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SPAWNING, GROWTH, AND SPATIAL DISTRIBUTION OF THE GEODUCK CLAM, *PANOPE GENEROSA* GOULD, IN HOOD CANAL, WASHINGTON.

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Zoology

SPAWNING, GROWTH, AND SPATIAL DISTRIBUTION OF THE GEODUCK CLAM, PANOPE GENEROSA GOULD, IN HOOD CANAL, WASHINGTON.

by

AVEN MAYER ANDERSEN, JR.

A thesis submitted in partial fulfillment of
the requirements for the degree of

DOCTOR OF PHILOSOPHY

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Approved by Richard R. Whitney
(Chairman of Supervisory Committee)

Department College of Fisheries
(Departmental Faculty Sponsoring Candidate)

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UNIVERSITY OF WASHINGTON

Date: June 10, 1971

We have carefully read the dissertation entitled Spawning, growth, and spatial distribution of the Geoduck Clam, Panope generosa Gould, in Hood Canal, Washington submitted by Aven Mayer Andersen in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

Mr. Andersen has carried out the first field studies of spawning, growth, and spatial distribution of geoduck clams. He determined age at maturity and length of the spawning season. He traced gametogenesis. Growth rate was followed and a von Bertalanffy growth curve calculated. Abundance and spatial distribution was mapped. He found that decaying aquatic vegetation probably smothers some geoducks.

Only a handful of publications dealing with this clam have appeared in the literature. Because of the scarcity of information, Mr. Andersen had to pursue his study with few guidelines. His vigorous field program produced results in spite of the necessity for using the trial and error approach in developing methods of study. Mr. Andersen's study has added significantly to the knowledge of the life history of the geoduck clam. This knowledge will be important in the management of the new commercial fishery which has developed and in the already well developed recreational fishery.

DISSERTATION READING COMMITTEE: Richard R. Whitney

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Signature Owen M. Anderson

Date 2 August 1971

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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INTRODUCTION

The Pacific Coast geoduck, Panope generosa (Gould, 1850) is the largest burrowing clam in North America. It occurs from Baja California to Southeastern Alaska and in Japan, living with its valves buried two to four feet deep in gravelly to muddy substrates from the lower littoral zone to at least 180 feet below mean low water (Abbott, 1954; Carpenter, 1864; Grant and Gale, 1931; Lindsay, 1966).

In Washington state, geoducks have been taken for personal use since before the white man came until the present day, and now the subtidal stocks are being commercially harvested. Yet the life history of the geoduck has never been studied.

In the absence of life history studies, Lindsay (1966) summarized, in a published abstract, the casual observations on geoducks by Washington Department of Fisheries biologists. Lindsay states: "Maximum adult size reported is about 13 lb. . . . Sexes are separate, but sex reversal may occur. Spawning is known to occur with rising water temperatures in May or June although mass spawning may not occur except during warmer years. . . . Setting of larvae is predominantly during the warmer years. . . . Growth is believed to be slow, and it is estimated the average geoduck reaches 3 lb. in a period of 10 to 15 years. Maximum age reached is unknown, but weight and thickness of shells of old clams indicate they probably survive beyond 20 years. . . . More than one clam per foot is usual."

Thus, with Lindsay's summary providing a baseline, this study was undertaken to document when geoducks spawned during the year, at what size they first spawned, if they changed sex, what their rates of growth and mortality were, and what their abundance and pattern of spatial distribution on an intertidal beach were.

THE GENUS *PANOPE*

The scientific names of clams change frequently and that for the geoduck is no exception. According to Grant and Gale (1931), this species has been called by 14 scientific names. Gould (1850) named it *Panopaea generosa*, apparently misspelling the name but assigning it to the genus *Panope* Menard de la Groye, 1807 (family Saxicavidae). In the latter part of the 19th century this species went under the name *Glycimeris generosa* (Gould) (Carpenter, 1864; Stearns, 1885). Dall (1912) argued for the name *Panope* on the basis of a pamphlet of Menard's dated January 1807. Vokes and Cox (1961), however, questioned the validity of Menard's January 1807 publication and, further, argued that *Glycimeris* Lamarck, 1799 should be rejected because Lamarck transferred that name to another pelecypod genus in 1801 and because of possible confusion with a third pelecypod genus, *Glycymeris* De Costa. Vokes and Cox proposed to the International Commission on Zoological Nomenclature that it place *Panopea* Menard de la Groye, April 1807 on the Official List of Generic Names in Zoology and place the names *Glycimeris* Lamarck, 1799; *Glycimeris* Lamarck, 1801; and *Panope* Menard de la Groye (after April) 1807 on the Official Index of Rejected and Invalid Generic Names in Zoology. To date, the Commission has failed to act on these proposals (Vokes, 1969).

Because the Commission has yet to decide on an official name for the genus, and because I do not want to add to the confusion, I will use the generally accepted spelling of *Panope* (Abbott, 1954; Morris, 1966) in this dissertation.

The genus *Panope* contains many species, both fossil and living, besides *P. generosa*. Extinct species, some living at least as long ago as the

Jurassic Period, have been found throughout the world (Grant and Gale, 1931; Imlay, 1957; Keen and Bentson, 1944; Olsson, 1964; Regteren, 1937; Speden, 1970). Living members are _P. aldrovandi_ Menard in the Mediterranean and _P. attenuata_ Sowerby in South Africa (Rogers, 1908), _P. australis_ Sowerby in Australia (Cotton, 1961), _P. bitruncata_ (Conrad) on the South Atlantic and Gulf coasts of North America (Johnson, 1956), _P. japonica_ Adams in Japan (Kira, 1955), and _P. zelandica_ in New Zealand (Morton and Miller, 1968). For none of these living species is the life history known.

HISTORY OF THE GEODUCK FISHERIES

Indians of the Pacific Northwest collected geoducks for food before the white man arrived, often drying them for future use (Underhill, 1944). Later, the settlers also dug geoducks for food. Some geoducks were even sold, with other clams, in the markets of Olympia and Portland (Collins, 1892; Doane, 1902; Ryder, 1882; Stearns, 1883a). The early white settlers were so impressed with the geoduck that attempts were made to transplant geoducks to the Atlantic Coast (Hemphill, 1882; Stearns, 1883a). Hemphill stated, in a letter to Ryder, that, "Its flesh is, I think, the most delicious of any bivalve I have ever eaten, not excepting the best oysters." (Ryder, 1882). Early attempts to ship geoducks to the Atlantic Coast by boat were unsuccessful (Stearns, 1883b). Later, plans were made to ship live geoducks via the recently completed Transcontinental Railroad (Baird, 1884; Ryder, 1885), but these plans were either dropped or failed; I am unable to find reports of their success.

Geoducks supported a small but enthusiastic personal use or recreational fishery in Washington for about 100 years--until 1926. Fearing that the fishery might make the geoduck extinct, the 1925 Legislature prohibited any person from taking or possessing geoducks (Kershaw, 1904; Pollock, 1930; State of Washington, 1926). Personal use fishing resumed in 1931 when the Legislature enacted regulations permitting geoducks to be taken for immediate personal use but prohibiting their use for canning or selling (State of Washington, 1931). This act allowed a digger to take up to three geoducks in any one day with a hand-operated fork, pick, or shovel, providing that "no person shall at any time maim or injure any geoduck or thrust any stick or other instrument through the neck or body of such geoduck before digging." (Ibid.). This act still regulates the personal use fishery.

New, significant legislation affecting the geoduck was written in 1969 when the Legislature passed House Bill Number 77 (as amended) authorizing limited commercial harvesting of subtidal geoducks (State of Washington, 1969). Commercial harvesting, under the joint control of the Department of Fisheries and the Department of Natural Resources, began in June 1970.

STUDY AREAS AND METHODS

Study Areas

This study was conducted in the State of Washington on two beaches in Hood Canal (Figure 1). The first beach, Big Beef, is located at the mouth of Big Beef Creek (122° 47'W by 47° 39'N). Big Beef was chosen as a study area because it had a natural, unexploited stock of geoducks, and because it is adjacent to the University of Washington's Big Beef Creek Research Station where living and research facilities were available. The Big Beef beach is privately owned by Mrs. John Emel. The second beach, Dosewallips, located four miles across Hood Canal at the mouth of the Dosewallips River (122° 53'W by 47° 41'N) is also known as Sylopash Point. It is a part of the Dosewallips State Park and contains a geoduck stock heavily exploited by park visitors.

