlated with geoduck age, exhibiting a log-log relationship.

Distribution at the site was clumped, but intraclump dispersion was either random or uniform. When dispersion patterns were examined in a time-series manner, they tended toward uniformity, but during years of highly successful recruitment, dispersion became non-uniform. The nearest neighbour of a young geoduck was always an adult, but size of the young was directly correlated with distance from that nearest neighbour. The size of recruits and their location relative to that of nearest neighbours, appears to be influenced by adult siphon activity.

DEDICATION

This work is dedicated to my parents, Charmaine and Alan, who provided encouragement and support, and to my wife Linda, who went through it all with me.

QUOTE

"The geoduck is distinguished from other clams by its meaty yellow siphon, a thick hose-like appendage that droops out of its shell in a dejected, phallic manner."

K. Freeman 1984.

"So thats a geoduck....For god's sake, don't let the children see!"

Hilliard 1982.

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Lastly, I thank my wife Linda, for her patience, her endurance and her support of my work, from beginning to end.

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I. Introduction

The geoduck clam, Panope generosa, is the largest burrowing bivalve in North American waters. In 1967, the Washington State Department of Fisheries began investigation into the possibility of a commercial geoduck fishery and papers describing the species became available shortly afterward. A study by Yonge (1971), describes functional morphology and adaptive radiation of the superfamily Saxicavacea, which includes the geoduck and Andersen (1971) has described their spawning, growth and spatial distribution. In light of these reports, a description of geoduck biology will not be presented here.

At present, geoduck clams are commercially harvested in the waters of British Columbia and Washington State and the management policy of the two areas is somewhat different (Goodwin 1973; Cox 1979). Washington State, with a smaller area to manage, concentrates the harvest within well-defined boundaries. This permits easier evaluation of the impact, while retaining a large number of virgin beds for comparative, as well as base stock use. In B.C. the fishery is spread over the whole coast, minimizing environmental impact in any given area. A study done in conjunction with B.C. harvesters (Blackman unpublished), showed that harvesting intensity in an area (% harvested), was inversely proportional to the density of geoducks. This would be less likely in the U.S., since harvestable tracts must be leased and therefore fishing intensity would tend to be high, to ensure a good return on the investment. The relative merits of an intensive harvest in discrete patches verses a moderate harvest over large areas, are presently unknown.

The high pressure water jet used to harvest geoducks, appears to be extremely disruptive to the immediate area but research to date has been unable to quantitatively assess the extent of it's disturbance (Goodwin 1978a). It appears however that once an area is harvested, recruitment is significantly reduced (Goodwin pers. comm.). Very low natural recruitment rates translate into a low sustainable yield, and thus low harvest quotas. Depending on the mechanism by which the fishery affects recruitment, different levels of disruption to post-harvest recruitment could result from differences in management approach.

Studies in Washington State indicate that the harvest reduces future recruitment into the fishable population by two means (Shaul and Goodwin unpublished). The first occurs during a harvest, as young are accidently uncovered while digging for adults. These generally go unnoticed and are left to be eaten by predators. The second is the apparent reduction of settlement and/or survival of juveniles in previously harvested beds. In one study (Goodwin unpublished), an unharvested (control) plot contained three times as many juveniles as an adjacent plot which had been harvested 43 months earlier. The method by which the commercial harvest reduces settlement and/or survival is not known.

The water jet has the potential to alter sediment structure, as well as the composition of the infaunal community. Potentially, the most significant aspect of altering the infaunal community, is the removal of adult geoducks. Two studies (Goodwin 1978a; Breen and Shields 1983) have shown that changes to sediment composition are insignificant and that meiofaunal communities are only altered slightly, for what is likely to be a short period of time. Low recruitment thus appears to be a response to the removal of adult geoducks. Supporting this is a study by Goodwin (unpublished), using hatchery seed. This experiment ran concurrently and within the two plots mentioned earlier. Three months prior to the final harvest, marked seed were scattered in both plots. More than twice as many juveniles were recovered from the control and most were found next to adults (≤4inches). This study suggests that young geoducks have an affinity for adults and/or survival is enhanced when they are next to adults.

Confounding the situation are results of work in an area that had been severely disturbed by a dredging operation, many years earlier. Few geoducks survived, yet the density and size of geoducks there is presently equal to or greater than that of a nearby control plot (Goodwin unpublished). These results appear to be fairly good evidence for geoduck larval settlement and/or survival being independent of adults.

At present, the conclusions drawn from these two studies seem to conflict with one another and further work is required before the nature of the relationship between members of the same geoduck population is clearly understood.

Interaction between individuals of any population may take one of three basic forms: Positive (ie. mutually beneficial), Negative (ie. mutually detrimental) or Insignificant (ie. no observed mutual influence). Furthermore, the effects of intraspecific interaction may be density dependant, so that with increased numbers, disadvantages commonly associated with competition increase and effectively overshadow any benefits attained by association. This sort of stress is often felt most, by those located closest to one another (Pielou 1962).

The overcrowding of any fixed sessile organism can cause sufficient stress to result in any or all of the following conditions: (1) a reduced growth and development of juveniles and adults, (2) a relocation of juveniles, (3) the death of juveniles and/or adults. If a reduction in growth or development were to continue for a period of several years, mean adult size may become notably smaller or reproductive output may be reduced. An indirect measure of such a conspecific influence might therefore be obtained by comparing relative size measurements or measures of reproductive fitness such as gonad indices. The assumption is made that energy required for shell production and gonadal development is relatively constant for the range of environments in which geoducks are normally found.

Movement or death of any individual directly affects the pattern in which organisms are dispersed. Should other members of the population be responsible, then dispersion patterns may also be used to indicate the degree to which conspecifics are coexisting (Morisita 1959). In a paper surveying the literature on adult-adult and adult-juvenile interactions, Woodin (1976) cites many reports which have shown that increased densities of bivalves can result in reduced conspecific growth rate, increased mortality and/or uniform spatial dispersion.

The aim of this study was to examine the influence of geoduck clams on conspecifics, with a particular emphasis on the influence of adults on juveniles. Primary objectives were: (1) Study seasonal variation in the ability to detect geoducks, and thus determine the percentage of the population represented by further study. (2) Evaluate environmental heterogeneity throughout the study site, in particular sediment particle size and organic content, as such heterogeneity can have a significant influence on various population parameters (Meadows and Campbell 1972). (3) Observe the effects of density and the relative position of geoducks on conspecifics, by measuring shell production. (4) Determine the effects of geoduck presence on the dispersion pattern of conspecifics.

On several occasions it will be necessary to compare various age groups of geoducks and therefore the meaning of a few terms as they have been used here, is given. Andersen (1971) estimates age-at-first-spawning to be approximately four years, but growth rate only tapers off at 8-10 years. Geoducks within this 4-10 year age group will be called 'young' or 'juvenile' geoducks. The term 'adult' will be used to indicate any geoduck >10yr old. 'Recruitment' will refer to those geoduck larvae which survived settlement. Since the detection of a 4 year old geoduck appears to be no less efficient than that of an older one and since younger geoducks were not located, it will be assumed that 'recruitment into the fishable population' occurs with this age class (or earlier). It will be noted when 'recruit' is used in reference to the fishery.

Since its description in 1850 (Gould), the geoduck has been referred to by several scientific names (Andersen 1971), and so the small amount of information that is published is often difficult to locate. Most recently, Bernard (1983a) claims that Panope abrupta (Conrad 1849), which was first described from Japanese waters, takes precidence as it is indistinguishable from the local geoduck. Panopea, is the most frequently encountered alternate generic spelling (Kozloff 1974; Barnes 1980). Since Panope generosa is most commonly employed and in the absence of clarification by the International Commission on Zoological Nomenclature, it will be the taxonomic form used here.

II. The Study Site

Several limitations were placed on the selection of sample sites, foremost of which was the decision to confine all sampling to one study site. While this may raise questions concerning the applicability of conclusions from this research to populations elsewhere, two major considerations lead to a study of this type. (1) A heterogeneous environment precludes any inferences based on a comparison of dispersion patterns or relative sizes. By restricting research to one study site, this environmental variability was minimized. (2) Little is known of basic geoduck ecology and population dynamics. It was felt that an indepth study of one area might reveal features of geoduck populations previously overlooked by studies based on data from several locations.

Using SCUBA, surveys were conducted to locate an appropriate study site in Clayoquot Sound, on the west coast of Vancouver Island. The following criteria were considered essential to a suitable site. (1) The geoduck population density had to be relatively high, to ensure that dispersion patterns were natural, and not the product of a previous harvest. Average unexploited beds usually contain less than one geoduck per square meter (Goodwin 1973). Provided that substrate type and current velocity do not preclude harvesting, a minimum density of approximately 0.3-0.5 geoducks per square meter, is required for an economic harvest (Blackman unpublished, Breen and Shields 1983). Much higher densities are therefore indicative of a virgin clam bed, as harvesting would likely reduce density to the 0.5/m^2 level or lower. Though repopulation by recent recruits could raise the density of geoducks in a harvested bed to preharvest levels, at the time of this survey the fishery had existed in B.C. for only four years, and a population with that size and age structure could not be mistaken for an unharvested one. (2) Depth had to be relatively uniform so that geoducks from all sample sites would have had similar food availability, and have been exposed to the same general water temperatures and regimes. By avoiding intertidal and shallow subtidal areas, problems arising from tidal exposure, thermoclines and freshwater runoff, could be avoided. A maximum depth of 12m was also preferred so that the no-decompression time limits associated with SCUBA, would not interfere with the intended work. (3) Areas with an irregular coastline were avoided due to a potential for turbulent water flow thus an uneven food supply and a high turbidity. (4) A homogeneous substrate was a particularly important requirement because infaunal invertebrate communities are highly influenced by substrate composition (Meadows and Campbell 1972).

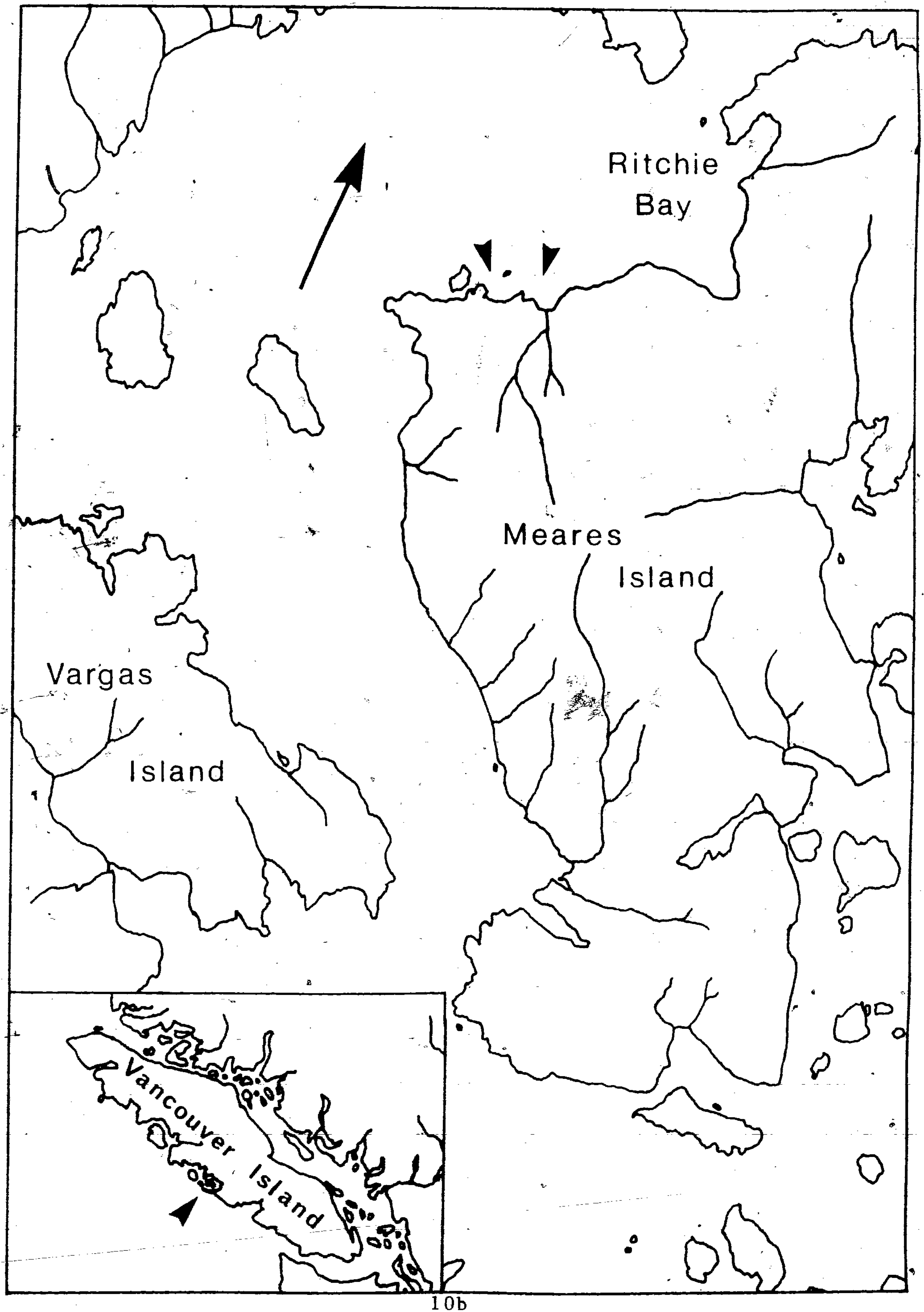
A site which met most of these required criteria was found at the north-west end of Meares Island (Fig. 1). The shoreline west of Ritchie Bay, forms the shallow bay where all work was done and as it is presently unnamed, it shall herein be referred to as Ritchie Bay. Upon request, the Department of Fisheries and Oceans closed Ritchie Bay to the commercial geoduck fishery, to permit this research.

A small stream empties into Ritchie Bay from Meares Island but it does not appear capable of influencing salinity at the depth in which this study was conducted. Though some old wood chips which presumably came from this stream were scattered on the bottom, research diving was conducted in a wide range of weather conditions and a halocline, indicative of significant runoff, was never visibly detected.

The bottom of Ritchie Bay is flat, except for a small rock island which rises steeply from its middle. Research was carried out on either side of this island. Underwater, a distinct boundary was noted which marked the start of the incline toward shore. The area between this boundary and the shore was characterised by a steadily decreasing depth and a sediment which was visibly more coarse than the fine sand which was typical of the rest of the study area. The bay was 13m deep beyond the sand/gravel boundary, where this research was conducted.

Overall geoduck density appeared to be high and as is often the case in geoduck beds (Goodwin 1973), the bright orange seapen, Ptilosarcus gurneyi, was common. Tresus capax, the horse clam (gaper clam), was also present in small numbers throughout. Between the study area and the shore, it was abundant and geoduck density was low.

Figure 1. Location of the study site at the north-west end of Meares Island. Inset shows the location of Meares Island in relation to Vancouver Island, British Columbia.


Ritchie
Bay
Meares
Island
Vargas
Island
Vancouver Island

Both water depth and sediment composition in that region were more characteristic of typical horse clam beds (Bourne and Smith 1972). One other bivalve which was readily visible in the study area was <u>Panomya ampla</u>, though it regularly occurred at low densities.

Geoducks are found in substrate ranging from soft mud to a sand-gravel mixture, but are most common in sand or a mud/sand bottom. They are also most abundant at depths ranging from 10m to 20m but can be found as deep as 50m (Goodwin 1973). The study site in Ritchie Bay is therefore thought to represent a typical geoduck habitat.

III. The Show Factor

The location of a geoduck is determined by visual detection of its siphon, termed a 'show'. The siphon tip normally protrudes from the sediment to permit feeding and respiration. As with other clams (Flowers 1973), the geoduck siphon need not always 'show'. When the geoduck siphon remains retracted for any period of time, the hole that it created when extended, fills in with sediment, leaving the clam undetectable. This presents a potential problem for the visual assessment of geoduck density and dispersion.

Methods of quantifying population dispersion patterns are based on the assumption that all organisms are available for inclusion in a census. While analyses usually only require a random sample of the population, all members must be equally available for the sample to be truely random. In addition, Nearest Neighbour Analysis, the method which was employed here to describe dispersion patterns, requires data on the true population density. Substituting a mean density estimate for this value can result in a loss of rigor in the associated tests of significance (Clark and Evans 1954).

The 'show factor', a percent value which attempts to relate observed density to actual density, was first discussed with reference to geoducks, by Goodwin (1973). In 1977 (Goodwin), the show factor was refined to account for seasonal variability, which was reported to range from a low of 5% visible in January, to a high of 60% of the siphons showing in May. Consideration of Goodwin's show factor has since become standard for all geoduck density and dispersion estimates (Goodwin 1978a,1978b; Goodwin and Shaul 1979; Cox and Charman 1980; Breen and Shields 1983).

Inclusion of a show factor greatly alters density estimates and most likely invalidates dispersion analyses which were not designed to take into account the fact that large numbers of the population may be excluded. If for example, a survey conducted in May reported 60 geoducks showing, the population would be estimated at 100 geoducks, since only 60% of the population is believed to be visible then. To obtain density estimates from surveys taken at other times of the year, observed numbers would be inflated further. Dispersion pattern analyses which are based on only those members of the population which are showing, a value which is reported to never exceed 60% of the total, would reflect only the dispersion patterns of visible geoducks. This may have little bearing on how the population as a whole is dispersed.

The duration of the period when geoducks are not showing is also of great importance to visual assessment (ie. if a 30 day 'show' period follows two days of siphon retraction, within a few days, all members of a population could be located). Inactivity (not showing) for long periods would make it extremely difficult to locate all individuals. Do the established monthly show factors apply to most geoduck populations? How long do periods of inactivity last? How frequent are such periods? If based on visual in situ assessments, can reliable inferences ever be made regarding the entire population?

Before study on geoduck density, dispersion patterns or conspecific interaction could be initiated, it was necessary to obtain an estimate of the percentage of the population which would be visible and to determine if this percentage would be different at different times of the year. The following work was designed to obtain such an estimate.

Method of Assessing Shows

In June of 1980, a 1m x 10m plot was established in the western end of Ritchie Bay (49°13'36",125°55'5") to observe 'shows'. The location of each geoduck was identified by a numbered flag, which was inserted into the sediment 5cm-10cm from the siphon tip, on its shoreward side. Each flag consisted of a numbered strip of yellow surveyors tape, tied to a piece of PVC tubing (6mm dia. x 30cm long). This means of identification ensured that all geoducks were accounted for, permitted the observation of particular geoducks, and facilitated locating all members at later dates.

For the duration of the summer, the plot was observed periodically, at intervals not exceeding two weeks. For every observation period, the number of each non-visible siphon was recorded. Dislodged flags were frequently found in or near the plot but determining which geoduck they corresponded to, was not always possible. Any numbered flag which was found uprooted, and did not clearly belong to a particular individual, was 'retired'. Geoducks subsequently found without an identifying flag were reassigned a newly numbered flag. In August, as a corrective measure, the location of each numbered geoduck was mapped.

In October 1980, the original flags were replaced by longer ones (50cm) which could be embedded deeper, thus reducing the time required to replace dislodged flags. Also at this point, the data collection method was altered. Recording only the numbers of the non-visible siphons did not permit distinguishing between geoducks which might be accidently overlooked, and those which were not showing. All subsequent surveys included noting whether or not each individual was showing.

Observations continued throughout the winter months but were less frequent. The length to which a siphon was extended, was much reduced during this period. Often the tip was flush with the sediment surface or slightly below it and covered by a thin sediment layer. Certain identification of these siphons required probing the bottom with a finger, in the depressions or 'dimples' (Cox 1979) which they created. Disturbance of the bottom in their vicinity, usually resulted in a partial retraction of the siphon, leaving a characteristic hole. These geoducks were considered to be 'showing', as contact with the surface was clearly being maintained. If a siphon could not be detected within a few centimeters of the sediment surface at the location indicated by its flag, and a hole from that retracted siphon was not visible, that geoduck was recorded as 'not showing'. Non-showing geoducks had therefore been retracted for at least as long as it took for several centimeters of sediment to fill in their siphon holes.

Observation and recording continued with greater frequency from May 1981 until mid-April 1982, when the study ended. In June 1981, due to a gradually evolved increase in surveying efficiency and a desire to increase sample size, the plot was extended 5m in length.

As the effects of temperature on geoduck shows was to be observed, a Peabody-Ryan model J, constant temperature recorder monitored ambient water temperature for 15 months of the study.

A rough estimate of turbidity in the ambient water was obtained on several surveys, by noting the horizontal distance at which a fixed object (yellow temperature recorder) disappeared from sight. Relative turbidity was considered to be inversely proportional to this distance. This method was used to permit relative comparisons and was not intended to be quantitative. The measurement is essentially a modification of the Secchi disc method of determining vertical water transparency (Tyler 1968), a method which has become standard practice but which is still subject to quantitative modification (Walker 1980), despite having been described as early as 1866.

Results

Repeated observation of the same population revealed that geoduck siphons tended to extend further above the sediment surface when there was a current. The siphons, which often extended several centimeters into the water column during the summer months, were more typically flush with the surface during the fall and spring. During the winter, siphons which were not completely retracted were often covered by a thin sediment layer.