These two beaches are generally similar habitats, but none of their qualities were measured for comparisons. Both are deltas formed by their respective streams, and in the area where geoducks occur consist mostly of sand covered with eelgrass (*Zostera marina*), although the intensive clam digging on the Dosewallips has removed the eelgrass from some areas. For a general idea of the temperature and salinity of the surface water, my observations and studies by Westley (1967, 1968) indicate the temperature probably ranges from 0 to 25°C during the year, with an average around 10°C; and the salinities range between 5 and 30 $^{0}/oo$, with an average near 25 $^{0}/oo$.

Geoduck Collection Methods

Geoducks were collected either by digging them from beaches exposed during minus tides or by diving, since the usual benthos collectors are ineffective. Vokes (1969), in fact, suggests that the Atlantic coast

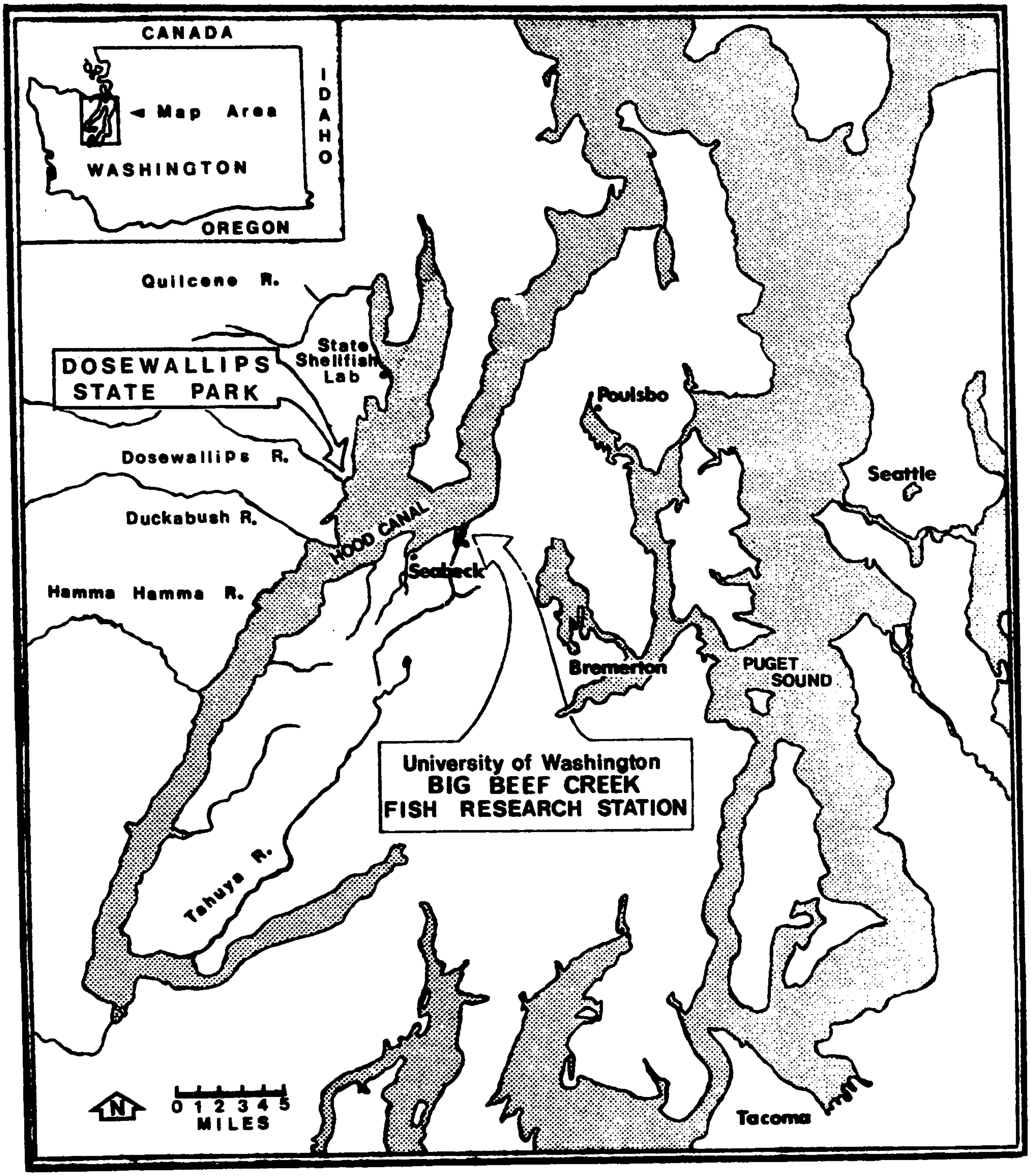

Figure 1. Locations of the study areas at Dosewallips and Big Beef.

geoduck, P. bitruncata, has rarely been collected because its habit of burrowing deeply into the substrate precludes its capture by the usual sampling gear.

When the beaches were exposed during minus tides, geoducks were individually dug after their "shows" (squirts of water, siphon tips, or siphon holes) were spotted. A tube similar to those used for digging razor clams but 20 cm in diameter and 40 cm long worked well for collecting small geoducks. Recreational clam diggers (park visitors at the Dosewallips and College of Fisheries faculty at Big Beef) provided additional geoducks for measuring. For some of the geoducks dug from the exposed beaches, the depths of their burrows were measured and the orientations of their shells to the shoreline were determined. Burrow depths were determined by measuring the distance from the surface of the substrate to the bottom of the burrow after the geoduck had been removed. Orientation was classified by the position of the hinge, whether it pointed towards, parallel with, or away from the shoreline.

Diving with SCUBA and using a "washout" nozzle permitted collecting geoducks at any time, and from subtidal as well as intertidal beds. The washout nozzle (based on a drawing furnished by the Washington State Shellfish Laboratory) was a high-pressure fire nozzle, modified by adding three back-jets and an on-off valve between the fore-jet and the back-jets. The nozzle, connected by 50 ft of hose to a water pump in a boat, was used to blow away the sand surrounding the geoducks. In contrast to digging geoducks from the exposed beaches, diving with the nozzle was an efficient process. Under optimal conditions one geoduck could be hand-dug about every ten minutes, whereas with the nozzle the rate was more like one each minute.

Except for the recreationally-dug clams that were measured and weighed on the beaches, the geoducks were taken to the laboratory at Big Beef Creek for measuring and study.

Shell Dimensions

Geoduck valves were measured with vernier calipers for length, the greatest anterior-posterior distance; width, the greatest dorsal-ventral distance perpendicular to the length, and breadth, a measure of the convexity of the valve. Dried valves were measured with an accuracy of 0.05 cm (i.e., measurements were repeatable to an accuracy of ± 0.05 cm).

Weights

Weights were obtained for the whole clam, meat, viscera, whole shell, and the dried right and left valves. Because some of the body parts were needed fresh, weights of the soft parts were determined from the damp tissues. The valves were weighed after they had dried. Geoducks less than 1200 g were weighed on a Mettler balance having a capacity of 1200 g with readings to 0.1 g. Larger clams were weighed with a 20 kg-capacity Chatillon spring scale, with readings to 25 g.

The total, or gross, weight was determined for the whole clam after the outer surfaces had been cleaned of extraneous material and dried with paper towels. Total weight included the shell, as well as the fluids and sand contained within the body cavity.

Some geoducks were butchered; for these, weights were also determined for the meat, viscera, and shell. The meat consisted of the siphon, the thick part of the mantle, and the "skin" covering the siphon and ventral surface of the mantle. The viscera consisted of the thin part of the mantle and the internal organs (Figure 3). The shell consisted of the hinge ligament and the two valves. The weights of the parts were determined after the parts had been cleaned of extraneous material and dried with paper towels. Weights of the individual right and left valves were determined after the valves had dried thoroughly in the air; the hinge ligament, however, was removed completely from both valves and was not included in the weights.

Tagging

So that growth of individual geoducks could be determined, all uninjured geoducks collected from Dosewallips and Big Beef--except those collected for gonad histology--were tagged and replanted. Most were small because the emphasis of most collecting trips was to dig small geoducks. Small geoducks were preferred for the growth study anyway, because they were likely to grow noticeably, whereas larger geoducks were likely to grow little if at all. Thus, of the 191 tagged, 78% were less than 10 cm long. Those tagged ranged in length from 2.08 cm to 17.27 cm, had a mode of 5.78 cm (n = 24), and a mean of 7.67 cm.

Before being tagged, the geoducks were cleaned of extraneous material, measured and weighed by methods described earlier, and the outer surface of one valve was allowed to dry.