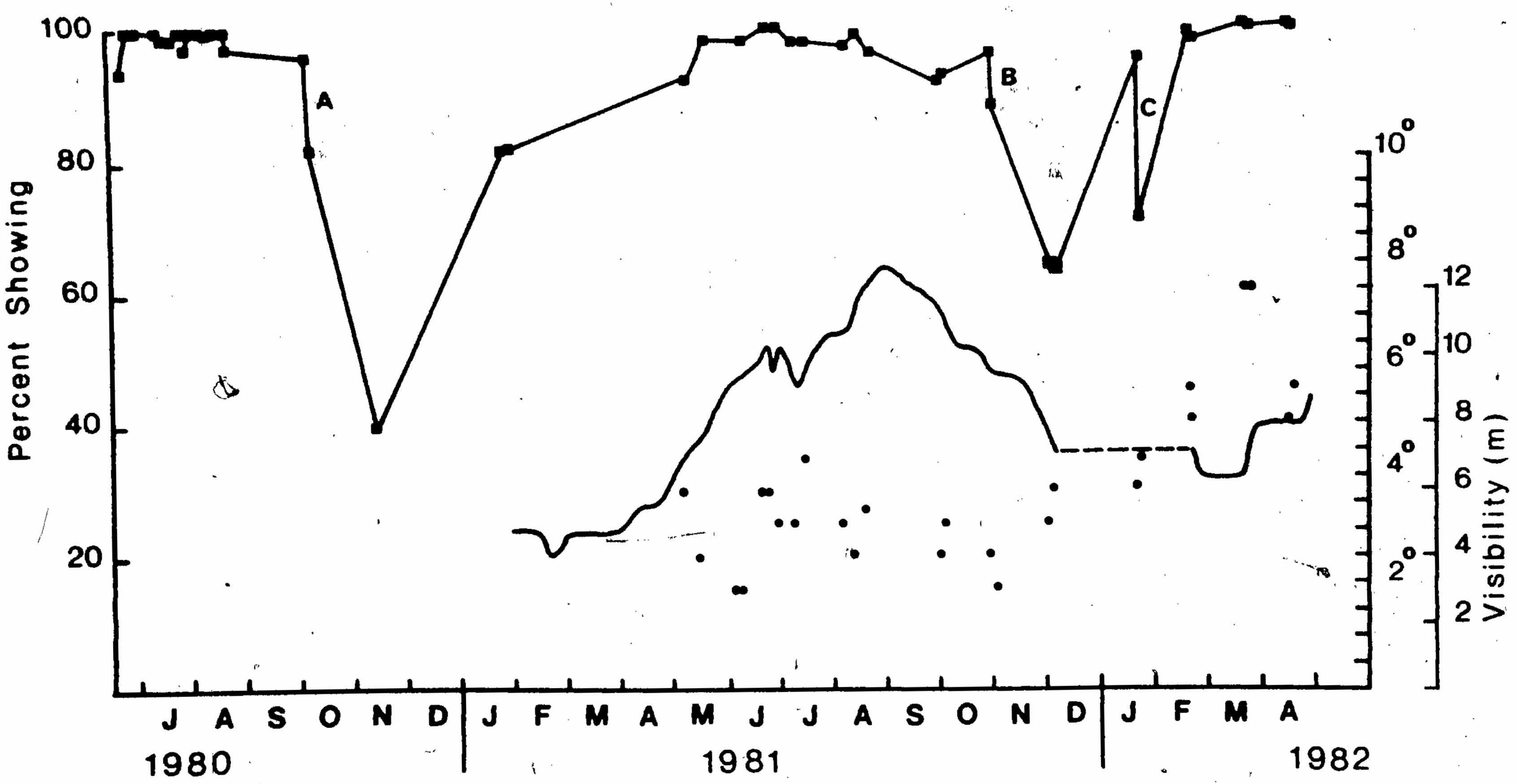
Data on geoduck siphon 'shows' throughout the 22-month period, are summarized in Table 3.1. These data are also illustrated in Figure 2, which includes water temperature and turbidity information. Temperature was not recorded for the period from December 1981 to mid-February 1982.

Twenty-seven geoducks ceased showing at various times since their initial observation and had failed to reappear by the end of this study. All such flagged positions were monitored for the duration of the study and only then was the assumption made that these geoducks had died, shortly after their last appearance. These numbers were therefore not included in the calculation of 'Percent Showing' values, for any given date. In Table 3.1, the 'Number Tagged (adj.)' is thus an adjusted value, which reflects the number of geoducks which had been identified by flags and are believed to have been alive on that date.

Table 3.1 Summary of Geoduck 'Show' Observations

Date Starting in 1980	Number Visible	Number Tagged (adj.)	Percent Showing	Comments
June 22	44	47	94	-plot partially labelled
26	70	70	100	
July 1	68	68	100	-3 died;1 found
11	73	73	100	-5 found
15	71	72	99	-2 died;1 found
17	70	71	99	-1 died
25	74	74	100	-1 died;7 found;3 flags lost
29	72	74	97	
30	72	72	100	
Aug. 5	67	67	100	-5 flags lost
7	69	69	100	-3 found;1 flag lost
8	68	68	100	-plot mapped;1 flag lost
19	66	68	97	-1 flag lost
Oct. 4	65	68	96	-long flags;note each clam
5	55	67	82	-1 died
Nov. 13	25	62	40	-5 died
Jan. 28	50	62	82	-1 died;1 found
31	49	61	82	-1 died
May 9	54	60	92	-1 died
18	61	62	98	-1 died;3 found
June 10	61	62	98	
26	62	62	100	-1 died;1 found
29	62	62	100	-plot exended
July 9	93	95	98	
14	92	94	98	-1 died
Aug. 8	91	94	97	
14	93	94	99	
21	87	91	96	-3 overlooked
Oct. 2	83	90	92	-2 died;2 overlooked
3	86	92	93	
30	88	92	96	
Nov. 1	77	88	88	-4 died
Dec. 4	43	67	64	-partial survey
5	55	86	64	-1 died;1 overlooked
Jan. 20	84	88	95	-1 juvenile found
21	55	77	71	-1 died;partial survey
Feb. 19	87	88	99	-1 juvenile found
20	64	65	98	-partial survey
Mar. 20	88	88	100	
21	88	88	100	
Apr. 16	86	86	100	-2 overlooked
17	74	74	100	-partial survey

Figure 2. Summary of geoduck show observations (jagged solid line) as recorded in Table 3.1, with water temperature (smooth solid line - °C), and visibility measurements (dots), from July 1980 until April 1982. Water temperature was not recorded between Dec. 4 1981 and Jan. 21 1982. Pairs of show observations labelled A, B and C represent an initial survey during which the sediment was frequently probed to detect siphons, and a subsequent survey, 1-2 days later, during which shows were markedly reduced.


Percent Showing
100
80
60
40
20
A
B
C
10°
8°
6°
4°
2°
12
10
8
6
4
2
Visibility (m)
J A S O N D
1980
J F M A M J J A S O N D
1981
J F M A
1982

The number of geoducks that died since the previous observation is indicated under the heading, 'Comments', as is the uprooting of flags, which in the first few months of the study resulted in relocating and renumbering the geoducks involved. The latter accounts for the large number of unmarked geoducks which were still being found, several months into the study. Also indicated are the dates when the plot was only partially surveyed, due to the time constraints imposed by the no-decompression time limits associated with SCUBA. To minimize any sampling bias which may have occurred as the result of a partial survey of the defined population, surveys always commenced from the same end of the plot. Occasionally, one or two geoducks were accidently overlooked in a survey and for the calculation of a 'Percent Showing' value, these individuals were omitted.

The three regions labelled 'A','B', and 'C' in Figure 2, represent three pairs of survey data points. The two surveys which form each pair, were conducted 1-2 days apart. Survey pairs A, and B occurred at the beginning of two inactive periods and the surveys represented by C, occurred at the end of an inactive period. A fourth pair of survey dates (unlabelled) occurred during the middle of the inactive period, on December 4 and 5, 1981.

Discussion

Mortality

An unexpected feature of this study was the large number of geoducks which apparently died over the 22 month period (n=27). At present, the natural mortality rate of geoducks is estimated to be very low (Andersen 1971; Breen and Shields 1983) and constant for adults of all ages (Shaul and Goodwin unpublished). While there is a slight possibility that some geoducks were falsely assumed to be dead, it is extremely unlikely that many would remain retracted for 3 months or more. Also, on at least 5 occasions the location where a geoduck was known to have existed, was covered with a patch of white film, similar to patches (bacteria or fungus) typically associated with decay in a moist environment. This occurred approximately 1 month after that clam first retracted permanently. The presence of these patches was not always recorded and so they may have accompanied the 'permanent disappearance' of all geoduck siphons. The submerged portion of a flag of at least one such geoduck was notably blackened and smelled of hydrogen sulphide (produced under conditions of anaerobic decomposition). These observations strongly support the assumption that these geoducks died and were not merely retracted.

Regardless of the exact number of geoducks that died, a significant proportion of the population was affected. The first possibility to consider is that this mortality was induced by the study itself. These geoducks experienced only two conditions which would not otherwise be encountered. (1) Many geoducks in the study plot were regularly 'poked' during the winter, to determine their position (showing vs. retracted). It is unlikely however that this disturbance could result in death, since geoducks elsewhere are often missing pieces of their siphon tips (predators?) and are in various stages of healing (Andersen 1971; personal observations). (2) All members of the study population had their locations marked by a numbered flag. There are several ways in which this may have affected the study population but none appears likely to have resulted in the observed high mortality rate. For example, potential geoduck predators were attracted to the flags (discussed below) but there was no evidence to indicate that such attacks occurred on the geoducks themselves, other than the occasional, slightly damaged siphon tip. Also, the flags may have disturbed water currents and thus feeding, but as these flags were placed neither directly upstream nor directly downstream of each siphon, such effects were probably minimal. Andersen (1971) suggests that an accumulation of vegetation may kill geoducks but he relates this to the anaerobic conditions of algal decay occurring intertidally. Though kelp became entangled in the flags, being constantly subtidal it was always loosely packed and presumably wasn't accompanied by a significant drop in oxygen content of the ambient water. The possibility that geoducks were fatally wounded due to puncturing by the flag staff was considered, but also appears to be remote. During this research almost 300 geoducks were similarly identified with flags and later harvested. None bore marks of such damage. One geoduck which was pierced by a plot-boundary stake appeared to be filtering normally several days later, when the plot was harvested.

Geoduck mortality appeared unrelated to the conduct of this study and the observed death rate is not considered to be representative of normal yearly mortality, since it greatly exceeds the rate of recruitment (inferred from population age structure data). There was also no indication that an environmental anomaly was responsible and the possibility of human influence is unlikely, as the study site was far from the nearest village. The observed mortality appears to have been natural and likely to have only existed for a short period. If this high mortality rate occurs regularly in geoduck populations, even if only infrequently and for periods of short duration, this phenomenon could severely alter present estimates of geoduck population stability and fisheries' estimates of sustainable yield.

Flag Loss

There were at least two separate factors thought to be responsible for dislodging the identification flags. Large pieces of the kelp, *Macrocystis integrifolia* and *Desmarestia ligulata* were frequently observed drifting across the substrate, particularly during the late summer and fall. When these became caught on the flags, they may have created sufficient drag to uproot them. Also, the tubing of several of the loose flags was misshapen and crushed in several places. While the PVC tubing used was fairly resistant to such damage, the red rock crab, *Cancer productus*, which was quite abundant throughout the study area, was found to be capable of producing similar results with its claws. Some markings on the tubing however, did not appear to have been made by crabs. The spiny dogfish, *Squalus acanthias*, which was particularly common during the fall, may have been attracted by the bright yellow surveyers tape and attacked some of the flags. This would account for those flags which were dislodged and oddly mangled. Lone dogfish were often encountered during surveys and would usually circle for 10 minutes or more, following any changes in diver position during that time. Though both dogfish and crabs may have been in part responsible for dislodging flags, no such attacks were ever observed.

Siphon Detectability

For reasons to be discussed later (see Shell Size and Age), it is believed that the data on siphon detectability represent all geoducks within the plot that were at least 4 years old.

Despite fluctuations in the number of geoducks surveyed (due to an increase in plot size, a loss of flags, mortality, etc.), a clear seasonal pattern of siphon 'shows', was evident. More than 90% of the geoduck population could be detected from mid-February until November ('active period'). During the summer months detection was even higher, never being less than 96%. November until mid-January was the period when the least number of geoducks could be detected ('inactive period'), representing as little as 40% of the population one year, and 64% the next.

These results differ greatly from those of Goodwin (1977). He observed a maximum of 59.8% and 5% of the population showing during summer and winter respectively. This discrepency however, is most likely in response to differences in experimental design, which reflect the different nature of the questions asked by each study. While both attempted to correlate the number of 'visible' siphons at any given time to actual population numbers, Goodwin's study more accurately estimates the percentage of the population likely to be observed by a surveyor. Fluctuations in siphon 'detectability' in this study, reflect fluctuations in siphon position due to geoduck activity. Here, geoducks with siphons that could be detected, despite not being readily visible, were considered to be 'showing'. The term 'show' as it is used in this study, is different from Goodwin's 'show' and appears to be the basis for Breen and Shields' recently (1983) proposed 'correction factor'.

As mentioned earlier, during the inactive period siphons were difficult to see and often the sediment had to be probed to verify the presence of a siphon, beneath a thin layer of sediment. In both cases A and B (Fig. 2), the number of detectable geoducks was significantly reduced on the second survey day. This would appear to indicate that the physical disturbance due to probing the sediment, caused several geoducks to retract and remain that way for a minimum of 24-48 hrs.

Of the ten 'A' geoducks which were visible one day and not the next, seven were still retracted on the following survey date, one month later. Of the nine 'B' geoducks which had similar such patterns in 1981, six were still retracted the following month. In both years, each such geoduck was subsequently observed on at least one occasion, so failure to reappear was not due to disturbance-related (poking) mortality. The effect (retraction) of a physical disturbance at this time of the year, persisted for a month or more.

On January 20, 1982, 95% of the population was detected, indicating the end of the inactive period. Many of these however could only be detected by probing the sediment. On the following day, only 71% of the population was showing, a drop to near mid-December levels. Physical disturbance was probably responsible for this reduction in number of 'shows' ('C' in Figure 2). Of the 20 geoducks that reacted this way, 15 had been 'not showing' earlier during the inactive period and so all may have been 'inclined' to retract. All but one of the 20 were showing on the next sampling date one month later.

Despite experiencing a similar disturbance on successive days in December 1981, there were no fewer geoducks showing on the second day. Perhaps this far along into the inactive period, all those which were going to retract, had already done so.

Analysis of these data should then take into account the likelihood that the onset of the inactive period, as indicated by points A and B, occurred earlier than normal, due to the physical disturbance required for geoduck detection. In 1982, onset of the active period may have been artificially delayed for the same reason.

The time geoducks spent in a retracted position varied. Some were not detectable on only one occasion during the inactive period and others remained undetected for several successive surveys. Because sampling during the winter months occurred at monthly intervals, the former situation could represent up to 2 months of inactivity and the latter, almost 4 months. In some cases, geoducks which had retracted early in the inactive period, could be detected on a couple of subsequent surveys, and then were retracted on the next survey date. The lower limit on time spent retracted, appears to vary between individuals.

Since each geoduck was assigned a number for the duration of the study, siphon retraction of individuals could be compared in successive years. Excluding instances in which retraction was only observed on the second day of survey pairs A, B and C, of the 56 geoducks followed through two inactive periods, 43% spent some time retracted both years, 29% were retracted only in 1980, 14% retracted only in 1981 and 14% showed throughout both winters. While a large majority of the study population spent a portion of at least one winter retracted, over half of them did not automatically retract with the onset of winter conditions. Also, a large portion of the population which retracted in 1980, failed to do so in 1981, despite another 14% 'not showing' for some time that year, after showing constantly during the previous one.

As Bernard (1983) points out, bivalves are not automata and some individuals may behave contrary to the rest of the population. Newell (1966) reported that despite experiencing no external disturbance, oxygen uptake of the cockle, Cardium edule, was not constant over time, noting that individuals alternated between active pumping and quiescence. Geoducks apparently have similar such individual tendencies with regard to showing during the winter months.

Almost 70% of the study population was 'not showing' on at least one occasion during the inactive period of 1980, and in 1981 this value was approximately 55%. If 'not showing' was a completely random event with respect to behavior of the previous year, roughly 39% (0.70 x 0.55) would be expected to be retracted on at least one occasion both years. Since 43% of the geoducks were, there was no reason to suspect that some were more likely to retract than others, based on the previous year's record. Also by random chance, almost 14% of the population (0.30 x 0.45) would be expected to show throughout both inactive periods. This is the value that was observed and so the probability of a geoduck showing throughout 1980 had no bearing on its record in 1981.

An Explanation for Siphon Retraction

Figure 2 illustrates how ambient water temperature varied while siphon 'shows' were monitored. In 1981, water temperature peaked late in August and began dropping in September. While 4% of the population was not showing on August 21, significant numbers of geoducks only retracted their siphons much later. For reasons discussed earlier, the distinct decrease in the number of detectable siphons, between October 30 and November 1 (198[illegible]) was probably artificially induced, so the actual onset of the inactive period likely occurred later in November. Seasonal siphon retraction appears to coincide with a decrease in temperature.

Oxygen consumption and ventilation rates have been measured for nine species of Northeastern Pacific bivalves (Bernard 1983). When exposed to temperatures below a 'lower thermal threshold', shell valves closed and metabolic activity was reduced to a level sufficient only for the maintenance of vital functions. This shift to low respiratory levels occurs naturally in response to, "...prevailing [environmental] conditions, matching ventilation (and therefore browsing rate) to food supply, or decreasing energy loss during periods of low temperature or starvation." -Bernard 1983.

Geoduck retraction from November to mid-February may be the result of functioning at this low level of metabolic activity. Though a 'lower thermal threshold' has not been determined for geoducks, that of the horseclam, Tresus capax, which of all species tested most approximates the general body structure and habit of Panope generosa, was 6°C. Winter temperatures in Ritchie Bay approach this, and could cause such a shift in metabolic activity, particularly if an adequate food supply is lacking. For a number of reasons, this is thought to have been the case.

In 1981, turbidity began to drop (visibility rose) in November (Fig. 2) and continued to do so until April of 1982. Since this corresponds to a decrease in water temperature, increased visibility is thought to have been caused by decreasing phytoplankton abundance, and not by reduced amounts of silt or suspended detritus.

In a brief study in 1980, Cotter (unpublished) found that the mean volume of geoduck stomachs and digestive diverticula combined, decreased significantly from October 10 to November 21, indicative of reduced feeding. He also noted that the material contained in these organs, which is normally dark green during the summer (personal observations), changed from a 'dark'-'medium' green in October, to a predominantly 'light' color by the end of the study, with none of the samples exhibiting the 'dark' green condition. Digestion appears to have occurred with little ingestion of new food.

In a concurrent study, Starcevich (unpublished) found that the crystaline style of geoducks weighed significantly less, after 3 days in a food-free environment, than those of a control population and after six days, styles were not present in the test clams. In some bivalves, the style dissolves when food is absent and is reformed when food becomes available. The crystaline styles of geoducks harvested on November 5 weighed less than those of geoducks harvested on October 1.

The findings of these two studies, in addition to observed trends in turbidity (a function of phytoplankton abundance), support the contention that food availability and the amount that geoducks consume, are drastically reduced during the fall and winter. This, in conjunction with low water temperatures, may result in a 'maintenance level' of geoduck metabolic activity. Other clams respond by closing their valves (Bernard 1983). Since geoducks are unable to do so, siphon retraction is proposed as an analogous response. This position may be beneficial to the geoduck, which otherwise may be forced to retract every time an animal attempts to feed on its siphon tip.

Unfortunately, several weeks of temperature data are lacking during the period when siphons began to extend. The data which are available however, for the winters of 1980-81 and 1981-82, clearly show that extension of the siphons preceeded the yearly rise in water temperature and thus was not caused by it. Possibly the shut-down of feeding and/or respiration may only be able to continue for a limited time and may therefore force geoducks to 'show' as early as they do, when water temperatures are at their coldest and phytoplankton densities appear to be at their lowest.

Conclusions

1) The large geoduck mortality which occurred during this study, did not appear to be due to either design problems or any other human influence. Should such mortality periodically occur in all geoduck populations, population stability may be greatly overestimated.

2) Periods of inactivity, during which many geoducks cannot be detected, occur seasonally between November and mid-February. Approximately half of the population becomes inactive each winter and individual geoducks vary greatly in the duration of retraction. For the rest of the year, more than 90% of the population is active. In June, July and August, this value was greater than 95%.

3) The discrepency between these results and Goodwin's (1977), are likely due to the inclusion here of geoducks which, while not readily visible, were detected by closer observation and probing of the substrate.

4) Geoducks appear to be particularly sensitive to probing just prior to and just after the inactive period. In the case of the former, the resultant retraction frequently persisted for more than one month. In January when disturbance resulted in retraction, only one of 20 geoducks was still not showing by the same date in February. Fifteen of these 20 had been 'not showing' on at least one survey date during that winter prior to the January survey and so in any one year, certain individuals may be more likely to retract in adverse conditions. Geoducks similarly disturbed midway through the inactive period did not respond by retracting for extended periods (24hr+).

5) There was no evidence to indicate that geoducks which did or did not show in 1980, were likely to do the same or the opposite in 1981.

6) Decreasing water temperature and food availability coincide with and may cause geoducks to retract their siphons seasonally. At that time, the food intake of those which show, was markedly reduced. The period of inactivity ended well before temperatures began to rise and phytoplankton bloomed. Some other factor, possibly a time-limited ability to remain inactive, was responsible for geoduck siphons re-emerging.

7) Based on these results, I concluded that density and dispersion analyses of surface-detectable geoducks would be representative of the whole population, provided that all such work be carried out between mid-February and November.

IV. Sediment Heterogeneity and Geoduck Distribution

Community structure of sedentary marine organisms is known to be influenced by environmental heterogeneity, particularly with respect to substrate particle size and composition. According to Stickney and Stringer (1957), substrate composition may be the single most important factor in the organization of a bottom community. Supporting this view are studies which conclude that particle size appears to be one of the most important settlement-inducing factors (Crisp 1974), and that the rate of recolonization depends to a large extent, on particle size (Boaden 1962). Swedmark (1964) concluded that the space between sand grains (a function of particle size), was the most important determinant of types and numbers of infaunal inhabitants.

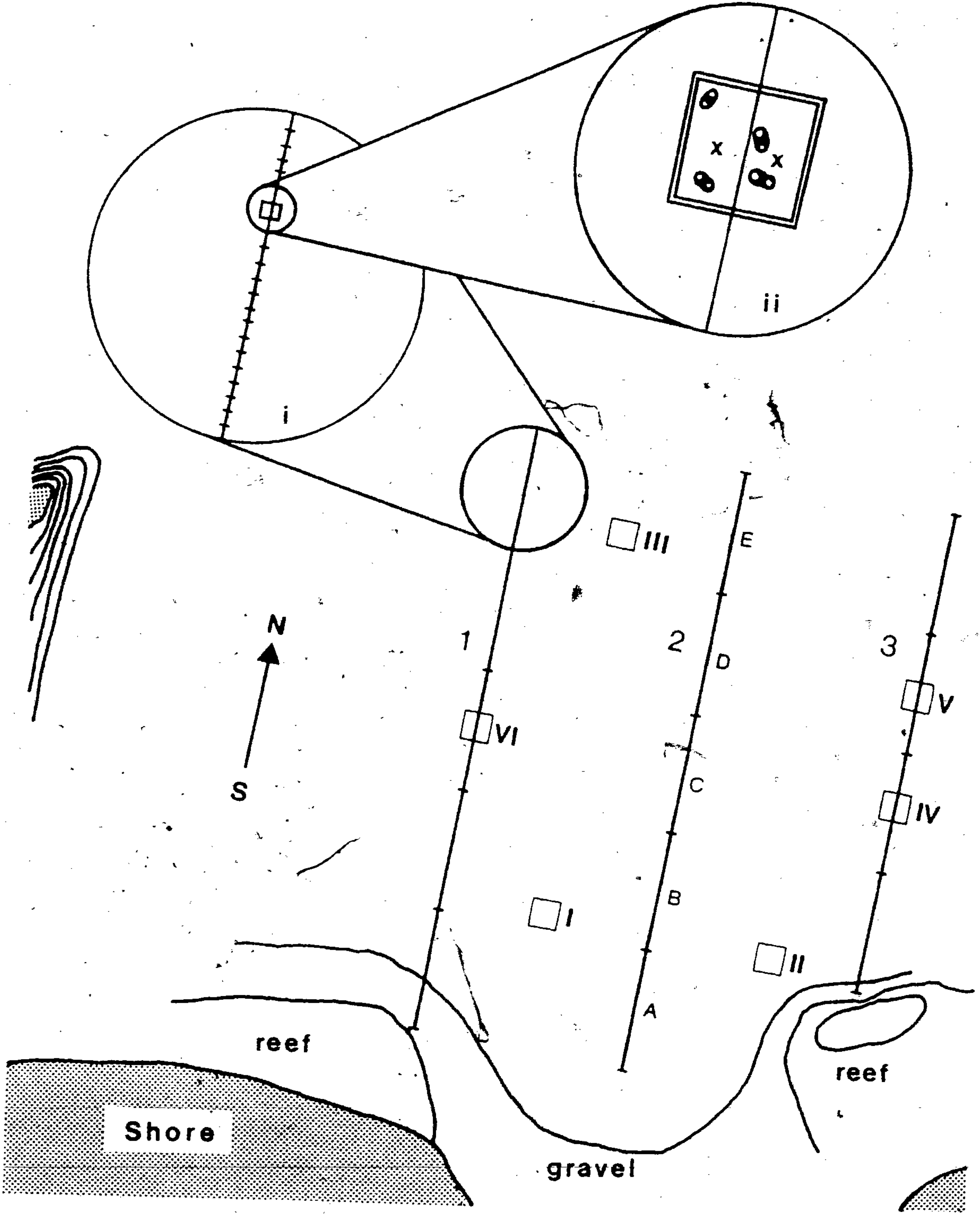
The terms 'distribution' and 'dispersion' have often been used interchangably but there are two distinct levels at which spatial configuration can be described and I will use one term for each. 'Distribution' will be used to describe relative densities while 'dispersion' will refer to the position of individuals relative to each other.

Methods

To determine variability in geoduck density and substrate composition, and assess the relationship between the two over a large portion of Ritchie Bay, a combination of systematic and random sampling was carried out east of the rock island (49°13'33",125°54'56"), with a portable 1m x 1m quadrat. Three parallel transect lines were set at 35m intervals, in a north-south direction, roughly perpendicular to shore (Fig. 3). Lines 1 and 2 were each 100m long. Due to a small rock reef which projected from shore, line 3 was only 80m long. Total area represented by this sampling was therefore slightly less than 7000 square meters. Each line was divided into five 20m segments or strata, labelled A-E, as is illustrated for line 2. Five numbers from 1 to 20 were randomly selected for each stratum, to correspond to the five 1m lengths along that line-segment, where sampling was to occur (inset i). The portable quadrat was placed over a designated portion of the line, so as to be bisected by it (inset ii). All geoducks within the quadrat were then counted and this number recorded. Additionally, for lines 1 and 3, two sediment cores (10cm deep x 3.8cm dia.) were collected from each quadrat, one from either side of the transect line (identified by X in inset ii). These were immediately combined to form one substrate sample, representing that $1m^2$ area. Thus the number of geoducks per square meter was recorded for 70 quadrats and sediment samples were collected for 45 of these.

Figure 3. Portion of Ritchie Bay, east of the rock island. The location of plots I-VI and transect lines 1-3 are indicated. Labelling of transect line segments appears on line 2. Inset 'i' shows enlargement of 1m intervals in segment 1E, with quadrat in place. Inset 'ii' indicates the location from which sediment core samples were collected within a quadrat.

✓


ii
x
x
i
N
S
1
2
3
E
D
C
B
A
III
VI
V
IV
I
II
reef
reef
Shore
gravel

Sediment samples were preserved by freezing and later dried in an oven at 50°C. Dried samples were weighed on a Sauter balance and each was mechanically shaken for 10 minutes in a Fisher-Wheeler Sieve Shaker. The following six size fractions were obtained for each sample: $>1000\mu$, $>500\mu$, $>250\mu$, $>125\mu$, $>63\mu$, $<63\mu$. These divisions represent the standardized size fractions of the Wentworth Size Classification for Sediments (Thomas 1973).

A sub-sample of 2.0-2.5g of each size fraction was weighed on a Mettler P160 balance and was combusted for 4-5 hours at 475°C, in a type 2000, Thermolyne muffle furnace. Loss of weight of marine sediments, after combustion by this method, accounts for 100% of the total organic matter present (Byers <u>et al.</u> 1978).

The first 7-10m of transect 1A and 3-4m of transect 3B, both extended into the coarse gravel substrate, mentioned earlier. Four sediment and density samples were collected from this area. As substrate type and varying bottom depth associated with this region were so obviously different from the rest of the site, density and substrate data for this small area were not included in calculations.

Results and Discussion

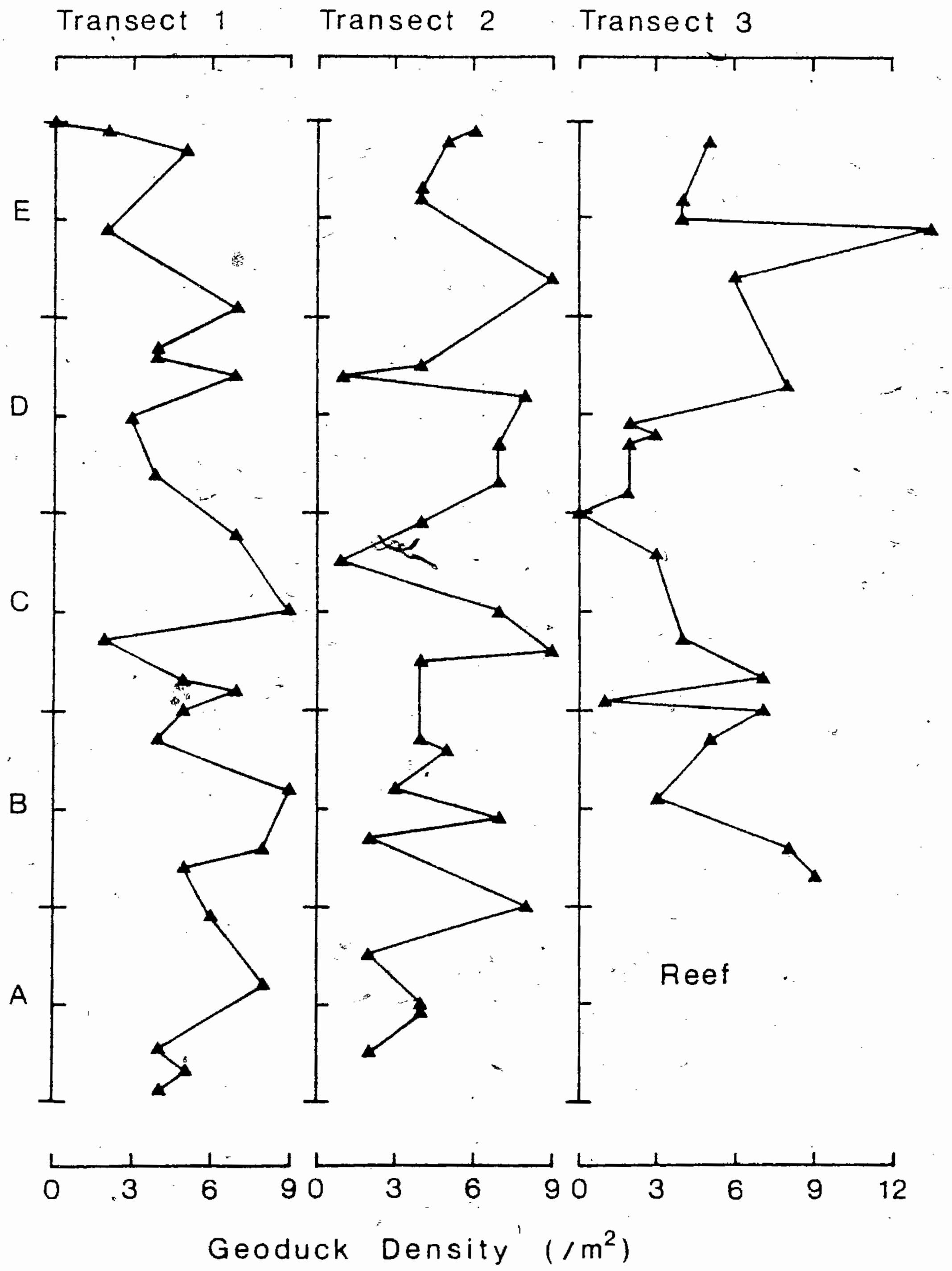
Density and Overall Distribution

Geoduck density per quadrat ranged from 0 to 13 /m^2 (Fig. 4), with a mean of 4.86/m^2 (σ^2=6.73; n=66). This is considerably greater than the average density of 2.5 geoducks/m^2, that Goodwin (1973) found in his high abundance areas. Though extremely high density patches may occasionally be found in Puget Sound and in the waters off the B.C. coast, rarely do geoducks occur in such densities over a large area (Goodwin 1978b; Cox and Charman 1980). The high density population in Ritchie Bay suggests that this bay had never been commercially harvested.

Using the χ^2-test (Elliott 1977), the population distribution was found to deviate significantly ($p<0.05$) from that of a Poisson series (random). Since sample variance exceeded the mean, I concluded that the geoduck population in the sample area was distributed in a clumped manner.

For some time it has been known that the use of quadrats to assess distribution patterns has several inherent problems (Greig-Smith 1952; Morisita 1959), a major one being that quadrat size greatly affects the outcome of such analyses. Furthermore, the spatial relationship of high and low density quadrats is often ignored (Pielou 1977).

Figure 4. Geoduck densities at 5 randomly selected locations within each line segment, for transect lines 1, 2, and 3.


Transect 1
Transect 2
Transect 3
E
D
C
B
A
Reef
0
3
6
9
0
3
6
9
0
3
6
9
12
Geoduck Density (/m²)

The clumped distribution of geoducks in Ritchie Bay could be produced by one of several patterns. Clumps may be numerous and small, roughly equal to quadrat size. Alternately, geoducks may occur in relatively few, large clumps or a grade of densities across the sample area is equally possible, representing the edge of one large clump. To determine where along this continuum, geoduck distribution in Ritchie Bay lay, quadrat density data was subdivided in several ways. In addition to clarifying the spatial relationship between the highest and lowest density quadrats found, the error associated with using a single quadrat size (Greig-Smith 1952), was thus also reduced.

To compare densities in the quadrats located closest to shore (inshore) with those set furthest away from the shore (offshore), data from all transect lines were combined. To form the 'inshore' sample, densities from stratum B and stratum C of each of the three lines were pooled. Data from strata D and E formed the 'offshore' sampling. A transformation (log(x+1)) was performed on these data to permit the use of a Student's-T test (Elliott 1977). No significant difference ($p=0.734$; $n=59$) was found between inshore and offshore geoduck densities.

Densities from transect lines 1, 2 and 3 were not significantly different from one another (ANOVA; $p=0.689$; $n=59$).

Geoduck density data were then combined by stratum and an ANOVA was used to test for differences in densities between strata. No significant difference was found ($p=0.229$; $n=59$).

When stating the distribution of any population, it is important to specify the scale on which this distribution is found. On a very large scale, geoduck distribution can be thought of as being clumped, in that the species Panope generosa occurs only in the north Pacific (Young 1971). Clumping is also observed on a smaller scale, with high and low density regions occurring in close proximity to one another (Goodwin and Shaul 1979). This is the case here, with geoducks clearly more abundant in Ritchie Bay than in some areas nearby (personal observations). Geoducks within the study area were also distributed in a clumped manner. Subdivision of the area (ie. inshore/offshore, line 1/2/3 etc.), and comparison of these densities failed to reveal any explanation for this clumping. Geoduck density 'inshore' was no different than that 'offshore'. Density along all three transect lines was similar and when the densities of all strata were compared, none were significantly different from the rest. Since the χ^2-test on individual samples indicated aggregation and testing with larger groups failed to detect this, clumps are likely to be considerably smaller in size than the length of a single stratum (20m). This conclusion is supported by data in Figure 4, which shows the relative location of each quadrat and the number of geoducks located there.

Sediment Composition

The decision to take sediment cores to a depth of 10cm was based on the depth distribution of recently settled geoducks. Geoducks spawn in the spring (Andersen 1971, Goodwin 1976), and at 14°C, larval metamorphosis and settlement occurs 40-50 days later (Goodwin _et al._ 1979). For the first 2-3 years of life, growth rate is about 30 mm/year (Goodwin 1973, 1976) and by the time that shell formation ceases for the winter (Shaul and Goodwin 1982), recruits-of-the-year are probably 20mm or less in length. Extrapolation of Andersen's (1971) data places geoducks of this size range at a depth of 10cm or less.

Mortality at the time of settling is generally believed to be very high for all larvae (Crisp 1974) and the first winter probably represents another major period of regular recruit loss. If sediment quality in any way affects recruitment, its surface layer likely plays a part in determining settling success, while the top 10cm influences ability to survive the first winter. Since mortality rate of the sessile form is probably greatest in this zone, sediment samples were collected to a depth of 10cm. It should be noted that some effects of surface sediment composition on settling success and thus distribution, may have been masked by taking sediment cores to this depth.

Results of sediment size fractioning and combustion are summarized in Table 4.1, as mean values for all samples. Figure 5 contains a histogram of these data with the standard deviation indicated for each size fraction.

Relative size fraction abundance comparisons were made based on dry weights. For all samples (n=41), the 125-249μ size fraction was dominant, representing 55%-70% of each sample. The 63-124μ size fraction, was second largest for all samples. When combined, these two fractions accounted for more than 75% of each sample. Sediment in this size range is described as fine to very fine sand. Particles <63μ are considered to be silt or clay. Each size fraction other than the two most abundant, averaged less than 5% of the total sample.

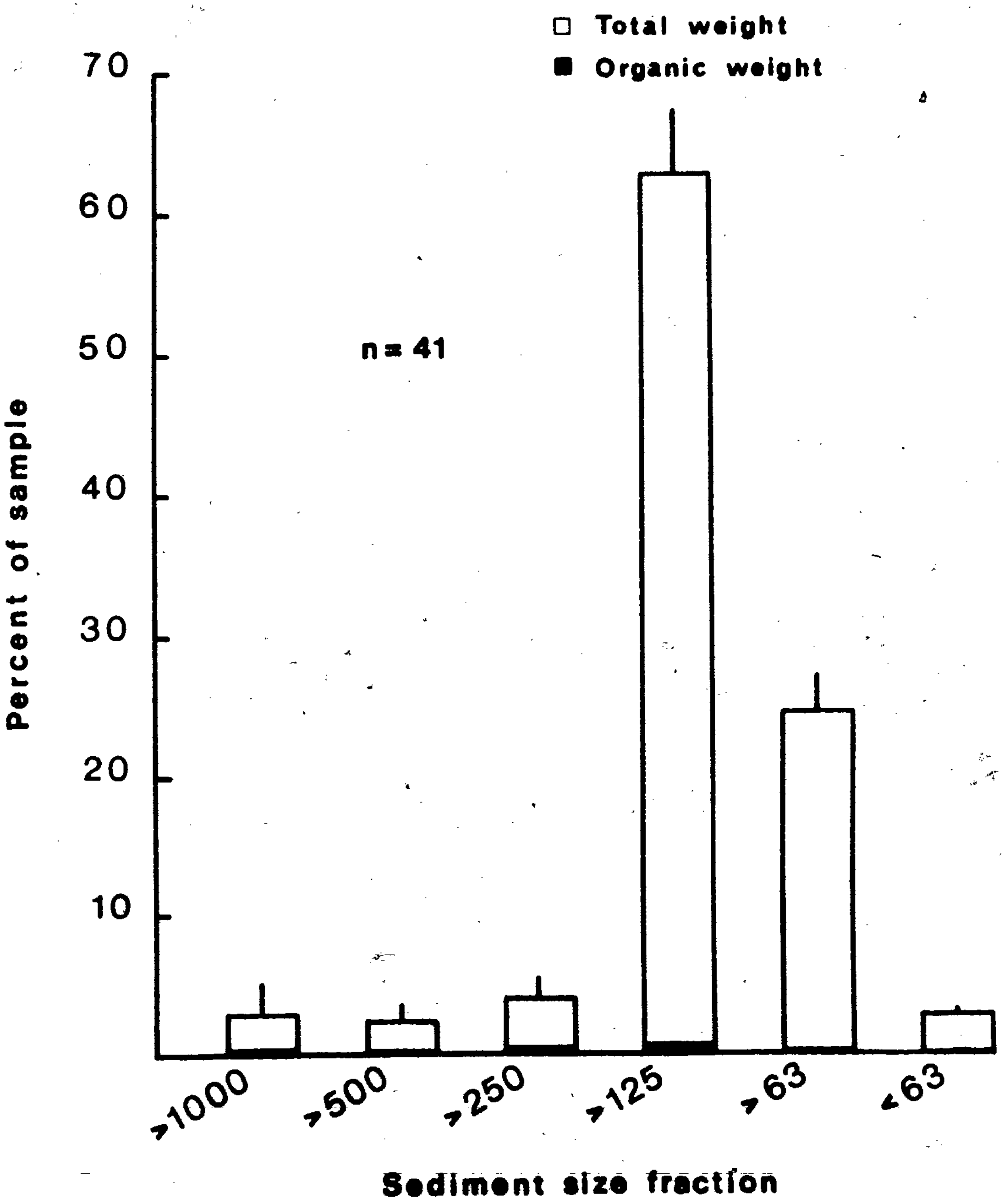
Table 4.1 Sediment Composition by Size Fraction (n=41)

Size Fraction (microns)	% of Sample (S.D.)	% Organic Content (S.D.)	g Organic per 100g Sediment
>1000	2.9 (2.1)	15.2*(7.5)	0.0041*
> 500	2.4 (1.2)	13.9 (6.8)	0.0034
> 250	4.1 (1.4)	8.5 (4.0)	0.0034
> 125	63.1 (4.1)	1.3 (0.3)	0.0080
> 63	24.7 (2.7)	1.3 (0.3)	0.0031
< 63	2.8 (0.6)	4.4 (1.3)	0.0013

* n=40

Percent organic content was inversely related to the abundance of each size fraction. The organic portion of the 63-124μ and 125-249μ size fractions averaged 1.3% each, with upper and lower values of 2.3% and 0.9%.

Figure 5. Sediment composition of Ritchie Bay, by size fraction. Bars indicate one standard deviation, for the total dry weight of each size fraction.


☐ Total weight
■ Organic weight
70
60
50
40
30
20
10
n= 41
Percent of sample
>1000
>500
>250
>125
>63
<63
Sediment size fraction

The two largest-particle size fractions consisted of an average of 15% organic matter. However even when combined, for any one sample these two size fractions accounted for no more than 15% of the total weight and so contributed little to the overall organic content.

When the relative weights of each size fraction were taken into account, the greatest amount of organic matter was in the 125-249μ size fraction (0.0080g per 100g sediment). The 0-62μ size fraction contained the least organic matter (0.0013g per 100g sediment).

The consistency of sample make-up, with respect to the relative weight of each size fraction and its respective organic content, supports the initial observation that sediment particle size throughout the study area was generally very small and well sorted.

The extent to which bivalves are able to detect minute differences between habitats is uncertain and consequently the influence of such differences is unknown. To more clearly define any substrate heterogeneity which may exist at the site and thus better assess the probability of it influencing distribution, further analysis of the available sediment data was undertaken on the basis of individual sediment size fractions.