Geoducks were tagged two ways. During the first two years of this project, 5/16-inch-diameter Petersen disc tags were cemented to the dried valves with fiberglass resin. The Petersen tags gave good results, but they were slow to apply and the resin had to dry for at least one hour before the clams could be placed into water. Therefore, during the last year an alphanumeric code was written on the dried valves with a waterproof ink. Marking with ink was fast, but the ink sometimes faded or wore off. However, numbers penciled on the shells when the clams were first dug were still readable two years later.

After being tagged, the geoducks were held in aquaria for several hours to several days until they could be planted.

Geoducks had to be carefully planted; the small ones were fragile and did not rebury themselves rapidly enough to avoid predators, and the larger ones, because their feet are nearly useless, may have been unable to rebury themselves. Care was taken to plant them uninjured and as deep in the substrate as they had been originally. Most planting was done using SCUBA and the washout nozzle to dig the holes, although some were planted when the beach was exposed during a low tide. Some soil was lost every time a hole was dug, and it proved most efficient to bring sand in plastic bags for refilling the holes after the clams had been planted. Geoducks are less dense than sand, and they floated out of the holes unless they were held in place as the holes were being refilled.

To study the growth of geoducks at different beach levels, the tagged clams were planted in rectangular plots at the -1-ft, -2-ft, -4-ft, and -10-ft levels. These plots were on a line normal to the beach line and 200 feet apart (Figure 2). To simplify finding the clams afterwards, they were planted one meter apart in rows one meter apart. As each clam was planted its position was recorded and then marked by sticking a 1-ft piece of plastic pipe bearing the tag number into the beach adjacent to the hole. To facilitate finding the plots at high tide and when diving, one corner of each was marked with a buoy and a line was strung along the bottom from one plot to the next.

The planted tagged clams were checked occasionally to evaluate the method of planting and to determine when mortalities occurred. Most of the checks were made using SCUBA. Usually the siphon tips could be seen, but frequently the ground nearby had to be poked to make them show, and even then some failed to show. The checks were made at irregular intervals, usually

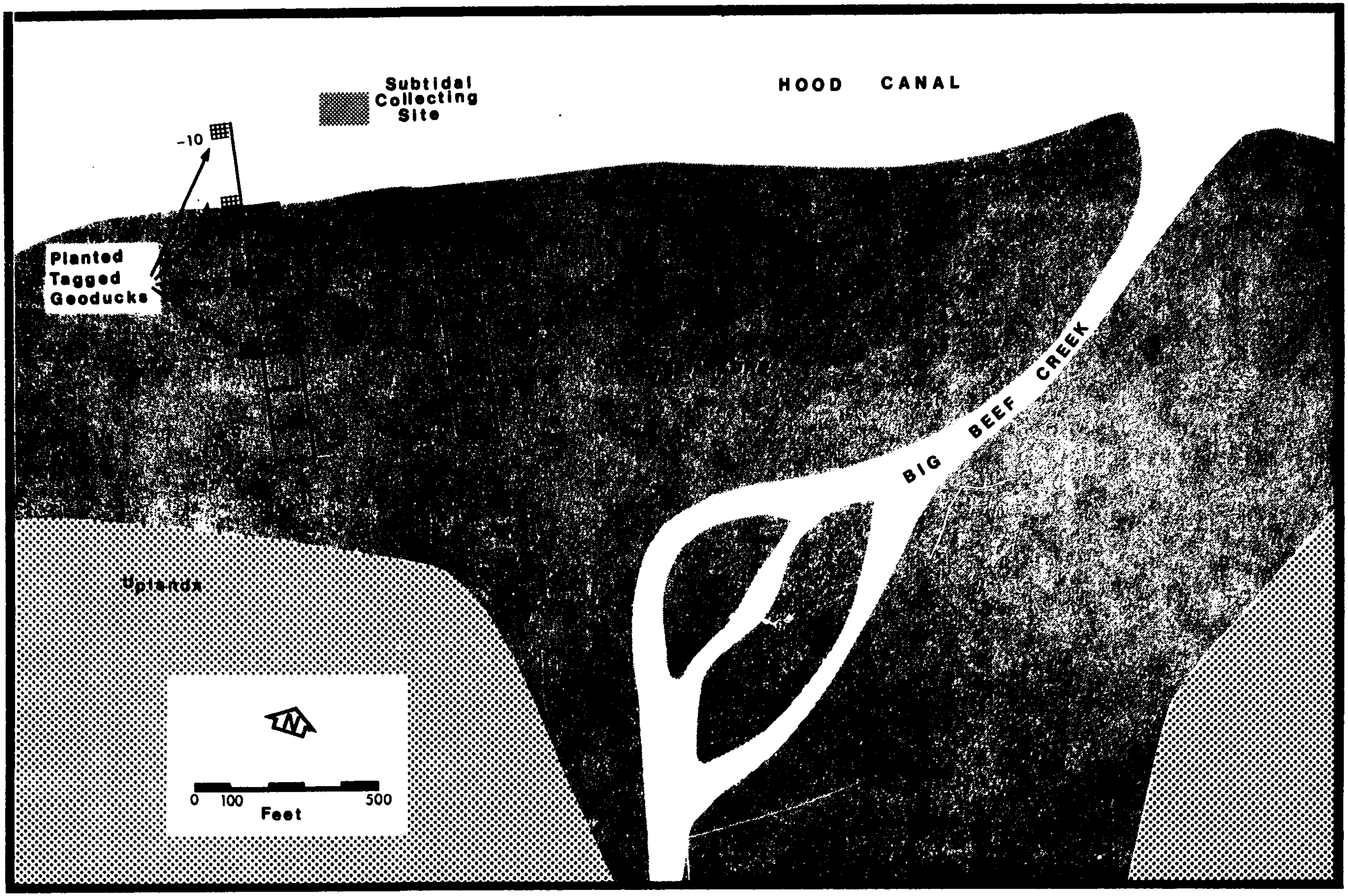

Figure 2. Details of the study area at Big Beef.

within a few days after the clams had been planted and at monthly intervals thereafter, although checks were difficult during the winter because of the frequent heavy silt loads caused by waves and the high flow of Big Beef Creek.

For determining seasonal growth, the experimental design called for planting and recovering clams each season. Two unanticipated factors, however, acted against this plan. First, because small geoducks could not be found and collected by diving as had been planned--except when one was accidentally washed out while a larger one was being dug--they were mainly collected from the exposed beaches during the daylight minus tides of May through August. Thus, 92% of the original plantings were made during those months. Secondly, tagging and planting caused the clams to stop growing temporarily, as will be discussed later, so the clams showed little growth until 6 months after being planted.

Tagged clams were recovered by redigging them, usually using SCUBA and the washout nozzle, although a few were redug using shovels or collecting tubes. A small venturi suction dredge was tried because it was feared that the small geoducks might be lost or badly broken if redug with the washout nozzle, but the dredge readily clogged with debris and was abandoned. The nozzle worked well even for small geoducks.

The recovered tagged clams were weighed and measured as before. If they were alive and relatively undamaged they were replanted where they had been dug, in an attempt to supplement the study of seasonal growth. If they were badly damaged they were butchered, and their meats, viscera, and shells were weighed, samples of their gonads taken, and their shells saved for later study.

Permanent Histological Preparations of Gonad Tissues

To determine when geoducks spawn during the year, the size (age) when they first spawn, and whether they undergo a change of sex, permanent histological preparations of geoduck gonads were made and examined.

Gonad samples were collected from geoducks dug specifically for the study of reproduction, from geoducks accidentally killed in the tagging study, and occasionally from recreationally-dug clams. Because subtidal geoducks were easier to find but apparently matured and spawned synchronously with the intertidal geoducks, and to keep from exploiting the intertidal population, most of the geoducks collected specifically for the study of reproduction were taken from the subtidal collecting site (Figure 2).

Because of these three sources there was a large range in the sizes of geoducks used in the study of reproduction. For the small geoducks, whole visceral masses were saved; whereas from larger ones, two adjacent cubes of tissue (each about 1 cc) were removed from the midlateral portion of the visceral mass.

The gonad samples were placed in coded containers, fixed and hardened, and preserved in 70% ethanol. The tissues were usually fixed and hardened with Davidson's acetic acid fixative (Shaw and Battle, 1957), but sometimes Ruddell's buffered formalin[1], 10% sea water formalin, or 4% Acrolein in sea water were used.