As is required for parametric testing of data expressed as percentage values, arcsine transformations were carried out on square roots of the raw data (Sokal and Rohlf 1969). All further statistical analyses dealing with sediment composition were performed on transformed data. In a manner similar to that used with geoduck density, data were pooled for inshore/offshore sediment composition analysis. With Student's-T tests, both locations were compared on the basis of abundance of each size fraction. The sediment in these two areas was similar with respect to size, for all but the >63μ size fraction, which was significantly more abundant inshore (p=0.014). Since the probability of this difference occurring by chance is relatively low, and this difference occurred in one of the most abundant size fractions, the difference is likely real, though the reason for this was not apparent. Despite transformation of the data, when inshore/offshore samples were analysed for organic content, the assumption of homoscedasticity of variance was in some cases, not valid. Differences for these particular size fractions, were then tested for by the Mann-Whitney U test, which does not require such an assumption. The >1000μ and >500μ size fractions contained significantly more organic material (p<0.001 and p=0.005) in the inshore samples than in the offshore samples. This was probably due to the presence of the woodchips, which were mentioned earlier. When the relative abundance of each size fraction was taken into account however, inshore/offshore differences were not significant.

Sediment from transect line 1 was compared (Student's-T) with that collected from along line 3. The abundance of all sediment size fractions except one, were similar (p>0.05). A significantly greater (p=0.021) amount of the >250μ size fraction occurred in samples from line 3, however this size fraction averaged only 4% of the sediment in all samples. Organic content of the <63μ fraction was significantly greater from samples collected along line 3 but also when the abundance of this size fraction was taken into account, sediment from either line did not differ with respect to organic content.

An analysis of variance by line stratum, was performed on the relative dry weights of each size fraction. For each fraction, differences were significant ($p<0.05$), particularly for the most abundant fractions (>125μ and >63μ), for which differences were highly significant ($p<0.001$). Similar analyses were performed on the total organic component by size fraction. Differences were significant for all but one size fraction (>125μ; $p=0.076$).

These analyses of the data revealed that inshore samples had more sediment in the 63-124μ size range than offshore samples and that samples collected along transect line 3 had a greater abundance of the 250-499μ size fraction than samples from line 1. Additionally, significant heterogeneity of both particle size and organic content existed between line segments.

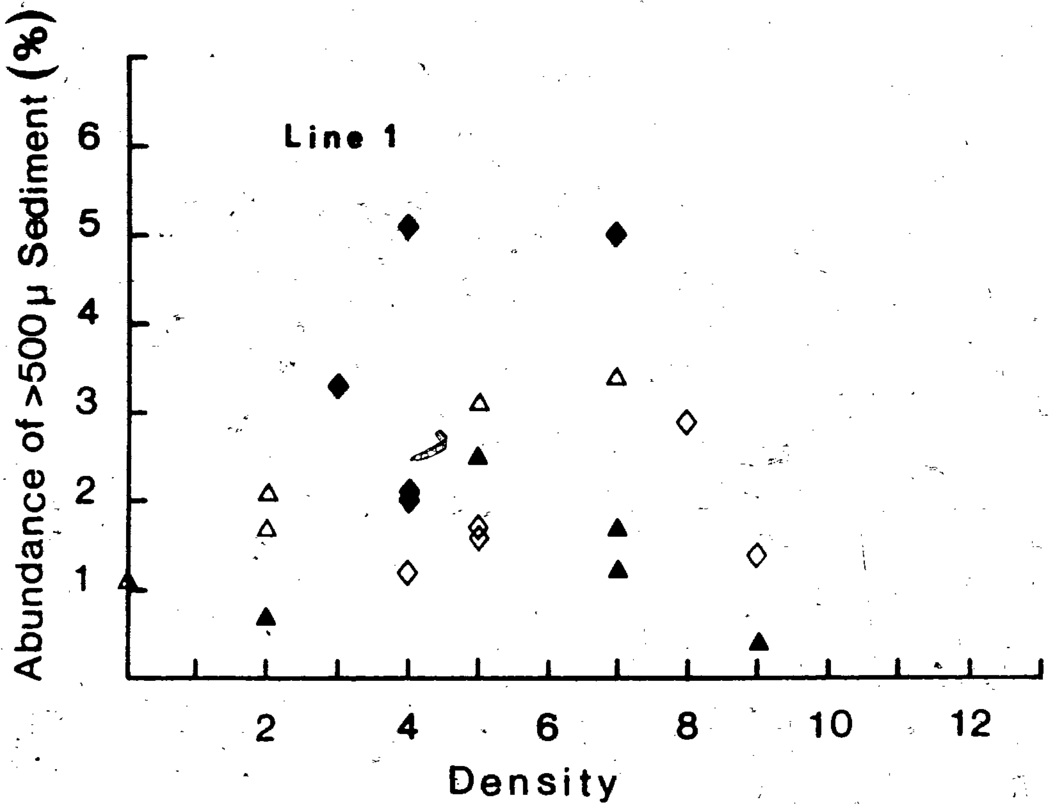
To determine the effect of this slight sediment heterogeneity on geoduck density and thus overall distribution, correlation analyses were performed between geoduck density and all sediment size and organic content variables, for each line segment. While some significant correlations were indicated, they varied from line-segment to line-segment and were therefore concluded to be an artifact of the large number of correlations attempted. Over small areas, geoduck density was not correlated with measured sediment parameters.

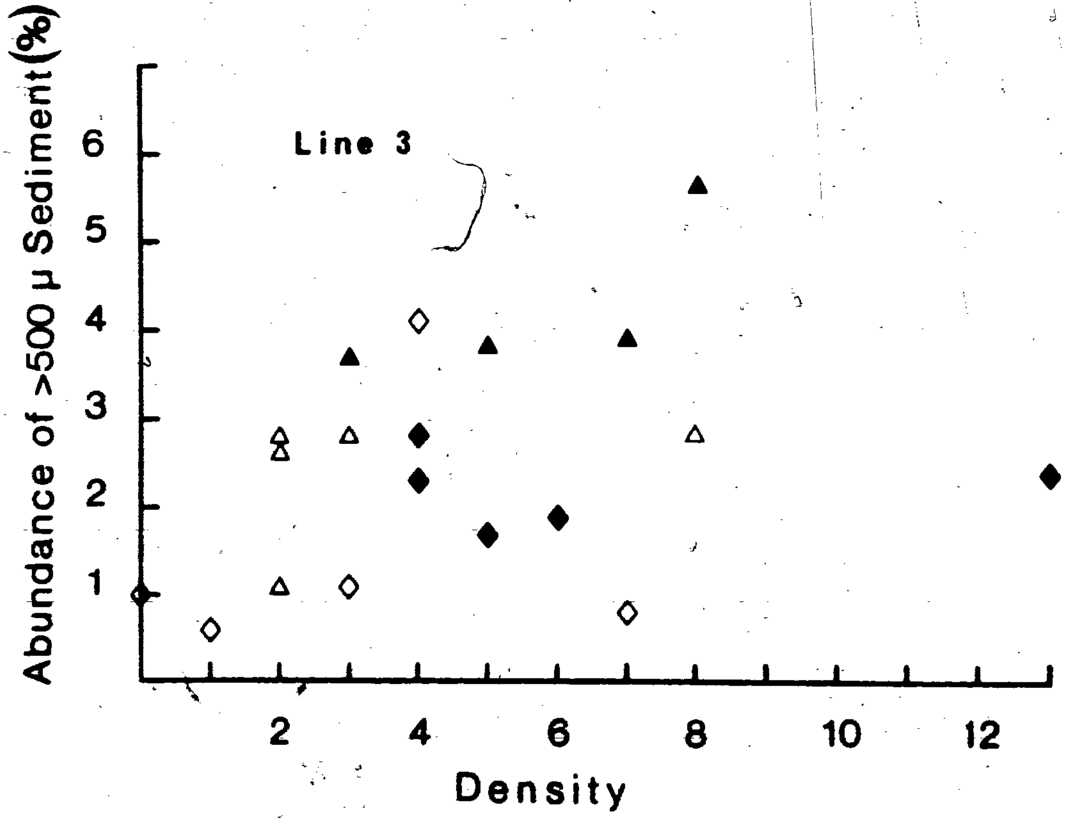
All sediment and density data from the site were compiled, and the only significant correlation was between geoduck density and abundance of the >500μ size fraction ($p<0.02$). Thus slight inshore/offshore, line 1/line 3 sediment differences observed, do not appear to have influenced density or distribution.

On average the 500-999μ fraction made up only 2.4% of each sediment sample, with a standard deviation of 1.2 (ie. abundance of this narrow size range of particles is small, with little overall variance in this abundance). The significant correlation above, can be interpreted in two ways. Either geoducks are sensitive to these minute variations or a type I error was made by setting the critical alpha level too low, at $\alpha=0.05$. In other words, a true null hypothesis may have been mistakenly rejected. As the relative cost of type I error appears in retrospect to be considerably greater than that of a type II error, a more stringent standard for avoiding the former should have been adopted, by setting the critical level at 0.01 (See Toft and Shea 1983, for a discussion on power analysis and statistical inference).

Given however that the original criterion for acceptance was met, geoduck density appears slightly, positively correlated with abundance of the >500μ sediment size fraction. Since no such relationship exists within line-segments (see Fig. 6), it

Figure 6. Abundance (%) of the >500μ sediment size fraction in relation to geoduck density (/m^2), for transect lines 1 and 3. Each symbol represents values within a particular line segment.


Line 1
Abundance of >500 μ Sediment (%)
1
2
3
4
5
6
2
4
6
8
10
12
Density


Line 3
Abundance of >500 μ Sediment (%)
1
2
3
4
5
6
2
4
6
8
10
12
Density

was concluded that the relative abundance of this size fraction may predispose an area for a certain geoduck density, but there is a high degree of variance in the actual density that occurs there.

Summary

1) To minimize environmental differences between sample areas, all sampling was confined to one, relatively homogeneous study site. Parameters such as water velocity, temperature, depth, salinity and food content were taken into account when choosing the site. The high potential for sediment composition to influence distribution lead to extensive analysis of this parameter to quantify its heterogeneity.

2) Geoducks within the study area in Ritchie Bay were distributed in clumps which appeared to be larger than 1m across but much less than 20m across. Geoduck densities did not differ significantly along transect lines and densities inshore were similar to those offshore.

3) Sediment throughout the site appeared relatively homogeneous. Surface (10cm) sampling revealed that the sediment consisted largely of small, well-sorted particles. The 125-249μ size fraction accounted for 63% of each sample on average and another 25% was in the 63-124μ size range. All other fractions each averaged less than 5% by weight.

4) Sediment samples contained little organic material.

5) When the relative abundance of all size fractions were compared, few differences were observed either between lines or between inshore/offshore regions. When line-segments were compared on the basis of abundance of each size fraction and its organic content, many significant differences were apparent.

6) The only significant correlation between geoduck density and any sediment parameter occurred with the >500μ size fraction. This fraction was the least abundant and the reliability of the relationship was questioned.

7) Environmental heterogeneity throughout the site appeared to be minimal and for that which was observed (abundance of various sediment size fractions), no clear relationship with geoduck density could be detected.

V. The Shell

Shell deposition occurs on the internal surface of the previous season's growth and extends beyond, to increase shell size as a clam grows. For geoducks, the rate at which shell thickness and surface area increase each year, decreases with age once they reach 3-4 years old. Beyond the age of 10yr, increase in size is minimal. The rate of this decrease in growth is not constant but varies slightly from year to year, as local environmental conditions fluctuate. Generally, elevated temperatures enhance shell production, while reduced temperatures inhibit production (Bourne pers. comm.). Severe disturbance may even result in a check of the growing phase (Goodwin 1976; Shaul and Goodwin 1982), which can often be seen on the shell surface. By comparing bivalve shells from different locations, environmental conditions at different sites can be inferred (Rhoads and Panella 1970; Panella and MacClintock 1968). The relationship between relative increment widths and past climatic conditions was realized prior to the turn of the century, with the growth rings in trees (Hitch 1982).

Minimal heterogeneity of all environmental variables between sample sites was sought to observe any possible effect of geoduck density on shell production. Shell length, height, weight and planar surface area were used as measures of this production.

Many bivalves are known to lay down internal bands which correspond to yearly growth (Rhoads and Panella 1970; Jones *et al.* 1978; Turekian 1978; MacDonald and Thomas 1980; Thompson *et al.* 1980). Distinct daily and even tidal growth increments have been reported for some species (Panella and MacClintock 1968; Richardson *et al.* 1979). The reason for this regular change in shell deposition is not clear (Jones 1983) and for some species, these repeating patterns may not even represent distinct time intervals (Jones 1981). Hughes and Clausen (1980) also report that increment patterns in shells from the same area and even patterns within the same shell are not always consistant, though increment width 'trends' appear to exist.

Geoduck embryos begin producing a thin protective shell within hours of fertilization (Goodwin 1979). The distinct banding within a geoduck shell corresponds to yearly growth increments (Shaul and Goodwin 1983). While the technique used for aging (cellulose acetate peels) appears reliable and can be accomplished in a fraction of the time required previously to hand grind thin sections, determining population age structure by this method is still quite labor intensive and requires considerable microscopy, particularly for such a long-lived species. In addition to a comparison of shell sizes at different population densities, a relationship between age and shell size was sought, to determine if the potential exists for relatively quick, rough estimates of individual ages.

Methods

To determine size and age structure for the study population, three sites were chosen from which to obtain representative samples. To assess the effects of density on shell size, the highest and lowest density regions encountered were chosen, with the aid of the transect density data.

A 4m x 4m plot was established at each of three locations (labelled I, II and V, in Fig. 3) to isolate areas from which all geoducks were to be removed. The selection of geoducks to be harvested was done in this manner to minimize the possibility of any size or age bias. Each of the three plots was divided into a grid of 16, 1m x 1m squares and all geoducks were located and their positions identified by marker flags. Flags were used to ensure the location and collection of all individuals, as the disturbance due to harvesting greatly decreases visibility and also causes geoducks in the vicinity to retract their siphons (Cox 1979). All geoducks in each plot were then removed. Variance in the number of clams/m^2 was used to statistically compare plot densities.

The equipment and method of collecting geoducks were similar to those of the commercial harvest (Cox 1979), and will only be summarized here. At the surface a 5 H.P. gasoline powered motor was used to drive a water pump, which in turn provided a steady flow of water to a SCUBA diver, by means of a canvas hose. This end was attached to a piece of steel pipe, outfitted with an on/off valve. The whole set-up is commonly referred to as a 'stinger'. The stinger was held in one hand and turned on, while directed at the base of a siphon. Sediment was blown away while contact with the retracting siphon was maintained with the other hand. If the siphon is not extended perfectly perpendicular to the sediment surface, and contact with it is lost, recovery of the geoduck can be quite difficult. The clam can only be removed after the body is reached and dislodged. The whole geoduck was then handed to a diving assistant, along with the corresponding numbered flag. This number was subsequently inscribed in pencil, at least once on the surface of each valve. Harvesting of the entire plot proceeded in this manner.

As these sites were also to be used for nearest neighbour analysis (discussed later), when a geoduck outside any plot was potentially the nearest neighbour of any one within that plot, it too was collected. A total of 269 geoducks were removed from these three plots.

Equality in size and shape of the left and right valves is a basic morphological character used in keys for the identification of bivalve species (Quayle 1960; Kozloff 1974). Measurements for left (n=68) and right (n=65) valves of the geoducks from plot V were compared. Length and height were measured to the nearest 1mm using Vernier calipers. Valves were washed and allowed several days to air dry. Hinge ligaments were then removed and weights were measured to the nearest 0.1gm on a

Mettler P160 balance.

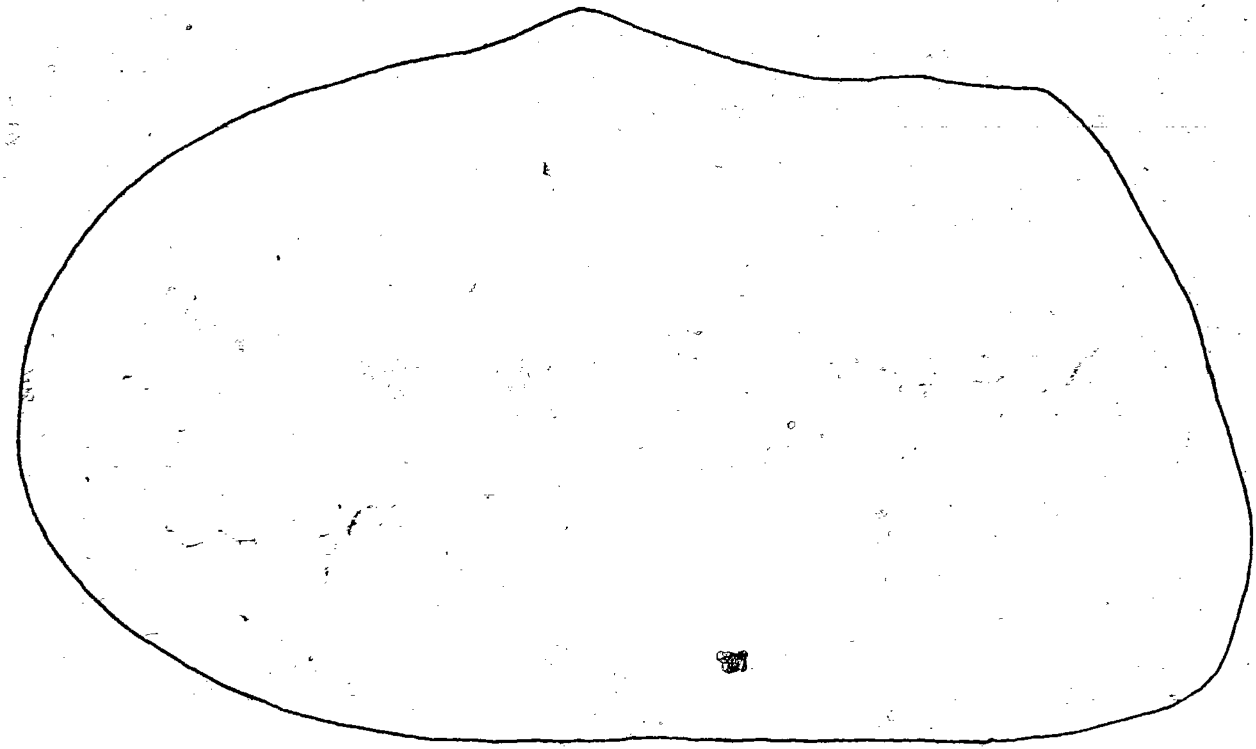
To best describe the valve size of individual geoducks, length and height measurements were combined for each, giving a measure of surface area. Due to the irregular shape of geoduck valves (Fig. 7a), the product of length and height does not adequately represent valve surface area. The shape of a typical valve was broken down into five component areas, each of simple geometric shape (Fig. 7b). Ten geoduck valves were then randomly selected from those obtained from plot V, and the relative dimensions of each subarea were calculated as percentages of length and height measurements. Next, percentages were averaged for the 10 values of each measurement and the following equation was derived to yield a predicted surface area (A_1):

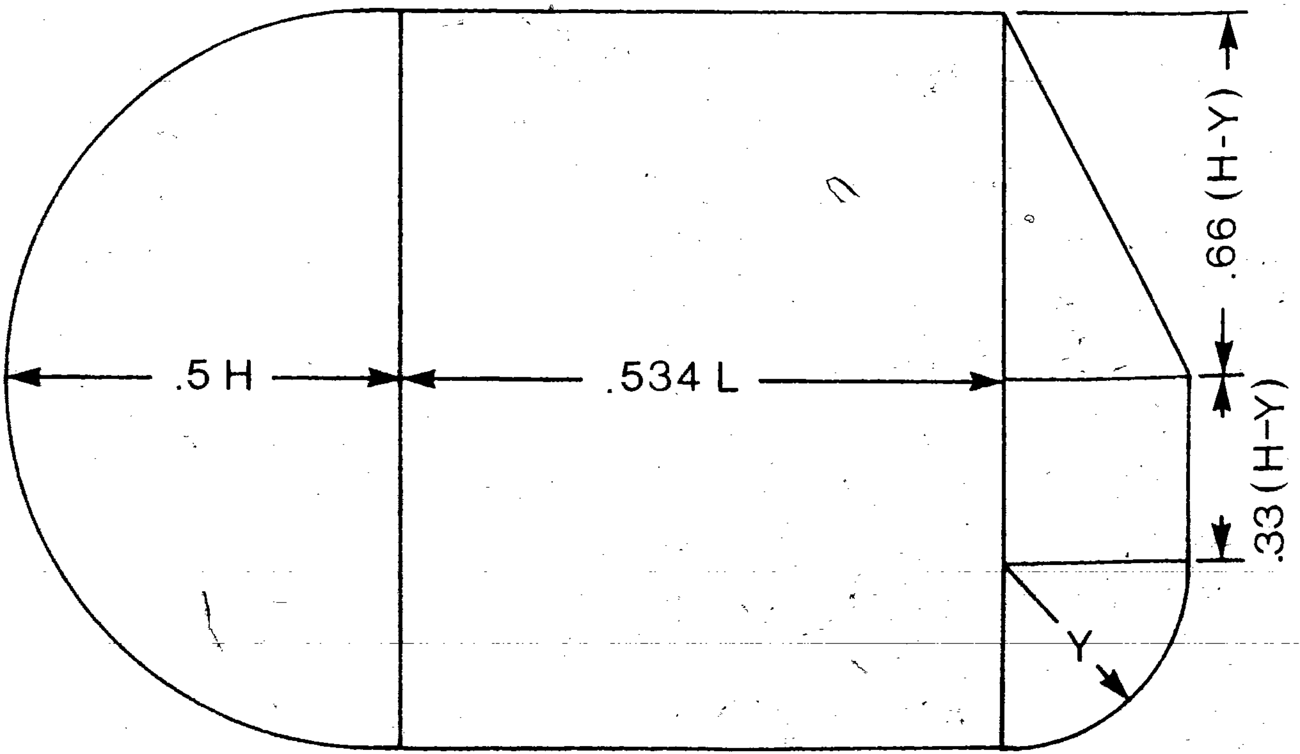
$$A_1 = 1/2\ (\pi \times H^2) + (0.534 \times L \times H) + 1/4\ (\pi \times Y^2) + 2/3\ (H \times Y - Y^2)$$

where L and H refer to valve length and height respectively, π is the constant 3.1416, and Y is a value related to both (see Fig. 7b). A labor intensive but likely more accurate estimate of planar surface area was determined for these 10 valves by the paper-weight method. This consisted of obtaining a 'standard weight' for a known area of paper and weighing a traced, cut-out of the valve, from a similar piece of paper. Area of the cut-out was then calculated using the cut-out/standard weight, ratio.

Figure 7a. Shape of typical geoduck valve (actual size).

Figure 7b. Geometric representation of shell above based on length (L) and height (H) measurements. 'Y' is a dimension with a value related to length and height as indicated.





$Y = L - (.5H + .534L)$

This was termed the 'actual area' (A_2). When predicted area was regressed against actual area, the following relationship was obtained:

$$A_2 = (A_1 - 11.18) / 0.9565 \qquad r=0.9078$$

A measure of planar surface area was calculated for all valves, using these two equations.

The cellulose peel technique has been used in paleontological work for years (Stewart and Taylor 1965) but has only recently been used to observe the internal growth increments of bivalves (Richardson _et al._ 1979; Thompson _et al._ 1980). Peels can be made using either liquid plastic or cellulose acetate. The latter method was employed in this study because of its apparent ease of application and the fact that its product can more easily be worked with and stored.

Since the hinge plate is internal on a live geoduck and thus experiences little abrasion, it is the best area in which to observe the growth rings of a shell. Right valves were sent to a lapidary, where they were cut ventrally through the umbone. The cross-sectional area of the hinge plate from the anterior portion of each valve, was then highly polished and the valves were brought back to the lab. These portions were washed to remove any remaining grit and then set in a modelling clay base to dry. Next, hydrochloric acid (1.5%) was dropped continuously on the polished surface for 35-45 seconds, to 'etch' it by dissolving away the calcium. To stop the etching process, the sample was submerged in a bowl of fresh water. Each valve was allowed to air-dry for a minimum of 20 min. Acetone was then gently dropped on the treated surface until the surface was entirely covered. Using forceps, a small piece (1cm x 1cm) of cellulose acetate (0.005 inch thickness) was immediately lowered into the acetone. Acetone partially dissolves cellulose acetate and with evaporation of the former, the organic matrix of the valve becomes embedded in the molten acetate. After a minimum of 20 min, the film was peeled from the surface to which it had become attached. This was usually done within 24 hours because if left for extended periods, the peel became difficult to remove and resulted in a poor specimen. Occasionally surfaces were treated a second time to obtain another peel if the first was inadequate. With the organic side downward, individual peels were placed on a microscope slide, covered with a coverslip and taped in place. This inhibited deformation of the peel, which occurred after short exposure to the heat from the microscope's light source. Growth increment rings were counted at 40-400x magnification.

The variance in different size measurements between geoducks was such, that a reliable age estimate could not be made based only on a single size measurement. Shell thickness however is a dimension which increases each year, since shell layers are added for the duration of a clam's life.

The inner surface of geoduck valves is often gritty and direct measurement of valve thickness would likely be more a reflection of this characteristic, than age. Rather than attempt to locate a particular region of the shell that had a thickness which was best correlated with age, valve weight was divided by total valve area, to give an average 'weight per unit area'. This value should be a function of shell thickness. The index (of valve thickness) was obtained by multiplying this wt./area value by a factor of 10, to prevent the log of the index from being a negative value. To utilize the data maximally, when both valves were available an average index was calculated.

Results and Discussion

Shell Morphometrics

Shell morphometric data often were not normally distributed (Fig. 8a-c), necessitating the use of non-parametric statistical analyses. There was no significant difference in mean length (p=0.7085), height (p=0.2706) or weight (p=0.6608), between left and right valves (Mann-Whitney U-Test). Left and right valve measurements were highly correlated in all three dimensions (Spearman's rho; p<0.0001; n=65). As a standardization, all other statistics were performed on left valve measurements when they were available. Though a bivalve shell consists of a left and a right valve, the term 'shell' will be used interchangeably with 'valve' unless otherwise specified.

Plot I contained the highest density of geoducks (mean=7.69/m^2) and plot V, the lowest (mean=4.00/m^2). Mann-Whitney U-tests indicated that the density of plot I was significantly greater than that of plot II (mean=5.13/m^2; p=0.0255), but plot II did not differ significantly from plot V (p=0.2606). A comparison of plot density and shell dimensions for the three plots appears in Table 5.1. Figure 8(a-c) contains histograms of shell length, height and weight, for each plot.

Table 5.1 Plot Density and Shell Measurements in Decreasing Order of Size.

Variable	Plot#	Signif.	Plot#	Signif.	Plot#
Density	I	0.026(*)	II	0.261	V
Weight	II	0.759	I	0.189	V
Length	V	0.012(*)	I	0.000(***)	II
Height	V	0.219	I	0.033(*)	II
Area	V	0.103	I	0.000(***)	II

If geoducks do exert a density dependant influence on the shell production of nearby conspecifics, then there are several ways in which this may be manifest. Comparison of valves was based on several dimension measurements. Total shell produced ie. valve weight, indicated no significant difference between plots (Kruskal-Wallis: p=0.4117). Total energy spent on shell production was therefore concluded to be similar for geoducks from all three densities.

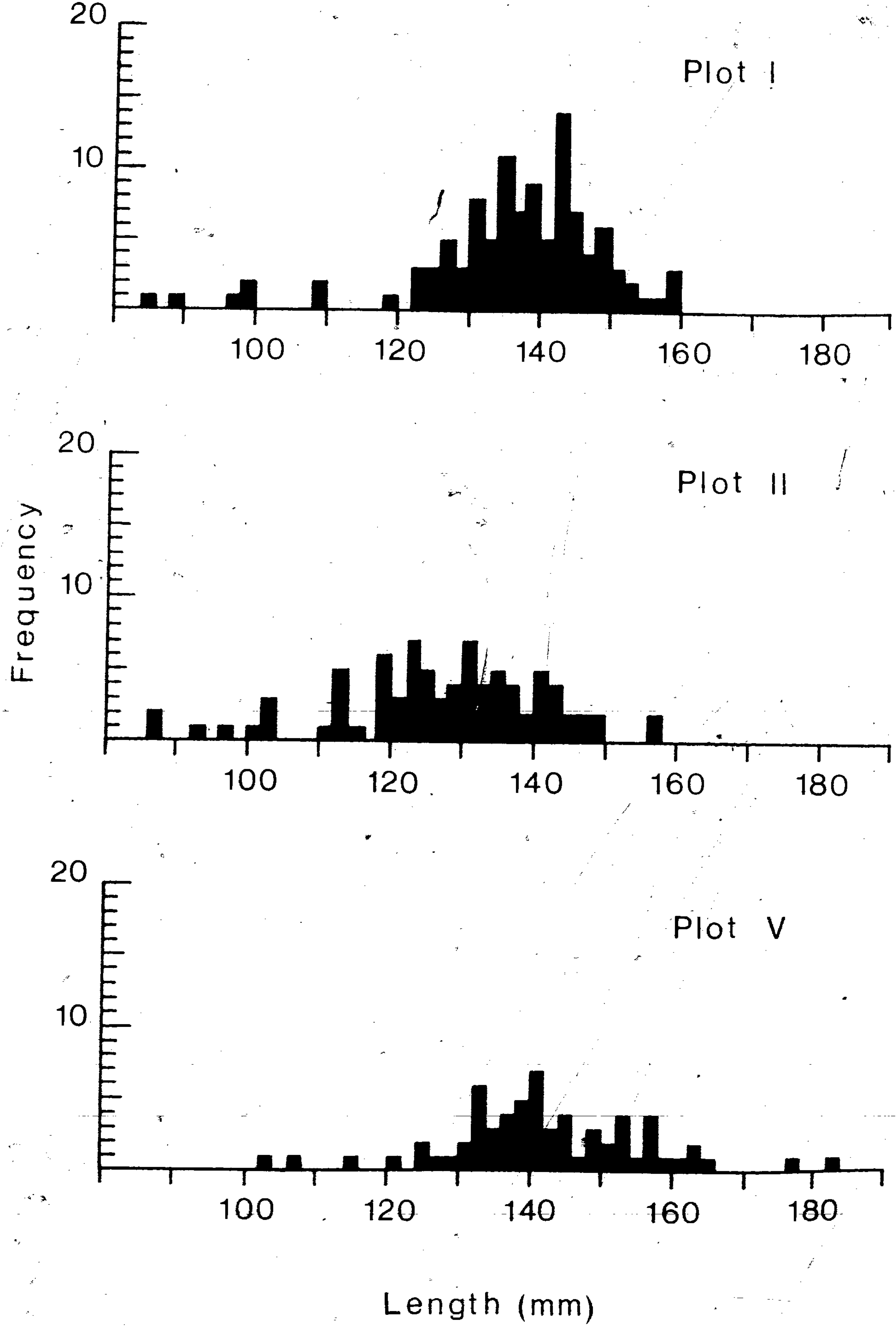
Plot comparisons (Mann-Whitney U) using shell length, showed that plot V valves were significantly larger (mean=143.0mm; p=0.0122) than those in plot I (mean=136.8mm) and geoducks from the latter plot were significantly larger (p=0.0000) than those from plot II (mean=127.9mm). The null hypothesis, that geoducks from each plot do not differ in size as determined by length measurements, was rejected.

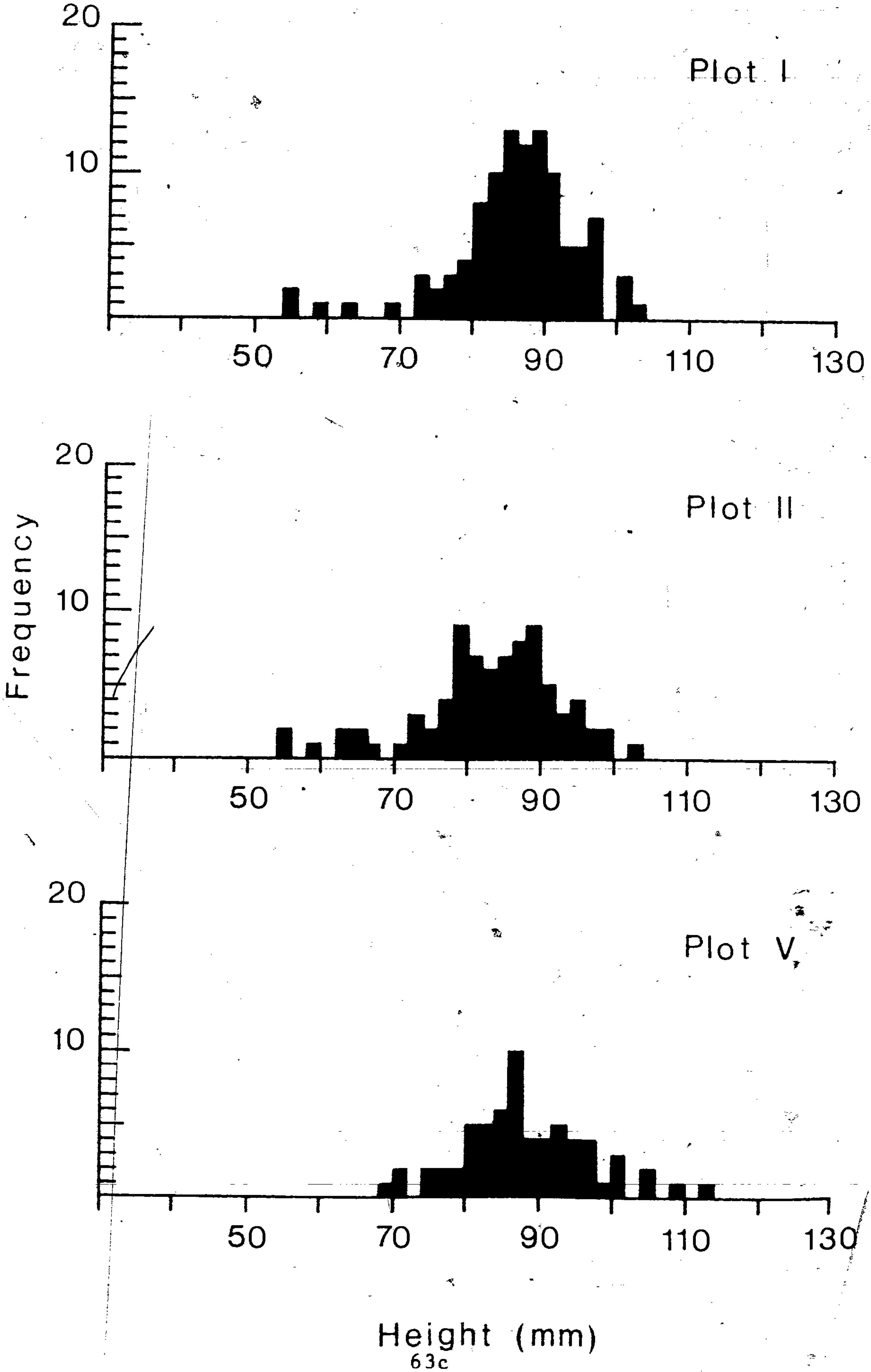
Shell heights were similarly compared and the same order of relative heights was found: plot V (mean=88.9mm) > plot I (mean=86.4mm) > plot II (mean=83.6mm). The difference between plots V and I however, was not significant (p=0.2189).

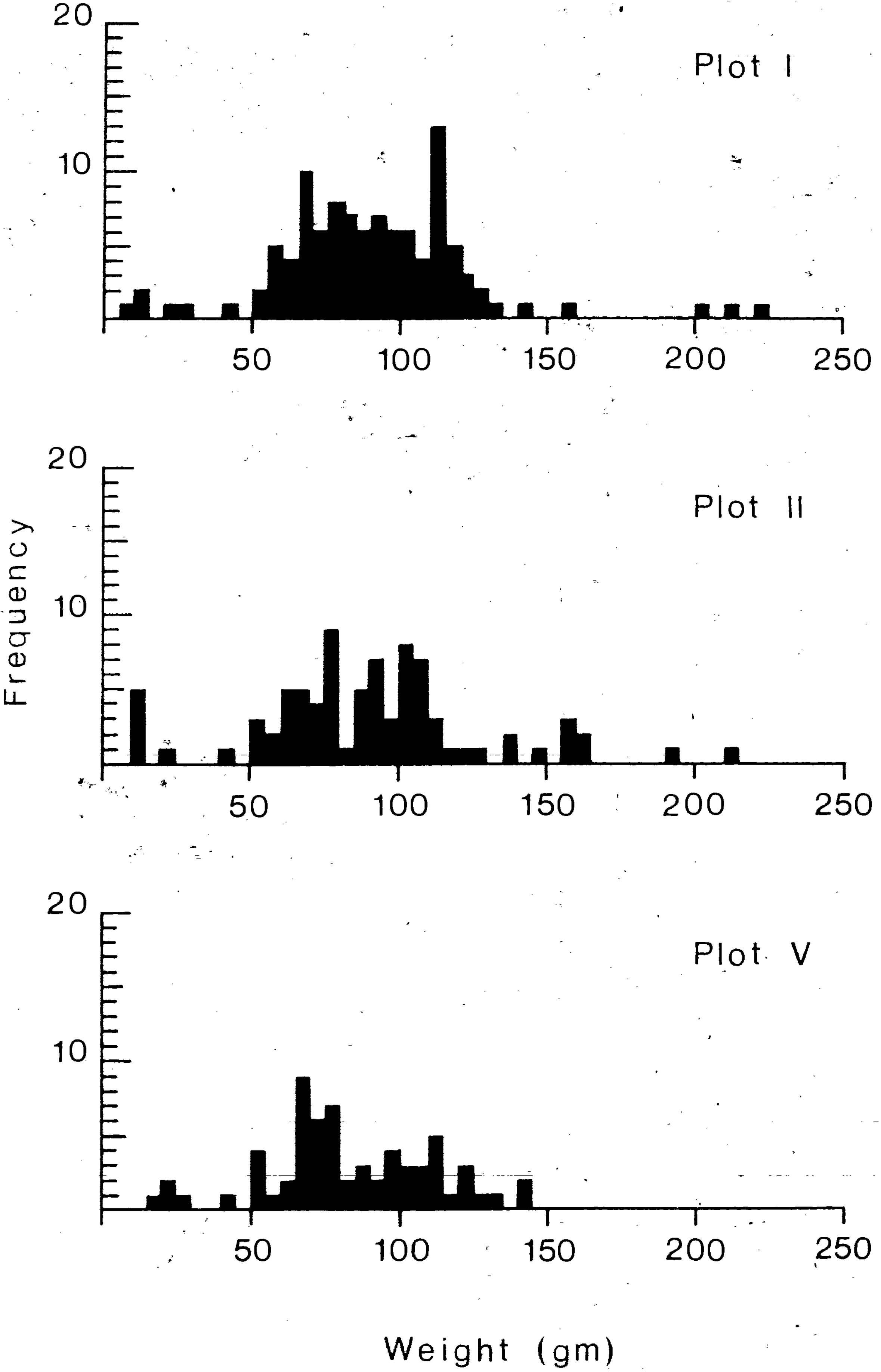
The three plots were then tested for differences in valve size measured as planar surface area. Geoducks from plot V were not significantly larger than those from plot I (p=0.1029) but both plot V and plot I contained larger geoducks than did plot II (p<0.0001 and p=0.0001). As length and height were both used to calculate this variable, area was probably a better measure of shell size than length or height separately.

A potential source of error lay in the assumption that the observed relative densities of these plots had remained the same for several years. Should this have not been the case, observed (present) density would likely have little bearing on shell dimensions, particularly since most growth occurs within the first 8 to 10 years. The mean age of each plot was considerably greater than this and so most growth had occurred many years earlier. To best observe relative growth over the most recent past and thus more directly evaluate the possibility of a relationship existing between shell size and present density,

Figure 8a-c. Histograms representing for each plot: length, height and weight.


20
Plot I
10
100
120
140
160
180
20
Plot II
Frequency
10
100
120
140
160
180
20
Plot V
10
100
120
140
160
180
Length (mm)


Plot I
20
10
50
70
90
110
130
Plot II
20
10
50
70
90
110
130
Frequency
Plot V
20
10
50
70
90
110
130
Height (mm)


20
10
Plot I
50
100
150
200
250
20
10
Plot II
Frequency
50
100
150
200
250
20
10
Plot V
50
100
150
200
250
Weight (gm)

mean sizes of the youngest age-class (4 years) were compared (Table 5.2). The mean valve surface area was also smallest for the young geoducks from plot II and largest for those from plot V. Due to the small sample sizes (n=3-5), two-sample statistical analyses could not be performed but the multisample Kruskal-Wallis test indicated that a significant difference existed between the samples considered (p=0.0483). Separately, length and height dimensions of young geoducks exhibited the same relative size relationship between plots, as did the dimensions of whole plots, but only differences in height were statistically significant (p=0.0232).

Table 5.2 A Comparison of the Mean Size Measurements of 4 Year Olds From Plots I, II and V (Kruskal-Wallis Tests).

Plot #	I	II	V	Significance
Area (cm^2)	51.9	40.3	64.0	p=0.0483
Length (mm)	103.8*	94.0	113.0	p=0.0610
Height (mm)	63.0	59.6	72.3	p=0.0232
Weight (gm)	16.9	12.5	22.2	p=0.0537
N	3	5	4	

* n=4

In summary, when all members from the three plots were considered, geoducks did not differ in mean shell weight. When valve sizes were compared on the basis of surface area, geoduck shells from plots I and V did not differ (p=0.1029), even though these plots represented extremes in geoduck density (over the range observed). Shells from plot II, which represented an intermediate density, were smaller than those of the other two plots and the difference was always highly significant, regardless of how size was measured. When young geoducks were isolated from each plot and similar analyses performed, the same size differential was observed, indicating that whatever stunted the growth of geoducks from plot II, 30-40 years ago, it was still present, and its effects became apparent in juveniles, by the age of 4yr. Population density and geoduck size do not appear to be related in any way.