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[1] Ruddell's buffered formalin fixative: 370 ml tap water, 20 ml commercial formalin, 13.7 g sucrose, and 5.4 g $MgCl \cdot 6H_2O$ or CaCl (Craig L. Ruddell, personal communication, 1967).

Following standard procedures, the preserved tissues were dehydrated, embedded in Paraplast, sectioned at 5 to 10μ with a rotary microtome, mounted on glass microslides, stained with Harris's or Meyer's hematoxylin, counterstained with alcoholic-eosin, and sealed with glass coverslips and Canadian balsam.

After drying for at least two weeks, the sections were examined with the aid of a compound microscope at 40 to 2000 diameters of magnification, and classified by sex and stage of gametogenesis.

Abundance, Distribution, Recruitment, and Mortality

A study designed to yield information on the abundance, distribution, recruitment, and mortality of geoducks by beach level consisted of marking and mapping the position of each geoduck in known areas, checking the marked geoducks periodically to determine if they were alive or dead, and marking all newly-discovered geoducks in the areas. Abundance and distribution could then be determined from the maps of geoduck positions, recruitment could be determined from the newly-added marks, and natural mortality could be determined from the disappearance of marked geoducks.

At the start of this study a 1,000-foot-long by 800-foot-wide section was gridded into square plots, each 100 feet on a side. After finding that the density of geoducks was much greater than had been expected, the study area was reduced to two 100-foot-wide strips of plots extending from about the +2-foot-level to lower-low water (Figure 2). The corners of each plot were staked so the plots could be relocated. The approximate beach levels of the plots were determined from the elevations of the corner stakes.

During low tides, the positions of individual adult geoducks within each plot were found, marked, and mapped. Since geoduck siphons were hidden among the eel grass leaves and had to be found and identified, few small (subadult) geoducks were found. The positions of those geoducks that were found were marked on the shoreward side of their siphon holes with one-foot-long pieces of black plastic pipe shoved for half their lengths into the beach. To make the pipes more easily seen, especially at night, their tops were wrapped with one-inch-wide white or yellow plastic tape. Marking was done during several low tides until most, if not all, of the adult geoducks in the plots had been found and marked. Then with the use of an alidade, plane table, and stadia rod (with the stadia rod placed right in the siphon holes) the position of each geoduck was mapped.

REPRODUCTION

The sex of geoducks and the timing and duration of their spawning season were determined by studying permanent histological preparations of gonad tissue. Other methods (Giese, 1959) were either impractical or imprecise. The methods of observing spawnings, collecting larvae, and collecting spat were impractical because the time of spawning was unknown and the larvae were undescribed. Examining the adults was also impractical: first, because geoducks are buried in the sediments with only the tips of their siphons showing, and secondly, because they lack secondary sexual characteristics. But even when they are removed from their habitat their sex and state of maturity are difficult to determine. Gross examination of gonads, a method used with some bivalves (Loosanoff, 1942; Tranter, 1958b), is imprecise and often useless (Porter, 1967; Ropes, 1968a; Wilson and Hodgkin, 1967). Fresh smears of gonads are also imprecise. They fail, for example, to distinguish the sex of a spent clam or distinguish between a hermaphroditic one ripe in the female phase and a ripe female.

Histological preparations not only provided a practical and precise method of determining sex and state of maturity, but permitted detailed study of the cytological changes occurring during gametogenesis, served as records, and permitted comparisons and reevaluations.

ANATOMY AND HISTOLOGY OF THE GONAD

Although this study was undertaken to define the reproductive cycle, a basic knowledge of the anatomy and histology of the gonad was necessary to understand the changes taking place during the year.

The gonad is an integral part of the visceral mass (Figures 3 and 4). It lies generally ventral to but also extends laterally upward around the digestive diverticula, is enclosed within the visceral epithelium, and surrounds loops of the intestine. It consists of anastomosing gonadal follicles and connective tissue. In a ripe individual the gonad makes up about one-third of the visceral mass.

Gonads in Juveniles

In immature geoducks, the gonad makes up a small part of the total viscera. In cross-sections it is seen to consist mostly of connective tissue, but small oval or flattened gonad follicles appear here and there. The follicles are distinguished from the other parts of the viscera by their position in the connective tissue, their small size and thin walls, and their contents of small, strongly-basophilic, primordial germ cells (Figure 5).

In larger but still immature geoducks, the epithelium of the follicles develops into two parts: one with cuboidal ciliated cells, and the other without ciliated cells and appearing to be germinal (Figures 6 and 7). Follicles like these have been reported in young oysters (Coe, 1932; Galtsoff, 1964) and mussels (Field, 1924), but not in clams; although Stickney (1963) noted a similar appearance in the terminal gonoducts of *Mya arenaria*. In geoducks, these follicles are not always positioned near the edge of the gonad with the ciliated epithelium closest to the visceral

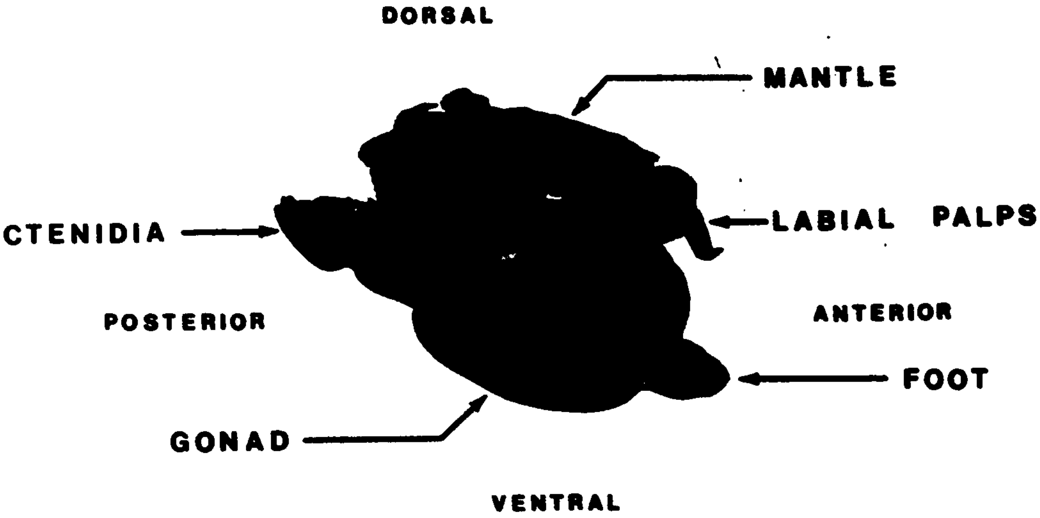

Figure 3. Side view of a visceral mass (life size).

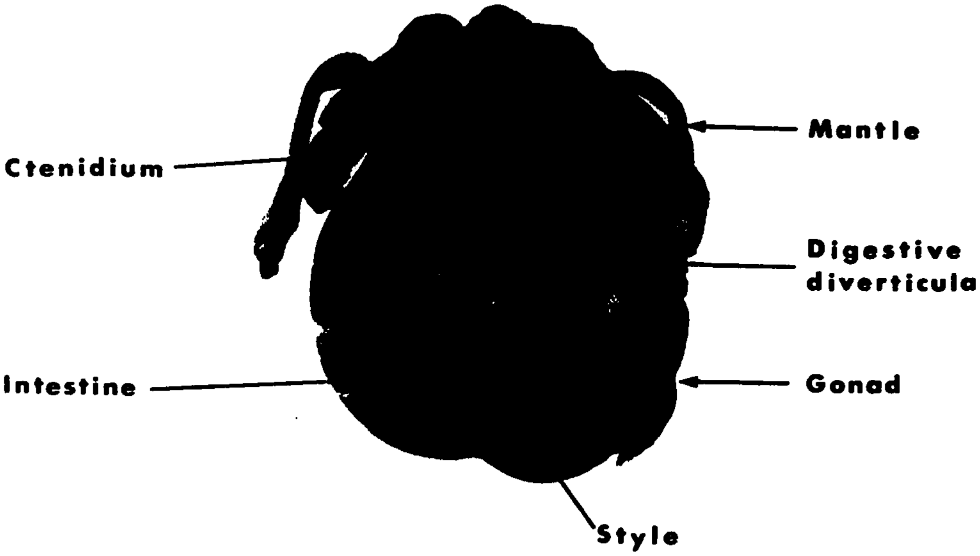

Figure 4. Cross section through the visceral mass (life size).

Figure 5. Photomicrograph showing primordial gonad tissue (at left) in a transverse section of a 2-cm-long geoduck (X240).