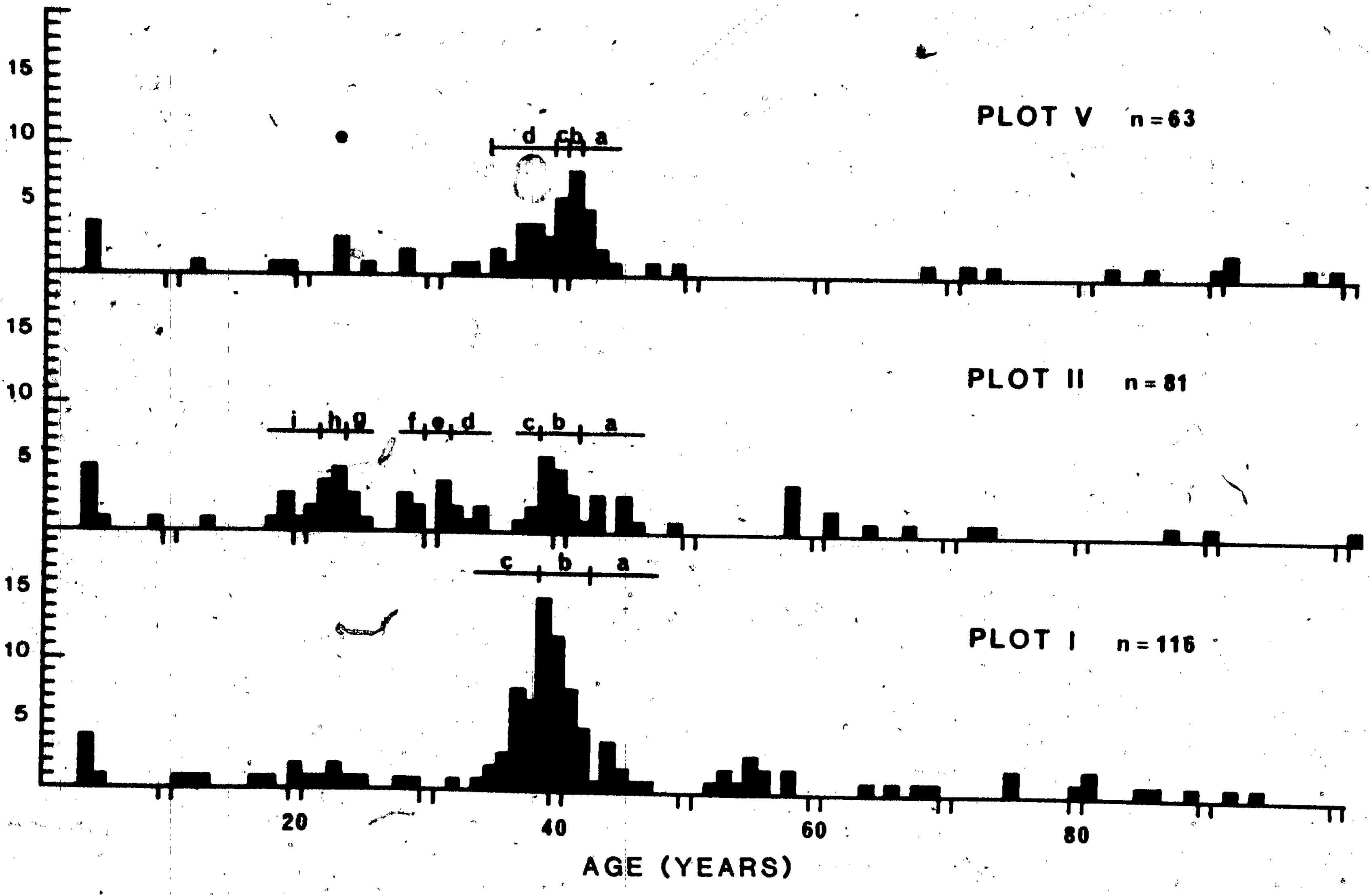
In the following chapter on population dispersion, conspecifics are shown to have had some influence on shell size but the relationship is not a simple function of density.

Shell Size and Age

Population age structure data, as determined by the cellulose acetate peel technique, appears in Figure 9. Ages could not be determined for seven geoducks from plot I and for one from each of the other plots. The age group into which each geoduck was placed was based on the age of that clam in 1981. No geoducks <4yr old were found.

It should be noted that an individual with, for example, 10 growth bands, corresponding to 10 growing seasons, was classified as a 10yr old. Some authors prefer to label such individuals as 9yr olds, assigning those with one band to a '0+' catagory.

Figure 9. Population age structure of plots I, II, and V. Each unit represents one individual of a given age. Changes in population dispersion patterns are indicated by labelled bars above each histogram, and are discussed in Chapter VI.

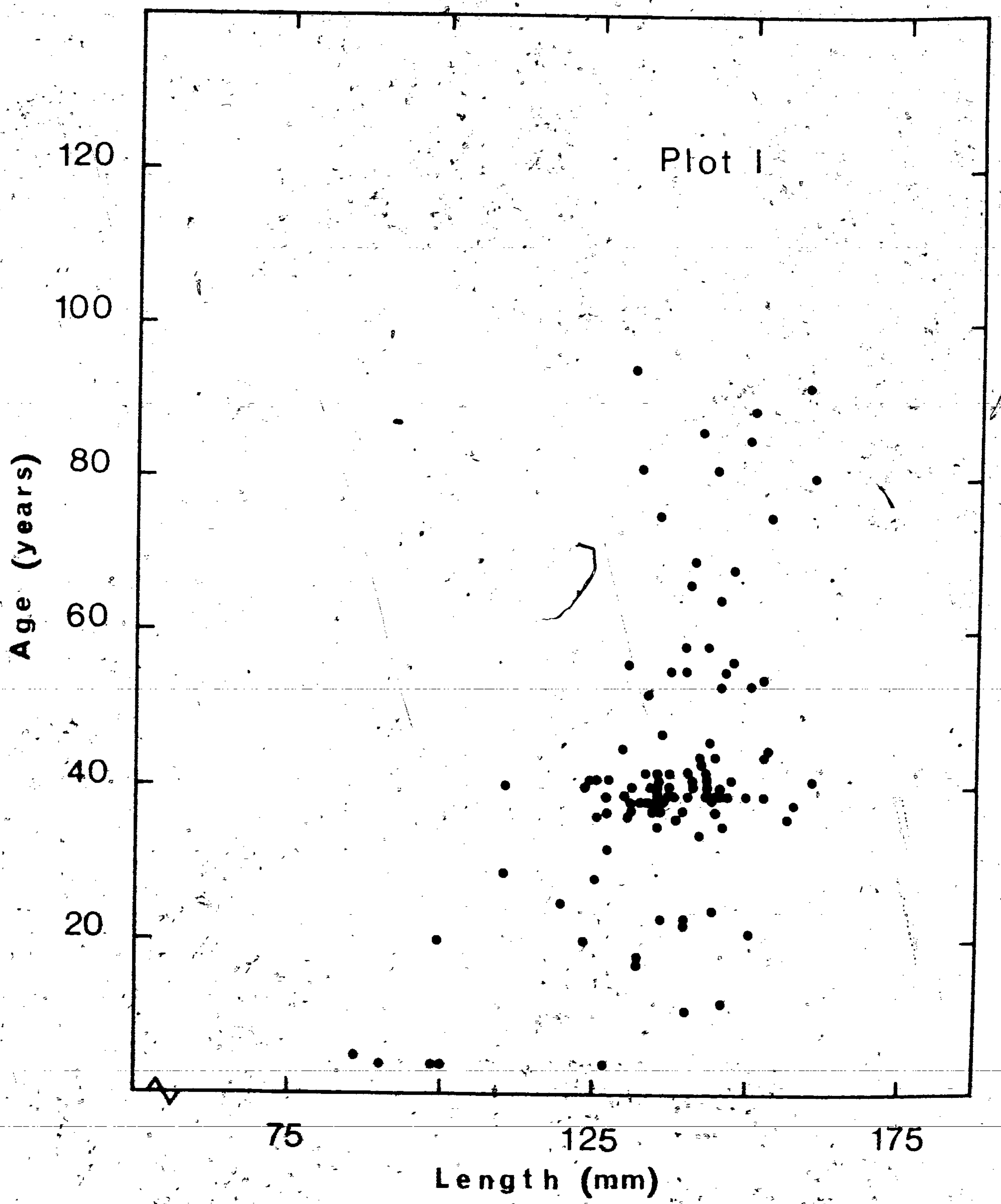

PLOT V n = 63
d ch a
PLOT II n = 81
i h g f e d c b a
PLOT I n = 116
c b a
15
10
5
15
10
5
15
10
5
20
40
60
80
AGE (YEARS)

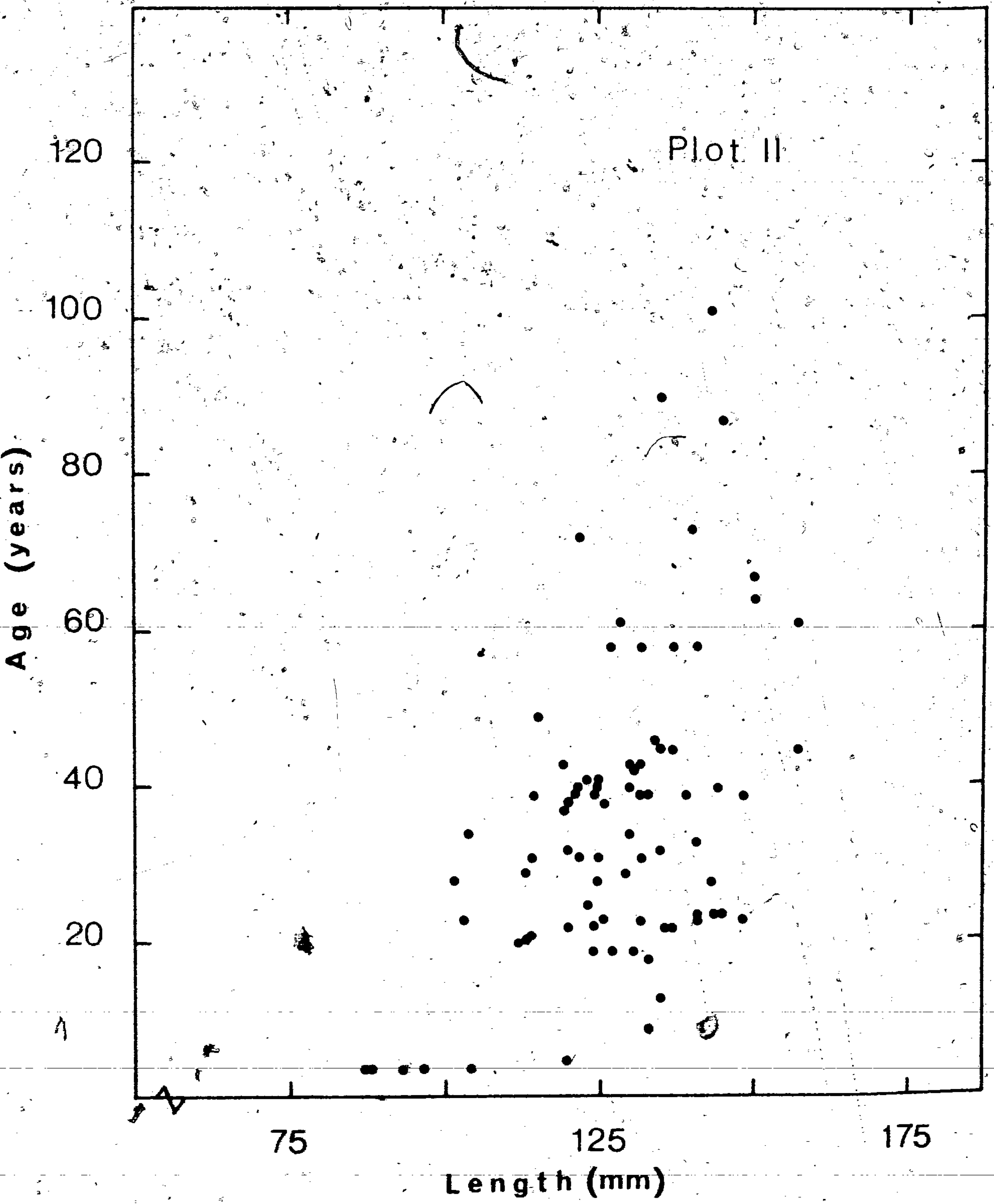
Certain years do not appear to have had any recruitment at all, however there are insufficient data to be certain of this. Wendell et. al. (1976) noted that certain age-classes of horseclams *Tresus capax* were abundant at one location and negligable only 300m away. A similar situation is noted when comparing the 20-25yr old geoducks in each of the three plots. The 35-45yr age-classes however, appear very strong in all three plots. The extremely small number of young geoducks present at the time of this harvest would not be able to produce this population age structure, which indicates that recruitment is not consistant from year to year and that recently, it had been extremely low in this area.

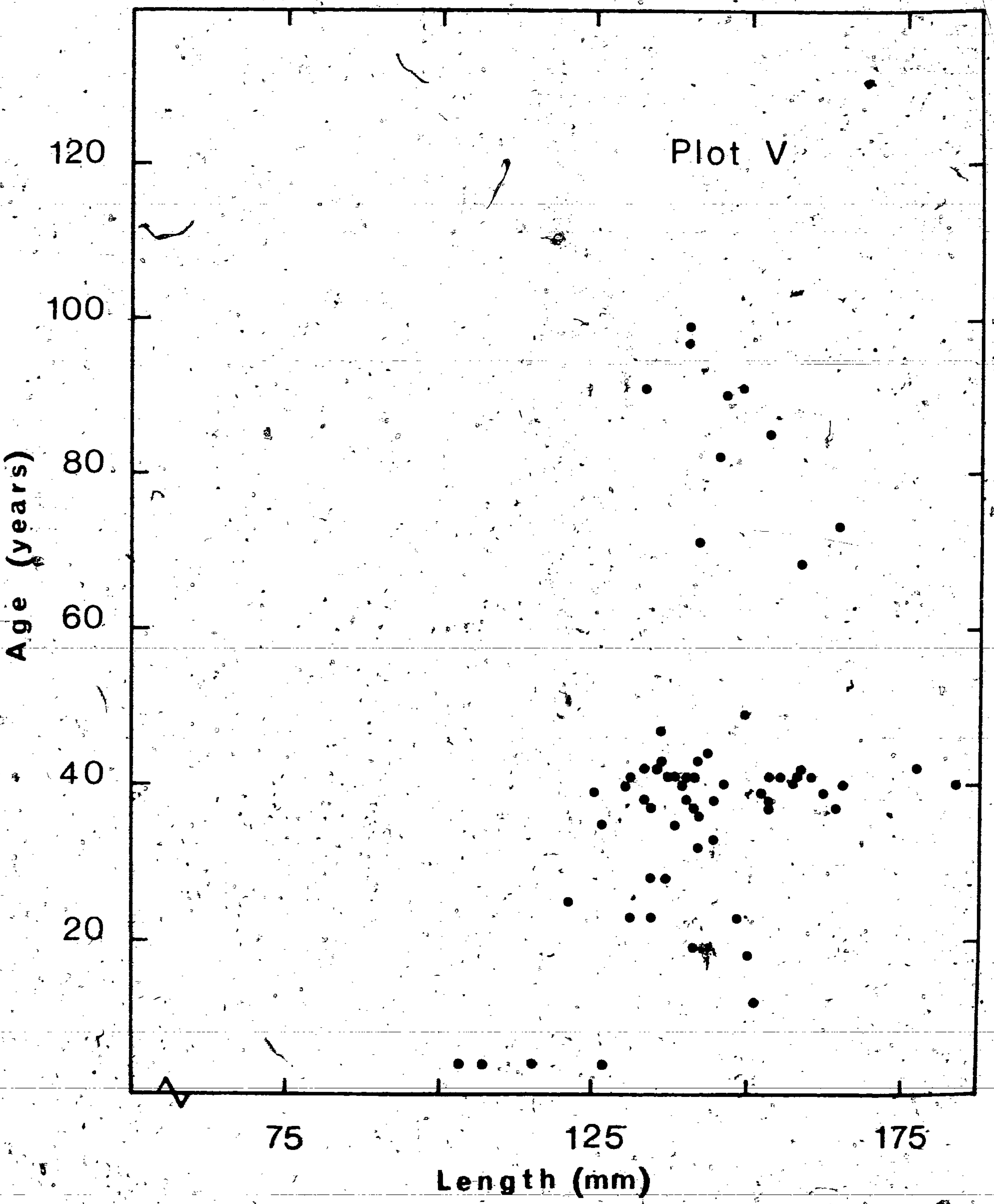
The relationship between length and age, for plots I, II and V, appears in Figure 10(a-c). Correlation between the two is highly significant (Spearman's rho=0.4178; p<0.0001). Height and age are similarly correlated (rho=0.4865; p<0.0001), as are surface area and age (rho=0.4769; p<0.0001). This however, only confirmed that young geoducks were small and old geoducks were large. From Figure 10 it can be seen that an estimate of age based on valve length, would be imprecise. Height measurements are equally poor in this respect.

Beyond 8 to 10 years, increase in size is minimal and may stop altogether when clams get older. As Andersen (1971) observed, the body cavity formed by the valves was often smaller in older geoducks. Abrasion of the unmaintained valve edges (termed recession), can result in the oldest geoducks being

Figure 10a-c. Relationship between geoduck age and total shell length, for plots I, II, and V.


Plot I
120
100
80
60
40
20
Age (years)
75
125
175
Length (mm)


Plot II
Age (years)
120
100
80
60
40
20
75
125
175
Length (mm)


Plot V
120
100
80
60
40
20
Age (years)
75
125
175
Length (mm)

smaller than those of an intermediate age. The recently developed ability to age geoducks with greater accuracy, has proven that earlier estimates of mean age were much too low and so Andersen's estimate of the age at onset of shell recession (20yr), is understandably low. The data in Figure 10 do not clearly indicate that shell recession is occurring at all, and this phenomenon may in fact be restricted to habitats where sediment particles are larger and more abrasive.

Geoduck age and the established index of shell thickness were related in a non-linear manner. Data transformations which are commonly applied in regression analyses, were used to simplify and permit description of this curvilinear relationship (Sokal and Rohlf 1969). Regression analyses were performed on pairs of data expressed in the following manner:

age vs. index
log(age) vs. log(index)
log(age) vs. index
age vs. log(index)
age vs. index^2 + index

As data which were log-log transformed fit a linear relationship better (highest correlation coefficient) than any of the other forms in which the data was expressed, the age/index relationship could be best described by the formula:

$$Y = 10^{(\log A + (B \times \log X))}$$

which is commonly known as the allometric growth curve.

Substituting age and index for Y and X respectively:

$$\text{age} = 10^{(\log A + (B \times \log(\text{index})))}$$

Correlation coefficients (r) for log(age) with log(index) were found to be: 0.871, 0.919, and 0.911, for plots I,II and V respectively. Corresponding coefficients of determination (r^2) were: 0.758, 0.844, and 0.829, thus 76%-84% of the variability in log(age) could be accounted for by the following linear relations with log(index), as determined by regression analysis:

Plot I: $\log(\text{age}) = (-0.1408) + 1.8295 \times \log(\text{index})$

Plot II: $\log(\text{age}) = (-0.2007) + 1.7257 \times \log(\text{index})$

Plot V: $\log(\text{age}) = (-0.4840) + 2.3329 \times \log(\text{index})$

A strong relationship exists between geoduck shell dimensions and age. To obtain a measure of the universality of these relationships, the three regression equations were compared by a one-way analysis of covariance. These equations were dissimilar, due to highly significant differences in their slopes ($p=0.0006$).

Differences in shell thickness for geoducks of a given age from different parts of the same bay, are sufficiently large to require knowledge of the age/size relationship of an area before age estimates can be made with confidence.

While y-intercepts are included in all three equations, that of the first is not significantly different from zero. In theory none should be different from zero since at age '0', the index of shell thickness should also be zero. The cause of this discrepency is apparent in Figure 10. Based on the available data points, a regression equation relating length and age, would not be expected to pass through the origin due to the lack of small individuals. Since the index of thickness is partially derived from these data, it also suffers from this problem. An equation relating log(age) and log(index) was then calculated such that it passed through the origin. This proceedure is frequently employed with growth curves, where the size of a structure is effectively zero at age zero (Sokal and Rohlf 1969). The following equations were derived as modifications to those listed above:

Plot I: $\log(\text{age}) = 1.6820 \times \log(\text{index})$

Plot II: $\log(\text{age}) = 1.5237 \times \log(\text{index})$

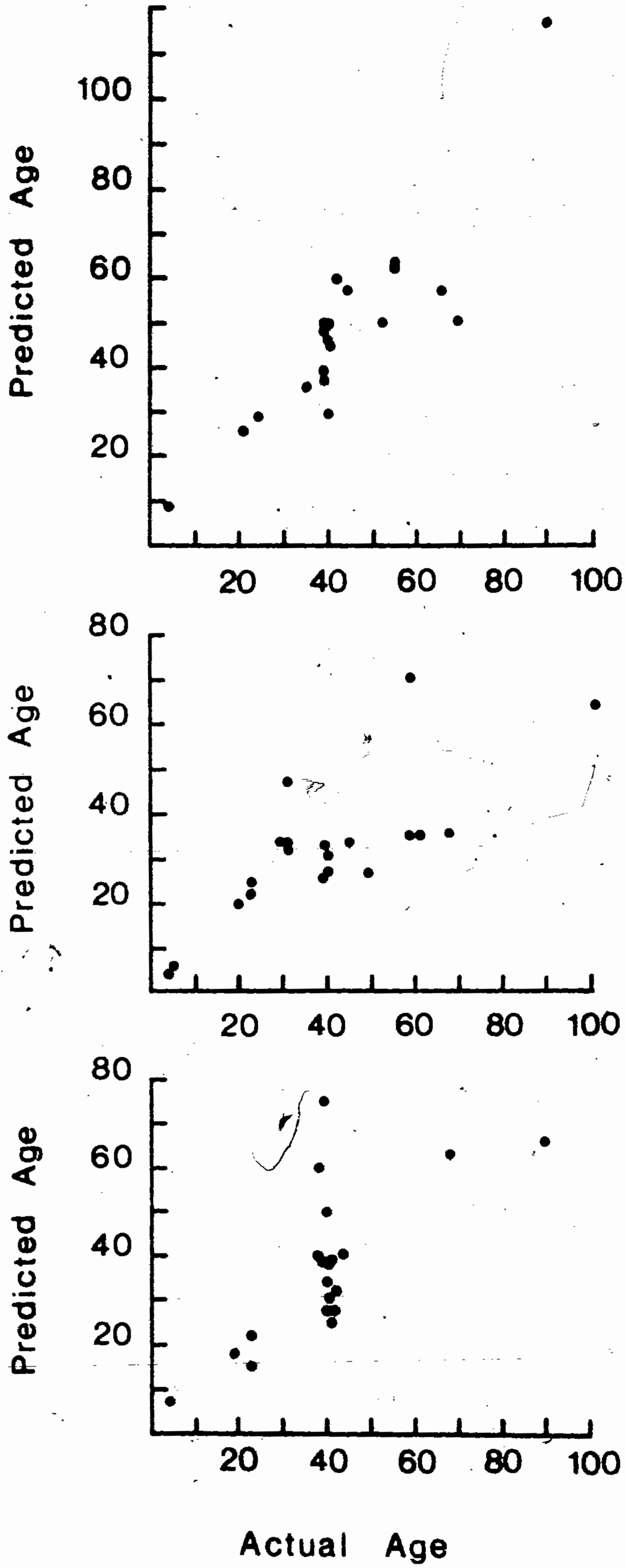
Plot V: $\log(\text{age}) = 1.7873 \times \log(\text{index})$

Equations of this form may have better potential for use in predicting rough estimates of a geoduck's age, based on a few shell parameters. The nature of regression analysis is such that confidence limits form a 'biconcave belt' around the regression line. This is due to both uncertainty about the true slope of the regression line and the requirement of regression analysis that the line pass through mean X and Y values (Sokal and Rohlf 1969). Consequently, strength of these relationships can not be expressed as a predicted age, plus or minus a constant number of years.

To demonstrate the applicability of this shell size/age relationship, and provide some indication of its reliability in years, the data were treated in the following manner, for each plot. Thirty geoducks were randomly chosen from a plot and a log(age)/log(index) relationship was developed through regression analysis. A second equation was then derived for that plot, with the stipulation that the line pass through the origin. Each of the two equations was used to predict the age of those 30 geoducks. A regression analysis was performed to assess which best predicted age. Only for plot II did regression through the origin yield a better age prediction. Twenty other geoducks were then randomly selected from among those remaining from each plot. The equation which was previously derived for that plot was then used to predict the age of each of these 20 geoducks. Correlation coefficients for predicted and actual ages, for plots I, II, and V were 0.8791, 0.7741, and 0.7141 respectively. These relationships appear in Figure 11. One or two points considered for plots II and V appear to be responsible for greatly lowering the correlation coefficients for these plots.

Knowledge of the age and shell dimensions of as few as 30 geoducks from a particular area could therefore be used to

Figure 11. Relationship between predicted and actual age of 20 randomly chosen geoducks from each of plots I, II and V.


Predicted Age
100
80
60
40
20
20
40
60
80
100
Predicted Age
80
60
40
20
20
40
60
80
100
Predicted Age
80
60
40
20
20
40
60
80
100
Actual Age

predict the ages of others in that area, provided that this level of confidence was acceptable. Increasing the number of geoducks for which age and shell dimensions are known would likely increase predictive ability. By increasing the number of geoducks for which age is predicted, the influence of 'outliers' would be reduced, thus increasing the correlation coefficients obtained.

VI. Population Dispersion

Throughout the study area in Ritchie Bay, environmental conditions were relatively homogeneous and geoducks appeared to be the most abundant macroinvertebrate present. Pielou (1960) states that in a habitat which is otherwise relatively homogeneous, most environmental variability may be due to the obvious heterogeneity caused by conspecifics. This location was therefore considered appropriate for studying the influence of geoducks on the dispersion of conspecifics.

Dispersion patterns are usually placed into one of three general catagories. Inference based on these patterns will be confined to that of broadcast spawners, in a relatively homogeneous environment. The catagories are as follows: (1) Clumping (aggregation), by far the most common pattern type (Pielou 1960), indicates an overall positive association. One of two general processes can bring about a clumped dispersion: (a) active attraction to others, which requires the ability to recognize either conspecifics (Knight-Jones 1951; Hidu 1969; Bayne 1969) or associated micro-organisims (Woodin 1976) or, (b) enhanced survival of individuals occurring in close proximity (Highsmith 1982). (2) Random dispersion, which is relatively rare, is by definition, one in which the location of each individual has no influence on the location of any other. (3) Uniform (regular) dispersion is extremely rare (Pielou 1960) and is evidence of a negative association, often present as stress due to severe competition or antagonism (Greig-Smith 1964). In a manner similar to the mechanism which creates clumping, uniform dispersion can result from either of the following (Williams 1980) (a) active avoidance of others (Knight-Jones 1951), or (b) reduced survival of conspecifics in close proximity (Woodin 1976).

Given the above conditions, a population of gregarious organisms which had existed at a low density without being disturbed for a period of time, would be expected to exhibit an aggregated dispersion pattern. Furthermore, if the organism was sessile and incapable of horizontal movement, several years of highly successful settlement (strong year class representation) may result in a dense population with intense intraspecific competition, and this would be apt to produce a uniform dispersion pattern. Since the change from an aggregated pattern to a uniform one occurs as a transition, at some point the establishment of recruits in a uniform pattern will likely create a dispersion which appears random. In fact however, it would actually consist of juveniles which are uniformly dispersed and adults which remain aggregated, since the original members are assumed to be incapable of movement. Dispersion analysis attempted during this transition, which may exist over a period of several years, would indicate a high density population exhibiting random dispersion. It is only with continued recruitment in a regular pattern, that the overall pattern would eventually become uniform. Conversely, a high density, uniformly dispersed population may undergo a period of substantial mortality, which is random with respect to individual positioning. This would leave the population uniformly dispersed, but with a relatively low density.

In either of these situations, the standard use of dispersion patterns to make inferences regarding conspecific interaction, would be inappropriate. The only individuals to be dispersed relative to each other and thus reflect the present level of competition or antagonism, would be those which had entered the population since any such changes in population structure occurred.

With this in mind, a dispersion index for adult geoducks alone was calculated and compared with that of the total population in that plot, permitting an indirect assessment of juvenile dispersion. Sensitivity to recent changes in dispersion pattern was thus increased. Carrying this one step further, an index of dispersion was calculated several times for all three plots, each time omitting increasingly larger (older) groups of the youngest individuals. In this manner, a time-series of dispersion indices was created for each plot. Previous such use of dispersion indices does not, to my knowledge, appear in the literature and is being proposed here as a method for utilizing field-collected data to see (1) if an influence by conspecifics on recruit location can be detected and (2) how this influence is manifest.

Should mortality rates be relatively high, then these indices may have little bearing on past dispersion patterns and thus provide little information on conspecific influence. Mortality however, is estimated to be quite low (0.01-0.05) and similar for all ages (Goodwin unpublished), except possibly the first year classes (Breen and Shields 1983). The high mortality rate noted while monitoring siphon shows occurred in the other end of the bay and did not appear related to position. If a similar level of non-position-related mortality also occurred where dispersion analysis was conducted, its only likely effect would be to increase overall randomness and thereby decrease the probability of detecting significant deviations from random dispersion. For this work, little emphasis was placed on precise identification of the extent to which dispersion deviated from randomness.

Methods

The three established 4m x 4m plots used in morphometric studies were also used to observe geoduck dispersion patterns. Transect survey data was utilized to select the best potential location for three additional 4m x 4m plots. Extremes in geoduck density were required to best observe any effect that density may have on dispersion. The relative location of all plots appears in Figure 3.

Prior to harvesting (plots I,II & V), each of the six plots was overlaid by a grid which divided it into 16, 1m x 1m squares, labelled A-P (Fig. 12). All squares were carefully examined for geoducks and when found, each was tagged in the manner previously described. Using a portable 1m x 1m quadrat, which was subdivided into four quadrants, the location of the center of each siphon was then measured to the nearest 1.0cm.

Analysis of Dispersion Patterns

Usually, distinguishing between the dispersion catagories of clumping, randomness and uniformity is not possible by observation alone. Many statistical methods exist to analyse dispersion patterns and assign them to one of these three catagories. Such tests generally provide a basis for deciding whether or not an observed pattern differs sufficiently from a random distribution, to assume some type of interactive effect. Obtaining a significant difference does not however prove interaction. Feller (1943), concluded that clumping or contagion could not be determined by dispersion alone, but that it was also necessary to consider how dispersion changed with time. An attempt to incorporate this time aspect into analysis of observed geoduck dispersion patterns will be discussed later.

Pielou (1977) separates the dispersion analysis of sessile, sedentary organisms into three, "..wholly different set-ups..". Two differ, based on whether habitable sites are discrete or continuous. The third is used when individual members of the population are not clearly delimited. The use of quadrats which are scattered randomly, is the most commonly employed method of assessing distribution in a continuum, as was the case here. Quadrats were employed earlier, in conjunction with transect lines, to observe overall geoduck distribution in the study area. In discussing those data, two major flaws associated with quadrats were noted, as were the attempts which were made to minimize their effects. While the method lends itself well to an overall analysis, it was considered to be inappropriate for the detail of pattern analysis sought here.

There are two distinct aspects to a pattern, which are referred to as 'intensity' and 'grain' (Pielou 1977). Intensity refers to the extent to which density varies from place to place. The grain of a pattern is a function of the size of the areas occupied by different densities. Grain and intensity are independant of one another. Measuring distribution with a single quadrat size provides only information on intensity. A series of quadrat sizes are required to assess grain.

Distance or plotless sampling consists of several different methods of analysis which avoid some of the problems associated with quadrats. Random-point to nearest-individual measurements are influenced by both intensity and grain (Pielou 1959). I considered the Nearest Neighbour method (Clark and Evans 1954) most appropriate for this analysis of geoduck dispersion patterns as it measures only the intensity of a pattern and is considered the best index for intra-clump dispersion (Pielou 1959, 1977). The two major draw-backs of this method are the very troublesome field-work involved in selecting individuals at random, and the inherent errors that arise from estimating density. By recording the location of all individuals within pre-defined plots, both problems were avoided.

The index obtained (R) is a ratio of the observed mean nearest neighbour distance to the expected mean nearest neighbour distance for randomly distributed points. The error inherent in using randomly distributed points rather than circles of a definite diameter was recognized by the original authors but only recently has a correction method been suggested (Simberloff 1979). For many populations, the relative area occupied by individuals is so small that they can be treated as points, but this is not the case for geoducks.

The dispersion index used here, considers the mean expected distance for randomly distributed circles of a diameter equal to the mean siphon diameter. The most appropriate diameter may well be larger and related to either cross-sectional body size or the area influenced by siphonal water currents. Lacking such information, the smallest dimension that should be used to modify classical nearest neighbour analysis should be mean siphon diameter. This corrected index will be labelled 'Rd'.

As was recommended by Clark and Evans (1954), if the nearest neighbour of a given individual lay outside the plot, its position was also recorded and used in calculations.

One minor problem associated with employing a plotless technique to a pre-defined plot, is that some individuals may lie with their centers exactly on a boundary line. As a standardization, prior to analysis it was decided that all geoducks lying on the P-M-D boundary (Fig. 12) would be considered within the plot, while those on the P-A-D boundary would be considered outside the plot.

Results

The density and associated index of dispersion (Rd) for each plot appears in Figure 13. Table 6.1 contains this data as well as R-values, to allow comparison of the two. The general type of dispersion pattern, as determined by R-values ($p<0.05$), is also noted. R-values of 0, 1 and 2.15 represent maximum aggregation, randomness and maximum uniformity, respectively (Clark and Evans 1954). As suggested, the significance of departure from the expected mean nearest neighbour distance was calculated by the following equation:

$$c = (r_1 - r_2) / \sqrt{\sigma_2}$$

where r_1 and r_2 are respectively the actual and expected mean nearest neighbour distances, σ_2 is the standard error of r_2 ($=0.26136 / \sqrt{(N \cdot \rho)}$), N is the number of distance measurements made and ρ is the population density. Values of ±1.96 and ±2.58 for c, represent the 5% and 1% levels of significance, respectively. It should be noted that when Simberloff's (1979) modification is used (Fig. 13), the overall dispersion of plot I is no longer significantly uniformly dispersed ($p>0.05$).

As previously discussed, the influence of conspecifics on recruit location and the relationship between a particular density and an observed dispersion pattern can be more closely examined by observing how the young are positioned relative to the rest of the population. In Figure 14, indices of dispersion (Rd) appear for several age groups, allowing observation of the similarities between plots at different times in the past. These graphic representations have been separated vertically in Figure 15 to illustrate differences which are unique to each plot.

Table 6.1 Indices of Dispersion for Plots I - VI

Plot No.	No. of Clams	Geoduck Density ($/m^2$)	Mean N.N. Dist.	Index R	Pattern (based on R)	Index Rd
I	123	7.69	18.8	1.1002	Uniform	1.0560
II	82	5.13	22.8	1.0303	Random	1.0016
III	75	4.69	24.5	1.0394	Random	1.0163
IV	86	5.38	23.8	1.1048	Random	1.0727
V	64	4.00	25.6	1.0231	Random	1.0004
VI	89	5.56	21.6	1.0168	Random	0.9862

No geoducks younger than four years old were found, therefore all geoducks for which age was determined, were included in the '4+' age catagory. Since ages could not be determined for a total of nine geoducks, slight discrepencies exist between indices for the '4+ yr' age group and the '0 years' age group (index for total population).

Figure 12. Labelling of plots.

Figure 13. Geoduck density vs. corrected indices of dispersion (Rd), for plots I-VI. In a random dispersion Rd=1. Values above or below this indicate more uniformity or more aggregation, respectively. The dashed line represents the 95% confidence level for uniform dispersion over a range of densities.

M	L	E	D
N	K	F	C
O	J	G	B
P	I	H	A

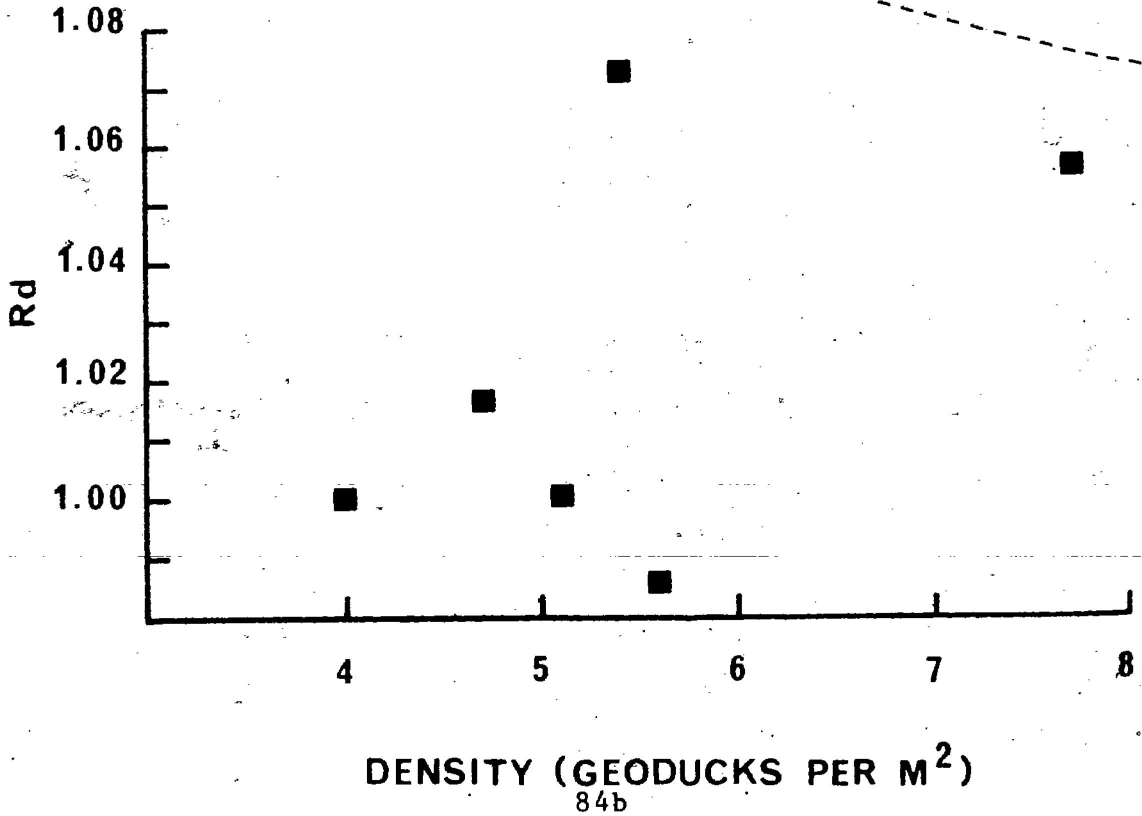


Figure 14. Dispersion indices (Rd) for plots I, II and V, expressed in a time-series manner, showing similarities between plots.

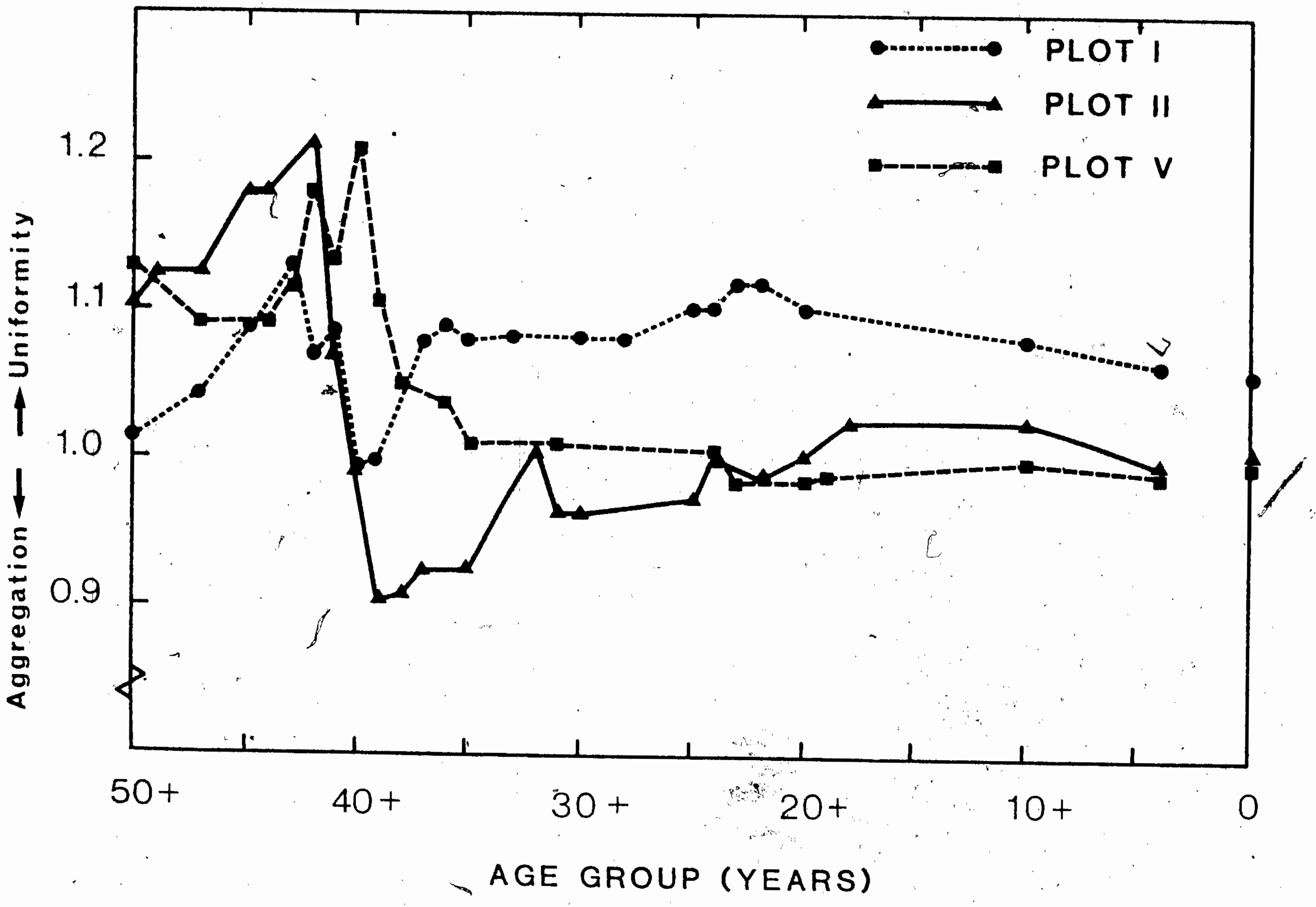
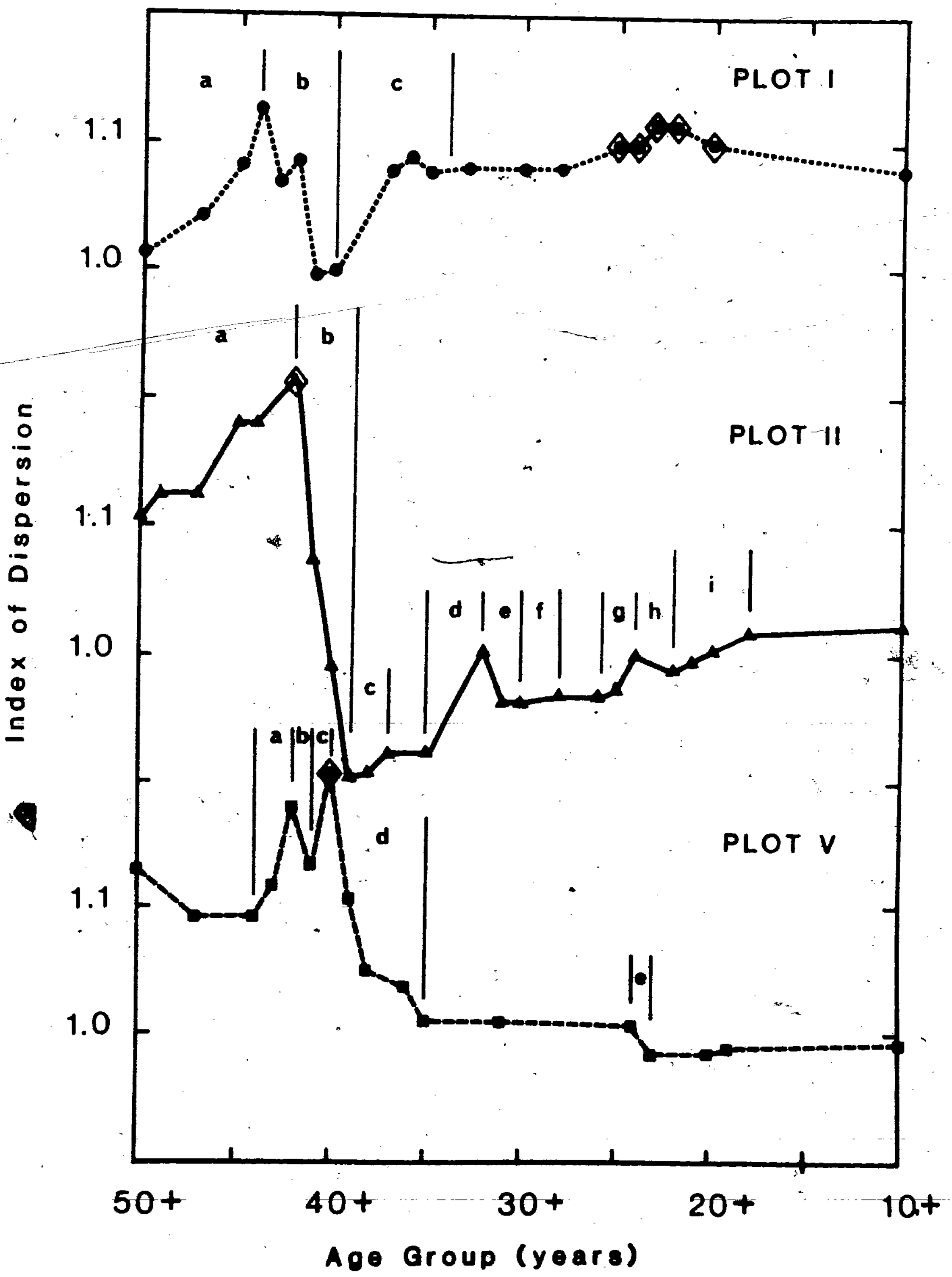

PLOT I
PLOT II
PLOT V
1.2
1.1
1.0
0.9
Aggregation ← → Uniformity
50+
40+
30+
20+
10+
0
AGE GROUP (YEARS)

Figure 15. Previous time-series data separated vertically, showing trends which are unique to each plot. Labelled regions are for comparison with Figure 9 (See text for discussion). Indices which represent significantly uniform dispersion ($p<0.05$) appear within a diamond-shaped symbol.