Figure 6. Photomicrograph showing juvenile gonadal follicles (F), a sperm duct (D), and a blood vessel (B) in a cross section of an 8-cm-long geoduck (X70).

Figure 7a. Photomicrograph showing the germinal section (at top and right) and ciliated section (at bottom and left) of a young gonad follicle (X300).

Figure 7b. Photomicrograph showing a mature sperm duct (at left) and a mature follicle in the Spent-Resorbing stage (at right) (X400).

Figure 8a. Photomicrograph showing spermatozoa-filled sperm duct in a poorly-fixed, spent male (c.f., Figures 7a and 13) (X300).

Figure 8b. Photomicrograph showing a spermatozoa-filled sperm duct (at left) and a partially-spawned follicle (at right) in a young male geoduck (X70).

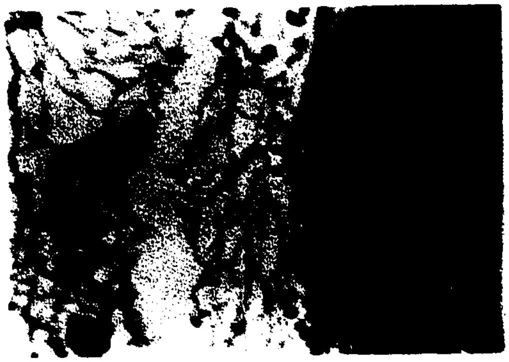

Figure 5.

Figure 6.

Figure 7a.

Figure 7b.

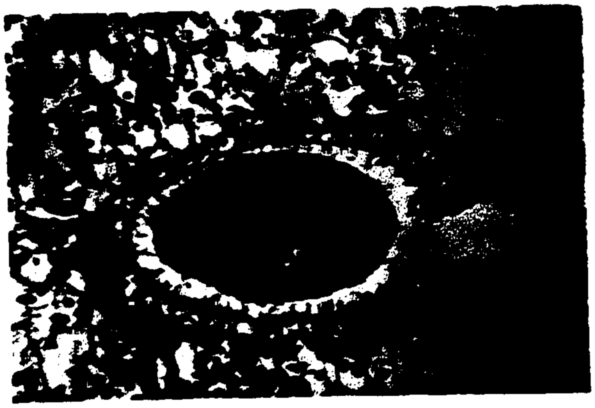

Figure 8a.

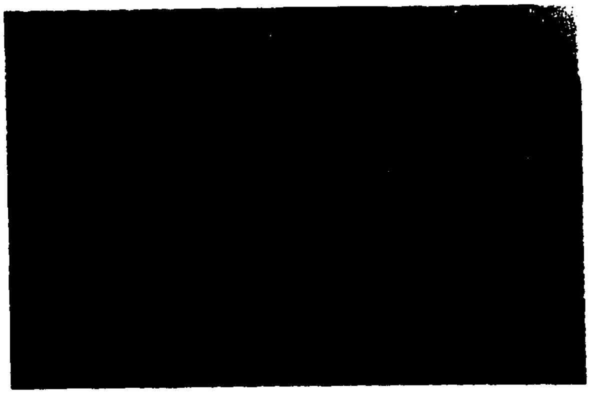

Figure 8b.

surface as they are in oysters (Galtsoff, 1964); they often occur throughout the gonad and either side may be closest to the visceral surface.

The two sexes are indistinguishable in juvenile geoducks. They have neither secondary nor primary sexual characteristics. The sex of the primordial germ cells (also called stem or indifferent cells)--precursors of ovogonia and spermatogonia--cannot be determined. Cole (1942) distinguished ovogonia from spermatogonia in *Ostrea edulis* at the earliest stages of development, but in most pelecypods this distinction is impossible (Coe and Turner, 1938; Galtsoff, 1964; Lammens, 1967; Quayle, 1943; Tranter, 1958b).

Gonads in Adults

In many respects the mature geoduck gonad resembles the mature gonad in other pelecypods, but there are some differences.

Follicles: A mature gonad has many follicles; the number of follicles and size of the follicles change seasonally. The follicle wall is not a true germinal epithelium but is composed of modified connective tissue, as in pearl oysters (Tranter, 1958b) and mussels (Wilson and Hodgkin, 1967). The follicle wall is thickest in spawned-out old clams and thinnest in ripe, young clams. In ripe ovaries, the wall between adjacent follicles often ruptures. In addition to the germ cells, the follicles often contain blood corpuscles. They do not, however, contain the "follicle cells" common in *Mya* and other pelecypods (p. 24).

Blood corpuscles: Bivalve molluscs typically possess two distinct groups of blood cells, although variation often occurs within a group (Galtsoff, 1964; Hill and Welsh, 1966). Two types of blood corpuscles occur within the gonads of geoducks; both are amoeboid.

The first type resembles the phagocytic hyaline cells of oysters (Galtsoff, 1964). They are usually eosinophilic, roughly-spherical, about 9μ in diameter, and have a roughly spherical, basophilic nucleus about 3 μ in diameter (Figure 14). In hematoxylin-and-eosin-stained tissues, the cytoplasm may be greyish-blue rather than the more typical pinkish-red. These cells are abundant and occur in all tissues. They are similar but considerably larger than the type B and C cells of pearl oysters (Tranter, 1958b). They appear to behave as and perform the same functions as the phagocytes of Yonge (1926) and Pauley and Sparks (1967).

The second type resembles the granular or brown pigment cells of oysters (Galtsoff, 1964; Pauley and Sparks, 1966). They are less abundant than the hyaline cells and occur mostly in the connective tissue, though they, too, are found in the follicles. In hematoxylin-and-eosin-stained tissues they vary in color from clear to grey to almost goldish. They often, but not always, contain granules. These cells are mostly ellipsoidal and larger than the hyaline cells. They measure about 1.8μ long. Generally, an elliptic, basophilic nucleus about 8 in maximum length is found at one end of the cell. They resemble the type A blood cell in pearl oysters (Tranter, 1958b) but are two to three times larger. These granular cells appear to be involved in phagocytotic and nutritive functions.

Nutritive cells: In the geoduck, connective tissue cells surrounding the gonadal follicles provide nutrition to the developing gametes. As gametogenesis progresses and the follicles increase in diameter, there is a corresponding decrease in the amount of connective tissue. Eosinophilic (lipid or glycogen) droplets in the connective tissue cells are probably a major high-energy source. These droplets are apparently homologues of the follicular cell inclusions found in *Mya arenaria* (Coe and Turner, 1938;

Pfitzenmeyer, 1965). Similar histological features occur in oysters (Galtsoff, 1964), mussels (Field, 1924; Wilson and Hodgkin, 1967), in pearl oysters (Tranter, 1958a,b,c,d; 1959), and apparently in some other clams (Ko, 1957; Loosanoff, 1937b, 1953; Porter, 1967; Ropes, 1968a; Stickney, 1963; Takahashi and Yamamoto, 1970).

In contrast, nutritive or follicle cells within the follicles provide nourishment to the developing gametes in three clams--*Mya arenaria* (Coe and Turner, 1938), *Paphia staminea* (Quayle, 1943), and *Macoma balthica* (Lammens, 1967)--and the jingle, *Pododesmus cepio* (Leonard, 1969).

Orton (1927) mentions that Sertoli or nurse cells connect sperm to the follicle walls in *Ostrea edulis*. Loosanoff (1937b) also noted that "fine protoplasmic strands connect the [developing sperm] cells with the follicle walls [as] undoubtedly the nutritive materials are delivered to the developing cells through the strands." Sertoli cells were not apparent in the follicles of male geoduck gonads. They did, however, have the fine protoplasmic strands Loosanoff noted.

Cells similar to the "partition cells" Porter (1967) describes in *Mercenaria mercenaria* occurred in maturing ovarian follicles. The mature and spent females lacked the partition cells but had an intra-follicular "tissue" similar to that in oysters (Korringa, 1952) and pearl oysters (Tranter, 1958b). Korringa suggested that this tissue was an accumulation of amoebocytes. Tranter agreed. In geoducks, this tissue is apparently a combination of the hyaline-type blood cells (amoebocytes) and remains of ovocytes.

Testes and spermatogenesis: Spermatogenesis in geoducks appears identical to spermatogenesis in other pelecypods. The primordial germ cells give rise to spermatogonia along the inner wall of the follicles. The spermatogonia, in turn, give rise to primary spermatocytes lying free in the lumina adjacent to the follicular walls. Progressing toward the center of the lumina are the secondary spermatocytes, spermatids, and finally the spermatozoa. The spermatozoa lie with their pointed and slightly-curved basophilic heads packed closely together and their eosinophilic tails streaming into the centers of the lumina.

In ripe males all stages of spermatogenesis are present. But in spent males or in those where spermatogenesis is just beginning, only spermatogonia are present. The spermatogonia--as in oysters (Galtsoff, 1964) and mussels (Wilson and Hodgkin, 1967) but unlike those in pearl oysters (Tranter, 1958b) and in the clam, *Paphia staminea* (Quayle, 1943)--are indistinguishable from ovogonia. Adult male geoducks, however, can always be identified from histological sections, regardless of what state of maturity they are in. Adult males have distinctive sperm ducts (Figure 8a).

The sperm ducts are characterized by a convoluted epithelium composed of lightly-basophilic, ciliated, columnar cells. These ducts closely resemble the ductus epididymis in mammals (Bloom and Fawcett, 1962). Because they are ciliated and are either empty or contain spermatozoa, they are definitely involved in moving sperm from the follicles. They might also produce secretions. Apparently they are derived from the ciliated part of the primary follicles in immature clams (see Figure 7). The tissues producing the convolutions closely resemble the "follicle cell stalks" Quayle (1943) noted in juvenile *Paphia* follicles.

Ovaries and ovogenesis: Ovogenesis, too, is similar to that in other pelecypods. Ovogonia develop from the primordial germ cells in the follicle walls. They, in turn, produce primary ovocytes. The primary ovocytes grow into the lumina as they develop, but remain attached to the walls until grown. Nourishment, apparently derived from the connective tissue surrounding the follicles, enters the primary ovocytes through their stalks (Eble, 1970; Takahashi and Yamamoto, 1970). When the primary ovocytes are fully grown they break off from the follicle walls and become free in the lumina.

The ovocytes do not undergo the final meiotic divisions that result in the production of polar bodies while they are in the follicles. In many pelecypods, final maturation occurs after the ovocytes are discharged and are fertilized (Allen, 1953; Galtsoff, 1964; Quayle, 1943; Stickney, 1963; Tranter, 1958a,b, 1959). In others, however, the primary ovocytes undergo the last meiotic divisions as they pass through the terminal gonoducts (Loosanoff, 1953; Stickney, 1963). Whether geoduck ovocytes mature before or after they are spawned is unknown.

Another feature of geoduck ovocytes is the presence of a gelatinous layer around each. In histological sections this layer appears as an invisible barrier separating the ovocytes. It stains neither with hematoxylin nor with eosin, although when the ovocytes are put in sea water the layer can be seen (Goodwin, 1970).

The presence of a gelatinous layer surrounding the ovocytes varies among the pelecypods. The layer is absent in oysters, jingles and some clams (Edmondson, 1920; Galtsoff, 1964; Leonard, 1969); it has been recorded as a part of the ovocyte in several pelecypods (Allen, 1953; Breese and Phibbs, 1970; Coe and Fitch, 1950; Edmondson, 1920; Field, 1924; Lammens, 1967); and it apparently occurs in others--it is evident in published photomicrographs--but it is not discussed (Calabrese, 1970; Loosanoff, 1937b; Quayle, 1943; Ropes, 1968a; Stickney, 1963). Allen (1953) reports that in Spisula the gelatinous layer can be stained with toluidine blue or Janus green B.

STAGES OF GAMETOGENESIS

Many schemes have been used to divide the continuous process of gametogenesis into stages (Lammens, 1967; Loosanoff, 1942; Ropes, 1968a; Tranter, 1958b). The scheme used here follows that of Ropes. Six stages of maturity were determined by the relative amounts of connective tissue, abundance of spermatozoa or primary ovocytes, size of follicles, and presence of phagocytes. Similar stages were used for males and females: early development (or early active), late development (or late active), ripe, partially-spawned, spent, and resorbing. Since the process is continuous the divisions between adjacent stages are indistinct.

To quantify the changes in size of the follicles, ovocytes, and ovocyte nuclei and nucleoli as the ovaries matured, the four items were measured in histological preparations. Tissues from five gonads in each of the first four stages of maturity (early, late, ripe, and partially-spawned) were used. Twenty-five measurements were made of each item in each preparation.

Because none of the items is a perfect circle in tissue sections, there was a problem of how to measure them. None of the other workers reporting on the linear dimensions of these items in clams discusses his measuring techniques. Clark (1925, 1934) obtained unbiased average diameters of fish eggs, however, by holding a micrometer in one position and measuring the diameter of an ovum on an axis parallel with the micrometer, regardless of the direction of the ovum's long axis.

To determine if Clark's method would yield unbiased averages for irregularly-shaped items in histological sections, vertical (N-S) measurements were compared with horizontal (E-W) measurements. For each of a sample of 16 tissue sections, 24 follicles, ovocytes, and ovocyte nuclei and nucleoli were measured. In each tissue section, 12 follicles were randomly selected and measured along their vertical axis and another 12 were randomly selected and measured along their horizontal axis. Ovocytes were selected and measured similarly, however, only the most mature (largest) ovocytes that clearly showed the nucleus and nucleolus were measured. For each ovocyte measured, its nucleus and largest nucleolus were also measured and they were measured along the axis the ovocyte was measured on. The means of comparable vertical and horizontal measurements were then tested for equality with "Student's" t-test.

The results of these comparisons were unexpected. For follicles and nucleoli the hypothesis of equal means was never rejected ($p > 0.05$). For ovocytes the hypothesis of equal means was rejected once ($p < 0.01$). And for nuclei the hypothesis was rejected ($p < 0.01$) four of 16 times.

The reasons for the differences in the ovocyte and nuclei means are unclear. Apparently the tissues were compressed slightly along one axis when they were cut by the microtome. The compression was not enough to affect the means of the large and highly variable follicles and the small and consistent nucleoli, but was enough to affect the means of the ovocytes and nuclei.

Therefore, the sample of 25 measurements for each item in each tissue section consisted of 12 measurements along one axis and 13 measurements along the other axis. Table 1 summarizes the measurements for follicles, ovocytes, nuclei, and nucleoli for each stage of maturity. Appendix 1 contains the values for each of the 20 tissue sections.

Figure 9. Photomicrograph of a male follicle in early development. The lighter spermatocytes occur along the borders of the follicle, with the smaller and darker spermatids toward the center (X400).

Figure 10. Photomicrograph of a cross section through a 9-cm-long male geoduck in late development. The follicles (right and top) have grown and now contain some spermatozoa. Note the two-part, young follicle in the center (c.f., Figure 7a). The visceral epithelium is at the right (X70).

Figure 11. Photomicrograph of ripe male follicles filled with spermatozoa. A sperm duct containing a few spermatozoa is at the upper right (x70).

Figure 12. Photomicrograph of partially-spawned male follicles and a spermatozoa-filled sperm duct (center) (X70).

Figure 13. Photomicrograph of a section from a spent male, showing the nearly empty follicles and one spermatozoa-filled sperm duct (c.f., Figure 8a) (X70).

Figure 14. Photomicrograph of male follicles containing spermatozoa being resorbed by phagocytes (X400).

STAGES OF SPERMATOGENESIS

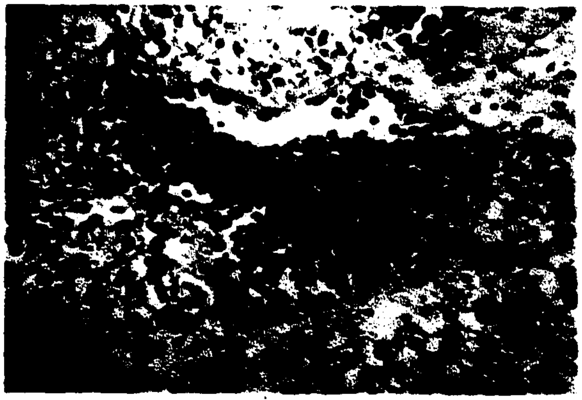

Figure 9. EARLY DEVELOPMENT

Figure 10. LATE DEVELOPMENT

Figure 11. RIPE

Figure 12. PARTIALLY-SPAWNED

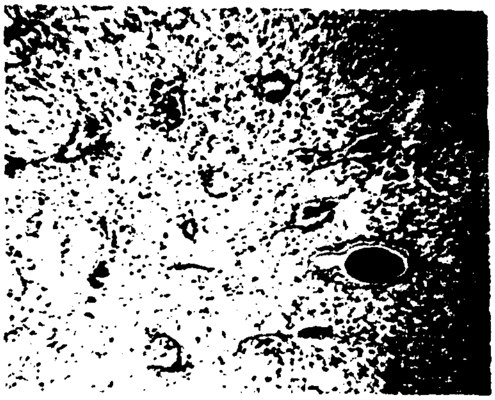

Figure 13. SPENT

Figure 14. RESORBING

Table 1. Summary of measurements (in microns) of four characteristics of geoduck ovaries in four stages of maturity. For each stage the values are averages of 25 measurements from each of 5 ovaries ($n_i = 5(25)$, $N = 500$; $\overline{X}$ = average, S_x= standard deviation).