PLOT I
a
b
c
1.1
1.0
PLOT II
a
b
c
d
e
f
g
h
i
1.1
1.0
PLOT V
a
b
c
d
e
1.1
1.0
Index of Dispersion
50+
40+
30+
20+
10+
Age Group (years)

A follow-up survey of plot I, 24 months later, failed to locate any new recruits, indicating that the lack of 3 year olds during the harvest was more likely due to their absence than to an inability to detect them. This also confirmed that all four year olds had likely been located when the plot was initially tagged, two years earlier.

Age groups shown in Figures 14 and 15 were subjectively selected, choosing smaller age group intervals when dispersion indices changed markedly over short periods of time.

As indices are calculated for increasingly older age groups, the reliability of these values decreases, due to a decrease in the number of nearest-neighbour pairs upon which these calculations were based. Though several individuals exceed 50 years of age (Fig. 9), and an index of dispersion can be calculated for subsamples of these older clams, they were not abundant and the inclusion of each additional individual can cause severe fluctuations in the calculated time-series of dispersion indices. Such indices are therefore of limited value and so the oldest group considered was 50+ years, for which indices were based on no fewer than 9 individuals per plot.

Table 6.2 contains data on the age difference between recruits of the last 10 years and their nearest neighbours present at the time of settlement. In two instances, the nearest neighbour of one of these recruits was younger than the recruit, and thus was not present when it settled. In both cases, the next nearest individual was then considered.

Table 6.2 Age Differences Between Recruits of the Last 10 Years and Their Nearest Neighbours.

Age of Geoduck	Age of Nearest Neighbour	Age Difference
4	44	40
5	25	20
4	37	33
4	46	42
4	unknown	--
4	25	21
4	97	93
4	42	38
4	38	34
4	20	16
4	31	27
5	31	26
9	40	31
4	24	20
4	9	5
4	42	38

Whereas shell size did not appear to be related to population density, even when only the young were considered, a single density value is a generalization and can not express any influence of conspecifics on the shell size of specific individuals. The 4 year age class was largest of all young geoducks, and since a single age class contains individuals having all had similar time in which to grow, statistics on these geoducks were pooled for all plots and observed for correlation with distance to nearest neighbours. Valve area was significantly correlated with distance to nearest neighbour ($n=11$; $p<0.03$). Valve length was similarly so correlated ($n=12$; $p<0.02$), however coefficients were not significant for either valve height (n=11; p<.06) or weight (n=11; p<0.06). The attained levels of significance suggest however, that even here a relationship may exist.

Discussion

Predation and Dispersion Patterns

Though population dispersion patterns may permit inference regarding how an organism is influenced by nearby conspecifics, this is only valid if mortality is relatively low and occurs at random with respect to the location of individuals. A moderate level of such mortality is only likely to result in a conservative estimate of the effects of conspecifics on dispersion and therefore may be acceptable in some circumstances. Mortality due to predation is likely to be non-random since mobile predators may travel in distinct groups or as well-spaced lone predators. Predation may thereby alter natural dispersion by greatly under-emphasizing or over-emphasizing the apparent conspecific influence or predation may even make the relationship appear to be opposite to what it is. The possibility of significant predator-related mortality should therefore be given particular consideration when making inferences of this nature.

Predation, an obvious cause of position-related mortality for some species, has rarely been discussed in the literature in reference to geoducks. Andersen (1971) concluded that predators had an insignificant effect on adult geoduck mortality. More recently, Sloan and Robinson (1983) suggest that predation by the asteroids Pisaster brevispinus and Pycnopodia helianthoides, could contribute significantly to geoduck mortality if the latter was prevented from burrowing deeper than 40cm. An impenetrable matrix layer of cobbles, shells and sand is the example given of such an obstruction. While this type of substrate circumvents the geoduck's primary defence mechanism (burrow depth), the proportion of geoducks occurring in such a habitat is probably quite small. In addition, P. brevispinus has previously been estimated to feed on prey not much deeper than 15cm in the substrate (Van Veldhuizen and Phillips 1978). Since their specimens were on average half the size of those studied by Sloan and Robinson, and burrow depth is roughly equal to the seastar's radius, a depth of 40cm probably represents an upper limit to the depth attainable by only the largest of the species. Sloan and Robinson also state that P. brevispinus is an opportunistic feeder, preferring prey items for which excavation time is reduced. It has been reported that a depth of 60cm can be reached by geoducks less than 2 years old (Goodwin 1973), and that adults are usually found 60-100cm deep (Cox 1979, personal observation), therefore the time required to excavate these bivalves is probably substantial (see below). Given that P. helianthoides is also known to steal food from P. brevispinus, where both species are present, it is unlikely that the latter preys on geoducks regularly, despite being capable of relatively deep excavation.

Predation on Panope generosa by the spiny seastar, P. brevispinus has however been observed on two occasions, during the course of this research. During the fall of 1980, several P. brevispinus were seen to feed almost exclusively on geoducks (pers. obs.) in the dense bed (Breen and Shields 1983) off Brady's Beach, near the Bamfield Marine Station, on the west coast of Vancouver Island. During this feeding period, at least one seastar remained on the same geoduck for more than one week, at which point, the cleaned, uprooted shell was found intact, sitting in a star-shaped excavation pit. Return trips to this site were made in the fall of 1981, and the spring and summer of 1982, as well as the spring of 1983 and 1984. Such predation was not observed again at this site. In the spring of 1984, the same occurrance was observed on a smaller scale, between the Ross Islets, also near the marine station. Though the seastar was common on earlier dives at this site, geoducks were never noted to be among its food items. Both of these locations are more than 40 miles from the study site where the body of this research was carried out.

During the spring of 1982, large spawning aggregations of the squid, Loligo opalescens were observed in and around Bamfield Inlet and extensive masses of spawn were reported in the waters off nearby Brady's Beach (Shimek et al. in press). Geoduck siphons often extended 20-30 cm beyond the sediment surface (pers. obs.), to maintain the tips above the egg mass or beyond its perimeter. A similar response was earlier reported by Andersen (1971), when decaying vegetation was allowed to accumulate over a bed. He also found one such geoduck completely uprooted, and concluded that it had surfaced to avoid being smothered. Observations at Brady's Beach are consistent with this, since such siphon extention is probably not possible for adult geoducks which occur at normal burrow depth. The site was also later observed in August of that year. Stakes used to mark a particularly large squid egg mass were still present though little remained of the mass itself. The area contained numerous sunflower seastars, P. helianthoides, many of which were in the process of eating uprooted geoducks. The shells of twenty-seven freshly eaten geoducks (ie. both valves were present, some with meat and/or siphonal periostracum attached and few with any barnacle set), were also found within the area. There was little evidence of digging on the part of the seastar, further suggesting that the geoducks which were once buried by a substantial squid egg mass, had surfaced and only then become accessable prey for P. helianthoides.

Over the course of this study, P. brevispinus was only rarely observed in Ritchie Bay and feeding on geoducks was not observed. The seastars, P. helianthoides, Crossaster papossus and Dermasterias imbricata were all fairly common but only the latter was ever observed feeding, and this was always on the seapen, Ptilosarcus gurneyi.

I believe that the mortality of geoducks due to predation is likely to have had a minimal effect on population dispersion patterns in this bay. As mentioned earlier, the high mortality rate noted while monitoring siphon shows did not appear to be position-related and is therefore also unlikely to have influenced dispersion patterns.

Density and Dispersion

It has been noted that if an organism's size is dependant upon the space available and the resultant size range is very large, then dispersion analysis may indicate any one of these patterns, despite an actual random positioning (Pielou 1960). This is not believed to be the case here however as size range is relatively small. Pielou (1960) noted that regular dispersion will only be detected if size range is small or density is low, and in this study uniform dispersion was only detected (using R) in the highest density plot.

While the correlation coefficients obtained for R and Rd were positive (0.59 and 0.46) when tested for correlation with density, neither of these values was found to be statistically significant (Kendall's tau-B; p>0.05). The data as presented in Figure 13 however, suggest that the paucity of such data and thus the necessary high correlation required for detection, may be partially responsible for this lack of significance. Another factor which may contribute to this lack of significant correlation is the apparent bimodality of the dispersion indices. While four values lie between 0.98 and 1.02, there are none between 1.02 and 1.05 and then there are two within 0.016 of each other. It is possible that a critical density may exist, beyond which all settlement is uniform. This however may also be an artifact of the low number of plots considered.

Reducing a dispersion pattern to a single value is often extremely useful but considerable information may be lost. For three (I,II,V) of the six plots, additional information was available in the form of age data (Fig. 9). This was used with dispersion indices in an attempt to see more clearly how conspecifics may influence geoduck dispersion. To utilize these data optimally, it was assumed that relative survivorship (population age structure) was related to recruit (year class) strength. The results observed indicate that this was a reasonable assumption.

Figure 14 shows indices of dispersion (Rd) expressed as a time-series for plots I, II and V. When all members are considered, the most densely populated plot (I) is most uniformly dispersed and the least populated plot (V), has the lowest dispersion index. In the lower density plots, recent recruit positioning is clearly random. These density/dispersion relationships appear relatively consistent for all recruitment in the last 20 years, despite approximately 15% of the present population having settled during these years.

When the data are presented as a time-series, two chronological trends appear for all three plots: (1) Dispersion patterns 43 years ago appear more uniformly dispersed than they were 50 years ago, as is evidenced by a few years of increasingly higher indices. (2) Beginning 41-39 years ago, yearly recruitment appears to have been consistantly more 'non-uniform' for a 3-5 year period. Dispersion indices used in the manner described, do not distinguish between random and clumped recruitment on a yearly basis, as either is capable of decreasing the overall uniformity of the population. The existance of these trends in dispersion patterns indicates that recruit dispersion was influenced by the position of adults.

While recruit dispersion 35-40 years ago appears to have changed markedly from preceeding years, recruitment during that period (as inferred from population age structure) also peaked. Since age structure and dispersion were determined independantly, changes in dispersion indices should only be reflected in the data on yearly recruitment if (a) dispersion patterns were influenced by conspecifics, and (b) this series of dispersion indices is a valid representation of the past, and (c) the effects of mortality on dispersion were small. As mentioned earlier, calculated indices of dispersion for these age groups were based on only those recruits that survived until this study was conducted. As indices are calculated for older age groups, it is increasingly likely that natural mortality may have obscured the original dispersion pattern.

Figure 9 contains population age structure data. Two major features of the data appear in all three plots. (1) A distinct period of successful recruitment, lasting several years, began almost 50 years ago, with peak recruitment preceeded by several years of increasingly high recruitment. Recruitment was 'successful' in the sense that the settled individuals survived in considerable numbers. (2) This period of high recruitment peaked 41-39 years ago. These features coincide with periods of change predicted by the time-series dispersion indices, indicating that conditions (a)-(c) have to some extent been met.

The extent to which dispersion patterns are influenced by conspecifics, was more closely observed by a comparison of changes in dispersion which are unique to each plot, with the population age structure of that plot. Indices for plot I (Fig. 15) rise, drop, then rise again, as indicated by (a), (b) and (c) respectively. In Figure 9, the line which corresponds to these years appears above the histogram for plot I. It can be seen that the position of this line coincides with the high recruitment portion of the histogram. The line is divided into the three sections that appear in Figure 15, which represent uniformity, non-unformity and uniformity, and is labelled the same as these time-frames in Figure 15. Over the beginning of the period of good recruitment, the indices indicate that dispersion tended toward uniformity. This shifted to non-uniformity as recruitment increased, peaked and began to decline. Thirty eight years ago, though recruitment was still high, it dropped off markedly from the previous year. Indices at this point indicate a reversal toward uniform dispersion. Recruitment 20-30 years ago was slight but consistent (Fig. 9) and the corresponding indices indicate uniformity (Fig. 15).

This relationship between recruit intensity and the dispersion pattern of recruits, is repeated in both plots II and V. Indices of dispersion for plot II show one large drop (non-uniformity) 41-39 years ago (b) followed by two small drops, 31 (e) and 23 (h) years ago. Each time, these were preceeded and followed to some extent, by higher index values. In Figure 9, these three periods of non-uniform settling are seen to correspond to peaks in three periods of high recruitment (b,e,h). Periods of more uniform dispersion correspond to recruitment prior to and following these peak recruitment years.

Indices of dispersion for plot V indicate non-uniformity for periods 41 years ago (b) and 39-35 years ago (d). The first year in which this is observed, coincides with the year of most successful recruitment (b in Fig. 9). Uniform dispersion is first indicated during the years that recruitment increases (a) and then later when it decreases (c). The 5 year interval, during which time recruitment was increasingly less uniform (d), occurs at the end of the period of high recruitment. In holding with the line of reasoning developed thus far, this would be expected only if a second peak in recruitment occurred at this time. Though this is not clearly demonstrated, the data are not inconsistent with this possibility. The age structure of plot V also shows that recruitment 33 years ago might have been slightly better than average (e in Fig. 9). Dispersion indices indicate a slight tendancy toward non-uniform dispersion at that time.

A characteristic of all three plots is that recruit dispersion from year to year occurred in a manner which was usually either similar to, or more uniform than, others within that plot. During years of exceptionally high recruit success, recruits of the year settled either randomly or gregariously. Recruit dispersion appears to be related to the level of recruit success in any particular year.

To determine whether recruit positioning was related to the location of adults or to that of other recent recruits, the age difference between each geoduck ≤10 years old and its nearest neighbour, was calculated and appears in Table 6.2. It can be seen that the nearest neighbours of successful recruits are usually full grown adults. Though recruit dispersion is influenced by recruit success of that year, their nearest neighbours are not likely to be other recent recruits.

Over the range of nearest neighbour distances encountered among 4 year old geoducks (4-41cm), the closer a 4 year old was to its nearest neighbour, the smaller was that geoduck. If young geoducks do obtain some benefit from association with adults, it is not apparent in their growth rates. Adults appear to have inhibited the growth of those in their immediate vicinity.

Though recruit dispersion appears to be associated with adult positioning and the success of recruitment that year, the mechanism by which this occurs is not readily apparent. Adult/adult and adult/juvenile interactions may take the form of competition for space, competition for food and interference via sediment destabilization, resulting in uniform distribution, reduced growth, and increased mortality (Woodin 1976). The latter two would be predicted by the trophic amensalism hypothesis (one group makes its environment less suitable for a potential competitor). Though no information was obtained regarding the density-related mortality of geoducks, increased density did not bring about reduced growth. An alternate hypothesis suggested by Woodin is that discrete assemblages or patches can result from interactions occurring between established individuals and settling or newly settled larvae, such that they are excluded from the immediate vicinity. The effects of these interactions have a more limited impact on individuals in a sparsely populated area, but just what constitutes a dense assemblage varies with individual characteristics such as size, and level of activity (Woodin 1976).

For some time it has been believed that ingestion by suspension feeders contributes significantly to the mortality of settling larvae (Korringa 1941). The extremely strong water currents generated by geoduck filtering may influence the particulate content of the water for a considerable distance in the vicinity of the siphon tip. In calm water, the exhalent current carries suspended particles 20cm or more away from the siphon (personal observations). With a force of this magnitude, the area (horizontal plane) influenced by a filtering individual is likely to be considerably greater than that of the siphon tip. This could greatly limit the area in which a larva may descend, for the purpose of settling. Woodin suggests that in dense populations of suspension feeders, settlement may be completely prevented, and cites studies in which discrete assemblages of bivalves are both persistant and age-class dominated, as evidence of this. In field studies with the manila clam, Tapes japonica, settling success was markedly reduced when adults were abundant, but settling was never completely prevented, dispite manipulation of adult densities to twice that which was observed in the area (Williams 1980).

The observations that geoduck recruit location was related to the position of adults and that the nature of this relationship was dependant upon the settling success of that year, are consistent with Woodin's (1976) hypothesis, provided that Williams' (1980) findings are also considered.

Higher densities do not appear to have resulted in greater competition between adults, since growth was not reduced in these populations. Geoduck density has been shown to display some of the patchiness that Woodin discusses, with intrapatch dispersion ranging between randomness and uniformity. Though when all six plots were considered, dispersion was not clearly related to density, this is thought to have been due to too few sample plots. Of the three plots which were studied in detail, the one with the highest density had the most uniform dispersion, while the other two of lower densities, had more randomly dispersed geoducks.

Highly significant is the fact that despite this, recruitment into each plot for the last 20 years has been in a manner which is virtually identical to that of the adult population. A larval geoduck which descends to settle in the immediate vicinity of an adult, would be either resuspended by the exhalent current or is captured by the inhalent current, to be ingested or wrapped in mucus and ejected as pseudofeces, which is also usually fatal (Williams 1980). Successful settlement could only be accomplished outside the adults 'sphere of influence'. In a population of randomly distributed geoducks, Woodin's hypothesis predicts that settling position relative to adults, would be random. This is consistent with what was observed. With a sufficiently high density, Woodin's prediction of total exclusion may occur but this situation was not observed here. In a relatively high density population of uniformly dispersed individuals, the areas available for settlement would be similarly dispersed. Pielou (1977; p143 Fig. 9.1) demonstrates this with patches, by artificially creating a pattern, and then visualizing it in reverse (individuals positioned in interclump spaces). By creating these settlement-free zones around themselves, adult geoducks could either maintain population dispersion at the same level of randomness or cause it to be slightly more uniform. In years of high settlement success, the number of larvae to escape inhalation and land within the same inter-adult space as other larvae is likely to be greater and thus would bring about the more random dispersion which was noted in all populations, during such years. Despite successfully settling within these zones around adults, competition for food with a larger adult siphon would account for the smaller size of juveniles located very close to adults.

While this mechanism appears to account for the observed relationships between adult and recruit dispersion patterns, it is proposed as the major structuring force and not as the sole one. For example, the ability of larval marine organisms to detect conspecifics with well developed chemosensory structures, and then disperse relative to them, has been studied in detail and in many cases the specific chemical is either known, or its physical properties are well discribed (Bayne 1969; Crisp 1967,1974; Highsmith 1982). Though the location of geoduck settlement appears to be largely dictated by inter-adult space, for a short period after settling, movement in relation to adults may be possible. Also, while mortality of adult geoducks due to predation is believed to be minimal, juveniles of the species may experience greater predatory pressures. Only a few papers on juvenile bivalve predators have been published (Loosanoff 1959; Breese and Phibbs 1972), but predation is considered by some researchers to be the dominant cause of mortality of young bivalves (Muus 1973). One or both of these mechanisms may slightly modify the final pattern of geoduck recruit dispersion.

Summary

1. Though the dispersion pattern of geoducks may be modified by predator-induced mortality, the influence of predators in Ritchie Bay appears to have been marginal.

2. Indices of dispersion were not significantly correlated with plot density ($p>0.05$), but small sample size is believed to have been in part responsible.

3. A time-series of dispersion indices was created by incorporating geoduck age into the dispersion analysis of three plots. Similar trends in dispersion over time, were seen in all plots.

4. Since dispersion indices and recruitment were determined independantly and the association between the two is strong, this representation of past dispersion is thought to be valid. Recruit dispersion in a given year was related to the level of recruit success that year. When recruitment was low, the dispersion of recruits either did not alter overall dispersion or it caused overall dispersion to be more uniform. When recruitment was high, recruit positioning was either random or aggregated. Slight dissimilarities between the time-series

created for each plot correspond to slightly different levels of recruit success in each.

5. Recruitment does not occur in discrete patches. In 14 of 15 cases, the nearest neighbour of a young geoduck (≤10yr) was ≥16yr older than that young geoduck.

6. At these densities, in these environmental conditions, geoducks have a negative influence on the growth of neighbouring conspecifics. The size of 4yr olds (largest age class of young geoducks) was positively correlated with distance from their nearest neighbour (n=11; $p<0.03$).

7. A mechanism is suggested by which siphonal current may account for observed trends in dispersion and shell size.

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