Characteristic		Stage 1	Stage 2	Stage 3	Stage 4
Follicles	$\overline{X}$	177.5	293.1	674.3	393.3
	S_x	106.0	206.5	468.0	248.8
Ovocytes	Minimum	11.9	9.6	43.0	40.7
	Maximum	35.8	83.5	102.8	153.0
	$\overline{X}$	22.3	37.3	61.6	63.8
	S_x	4.0	7.5	9.9	13.8
Nuclei	$\overline{X}$	12.5	20.5	35.8	32.5
	S_x	1.8	2.9	3.6	4.7
Nucleoli	$\overline{X}$	4.6	6.3	11.7	11.0
	S_x	0.5	1.0	1.6	2.0

Stages of Spermatogenesis

Stage 1. Early active (Figure 9). Testes in the early active stage are characterized by large amounts of connective tissue and small follicles partially filled with early spermatogenic stages. Spermatozoa are rare or absent.

Stage 2. Late active (Figure 10). By the late active stage, the amount of connective tissue has diminished and the follicles have grown in size and increased in number. The follicles are nearly filled and contain numerous spermatozoa. Generally, there is a greater volume of early spermatogenic stages than of spermatozoa.

Stage 3. Ripe (Figure 11). Ripe testes are easily recognized. They consist of large, full follicles separated by thin bands of connective tissue. Spermatozoa are dominant. Many spermatids and fewer spermatocytes, though, are still evident. The sperm ducts often contain mature spermatozoa.

Stage 4. Partially spawned (Figure 12). Partially spawned testes are distinguished from ripe testes by the less-dense appearance of the follicles and the sperm-filled sperm ducts. In late Stage 4 testes, the follicles have open lumina and contain few spermatozoa. Early spermatogenic stages are often present.

Stage 5. Spent (Figure 13). In spent testes, the follicles have become much reduced in size and contain few spermatozoa, some are empty. The sperm ducts are often distended but contain few spermatozoa. Connective tissue has become the dominant tissue in the gonad.

Stage 6. Resorbing (Figure 14). Stage 6 testes differ from those in Stage 5 only by having numerous phagocytes in the follicles and connective tissue.

Stages of Ovogenesis

The stages of ovogenesis corresponding to the stages of spermatogenesis are defined as follows:

Stage 1. Early active (Figure 15). Geoduck ovaries are characterized in the early active stage by vast amounts of connective tissue and small ovarian follicles. The follicles average 177.5 μ in diameter, have obvious lumina, and relatively thick walls. Ovogonia are attached along the inner surface of the follicle walls. There are also a number of young primary ovocytes; these average 22.3 μ in diameter and contain nuclei averaging 12.5 μ with nucleoli averaging 4.6 μ in diameter.

Stage 2. Late active (Figure 16). The ovaries now characteristically have a greater number of larger follicles than Stage 1, and the follicles contain a greater number of larger primary ovocytes. The follicles average 293.1 μ in diameter. Their walls have become thinner, and the lumina are becoming filled with primary ovocytes. The ovocytes average 37.3 μ in diameter and contain nuclei averaging 20.5µ with nucleoli averaging 6.3µ in diameter. Often a nucleus contains more than one nucleolus, a normal condition according to Bloom and Fawcett (1962).

Stage 3. Ripe (Figure 17). The ripe ovaries are easily recognized. Connective tissue has almost disappeared, except where it occurs in bands of varying thickness separating the follicles. The follicles have not only grown larger, but in many instances the wall between adjacent follicles has ruptured. The follicles now average 674.3µ in diameter.

The primary ovocytes have also grown and become more numerous. Many have broken away from the follicle wall and are free in the lumina. The primary ovocytes average 61.6µ in diameter and contain nuclei averaging 35.8µ with nucleoli averaging 11.7µ in diameter. The nucleoli are generally of two parts--one staining lightly and the other a dark, basophilic nucleolinus--the amphinucleoli of Allen (1953). Frequently a nucleus contains more than one nucleolus.

Stage 4. Partially spawned (Figure 18). In Stage 4 ovaries the follicles have begun to decrease in size, they average 393.3µ in diameter, and some are without primary ovocytes. Most of the remaining ovocytes are free of the follicle walls, although some small ones remain attached and appear to be growing. The large ovocytes average 63.8µ in diameter and contain nuclei averaging 32.5µ with nucleoli averaging 11.0µ in diameter.

Stage 5. Spent (Figure 19). The ovaries of spent geoducks characteristically have many small, empty follicles surrounded by vast amounts of connective tissue. Although most are empty, a few follicles still contain one or two residual grown ovocytes; occasionally they contain ovogonia and small, growing ovocytes.

Figure 15. Photomicrograph of a geoduck ovary in early development. The small follicles contain small primary ovocytes. The ovogonia line the follicle walls, but are difficult to identify (X70).

Figure 16. Photomicrograph of a geoduck ovary in late development. Primary ovocytes are filling the follicles (X70).

Figure 17. Photomicrograph of a ripe geoduck ovary. The follicles are nearly filled with large primary ovocytes, some still attached to the follicle walls. The spaces between the ovocytes are caused by an invisible (with hematoxylin and eosin) gelatinous layer surrounding each ovocyte. The connective tissue is greatly reduced in abundance (X70).

Figure 18. Photomicrograph of a partially-spawned geoduck ovary. In some places the walls between adjacent follicles have ruptured. Connective tissue is sparse (X70).

Figure 19. Photomicrograph of a spent geoduck ovary. The follicles are shrunken and contain few primary ovocytes. Connective tissue is becoming more prevalent (X70).

Figure 20. Photomicrograph of a geoduck ovary with phagocytes resorbing the remaining ovocytes. Connective tissue predominates (X70).

STAGES OF OVOGENESIS

Figure 15. EARLY DEVELOPMENT

Figure 16. LATE DEVELOPMENT

Figure 17. RIPE

Figure 18. PARTIALLY-SPAWNED

Figure 19. SPENT

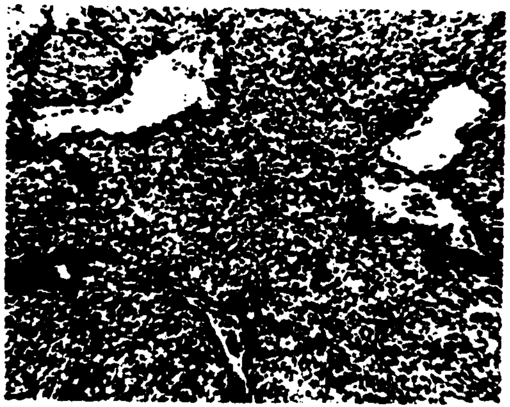

Figure 20. RESORBING

Stage 6. Resorbing (Figure 20). Ovaries in the resorbing stage differ from spent ovaries only because they contain noticeable numbers of phagocytes in the follicles and connective tissue. In some cases, ovocytes are being phagocytized. Occasionally the blood vessels are filled with phagocytes.

SIZE AT MATURITY

Since gonad samples were taken from geoducks ranging from 2.8 to 19.7 cm in shell length, the size at maturity could be determined (Figure 21). The percentages of those mature at various sizes are as follows:

Shell lengths (in cm)	< 4.5	4.5-5.5	5.5-6.5	6.5-7.5	7.5-8.5	≥8.5
Percentage mature	0	19	25	26	88	100

Interpolation gives 50% maturity at 7.5 cm.

Immature geoducks were as long as 8.2 cm. Although these immature clams had recognizable gonad tissue, their sex could not be determined.

Identifiable males ranged in length from 4.8 cm to 18.9 cm. Of the 175 males, 51 (29.1%) were shorter than 10.0 cm.

Identifiable females ranged in length from 8.5 cm to 19.7 cm. Two clams (6.2 cm and 7.1 cm) may also have been females, but their sex could not be positively determined. Of the 119 distinctive females, only three (2.5%) were shorter than 10.0 cm.

THE QUESTION OF PROTANDRY

The ratio of males to females (51:3) in geoducks having shells shorter than 10.0 cm indicated that geoducks might be protandric hermaphrodites.

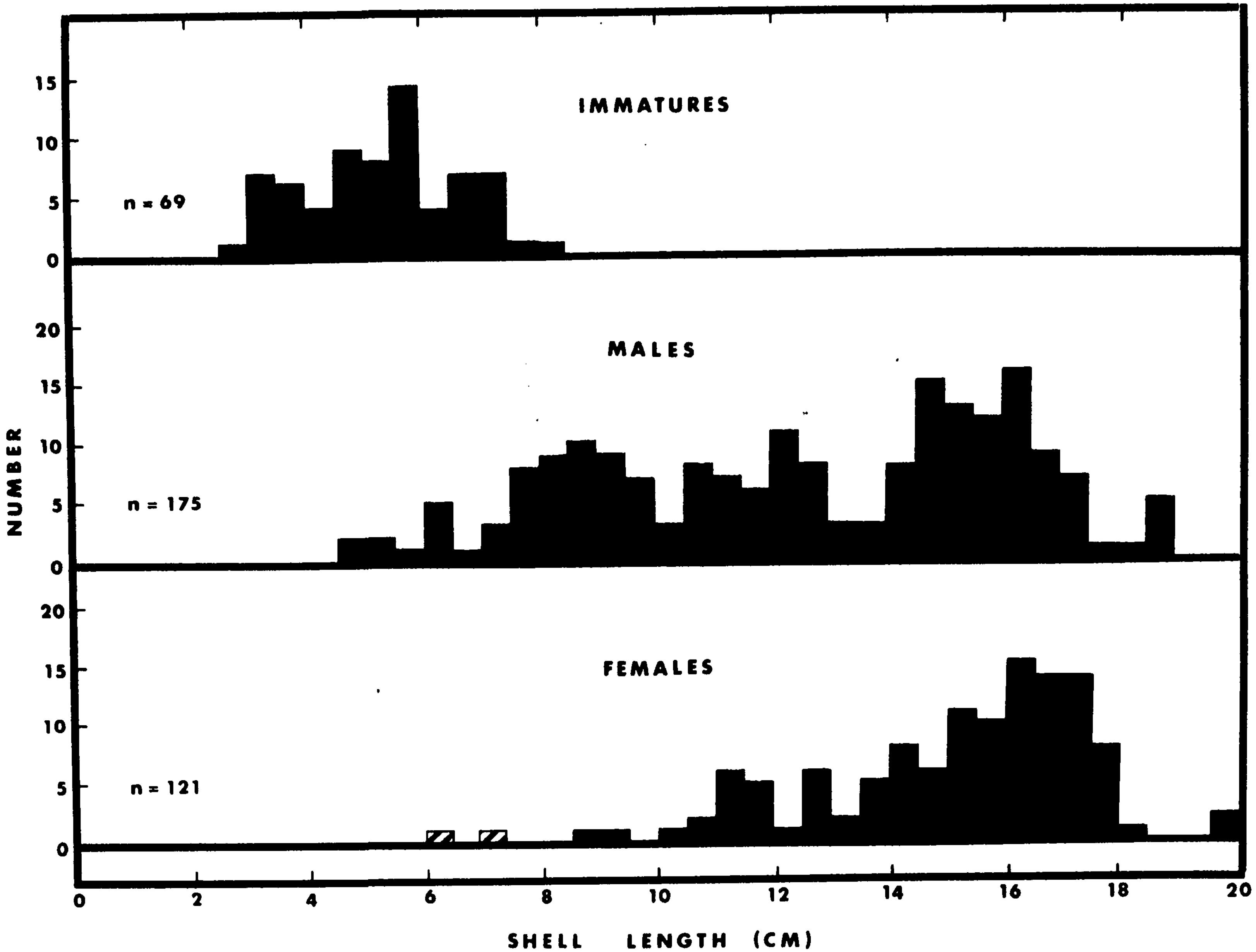

Figure 21. The relationship between size and sex in geoducks. The two hatched histograms with the females represent two possible, but not certain, females.

Similar ratios have been found in marine molluscs known to be protandric. Burkenroad (1931) reports that of American oysters, Crassostrea virginica, shorter than 2.0 cm. the ratio of males to females was 10 to 1. Leonard (1969) in his study on jingles, Pododesmus cepio, reports that 95% of those shorter than 4.0 cm were males. Many other examples are available: Coe, 1932; Fretter and Graham, 1964; Loosanoff, 1937a; and Tranter, 1958a, 1958b, 1959.

The histological evidence, however, fails to support the hypothesis of protandry indicated by the length-frequency distributions.

In the first place, none of the tissue sections contained hermaphroditic follicles. This evidence, however, is weakened somewhat by the infrequent collections and the small number of clams examined. During the 31 months of this study gonad samples were collected on only 56 days, with major collections one month or more apart. Tranter (1958d, 1959) collected pearl oysters twice a month. He believed he would have detected more hermaphrodites if he had sampled more frequently. Furthermore, in some clams hermaphrodites apprently occur infrequently. Fraser and Smith (1928), examining fresh smears of gonads, found only seven hermaphrodites in 3200 Paphia staminea. Quayle (1943), on the other hand, found no hermaphrodites in 1200 histological preparations of P. staminea. In a similar situation, Coe and Turner (1938) found three hermaphrodites in their study of Mya arenaria and report that less than 0.5% of the population was hermaphroditic. Other papers on M. arenaria make no mention of hermaphrodites (Pfitzenmeyer, 1965; Rogers, 1959; Ropes and Stickney, 1963). Ropes (1968b) examined histological sections of surf clams, Spisula solidissima and found only one hermaphrodite among 2500 clams. In this study, 396 geoducks were examined for sex and stage of maturity. Perhaps if hermaphrodites are rare in P. staminea, M. arenaria, and S. solidissima, they could be rare in geoducks too and be easily missed in small samples of the population.

Secondly, and more important, male geoducks were shown to possess well-developed and distinctive sperm ducts. These sperm ducts constitute a primary sexual characteristic useful for distinguishing males from females even when the sex of the gametes is in doubt.

In summary, geoducks are most likely gonochoristic. The question of protandry posed by the length-frequency distributions could be explained if female geoducks mature at a larger size than males. Furthermore, the absence of hermaphrodites and the presence of distinctive sperm ducts in males indicate that once a geoduck matures it does not change its sex.

AGE AT MATURITY

The size at maturity could be determined accurately. Not so the age at maturity. But on the basis of the size at maturity and the age-length relationship developed in the next section, the following conclusions could be drawn.

Geoducks are immature during their first year of life and many remain immature during their second year. By the end of their third year all have matured, but not all have spawned. Males mature faster than females.

For the males, some begin developing testes during their second year but apparently do not spawn. Most males spawn for the first time in their third year. Some may wait until their fourth year.

A few females develop ovaries and spawn in their third year. Most females, however, spawn for the first time in their fourth year when their shells are more than 10.0 cm long.

At these rates of sexual maturation, generations of geoducks would be about four years apart.

THE ANNUAL CYCLE OF REPRODUCTION

Gonad samples were collected from June 1967 through January 1970. In some months, however, none or few geoducks were collected. Because samples from months common to each year showed little yearly variations, the data for all years were combined by months for analysis.

The histological studies revealed a simple annual reproductive cycle in geoducks (Figure 22). Spawning occurs in a single mode from March to July. By late summer the residual gametes have been resorbed and gametogenesis begins anew. No period of rest or inactivity occurs. The cycle is continuous: developing, ripening, spawning, and resorbing.

The annual cycle begins in September when gonads in early stages of spermatogenesis and ovogenesis begin to occur in the samples. The percentage of early stages reaches a peak in October and then declines. Two males in May were still in the early stages, but most gonads had ripened by February.

Ripe gonads first appeared in November and were found until June. The percentage of ripe gonads reached a peak in March. The state of ripeness implied in the histological sections is supported, at least in males, by two direct observations. In the first case, a large male dug 23 January 1968 voluntarily discharged active sperm into an aquarium. In the second case, active sperm were observed in fresh smears taken from gonads of clams dug during December 1969 and January 1970.

Partially-spawned gonads first appeared in the samples in December. The percentage of spawned-out gonads gradually increased to a peak in May, then declined to July when the last were found.

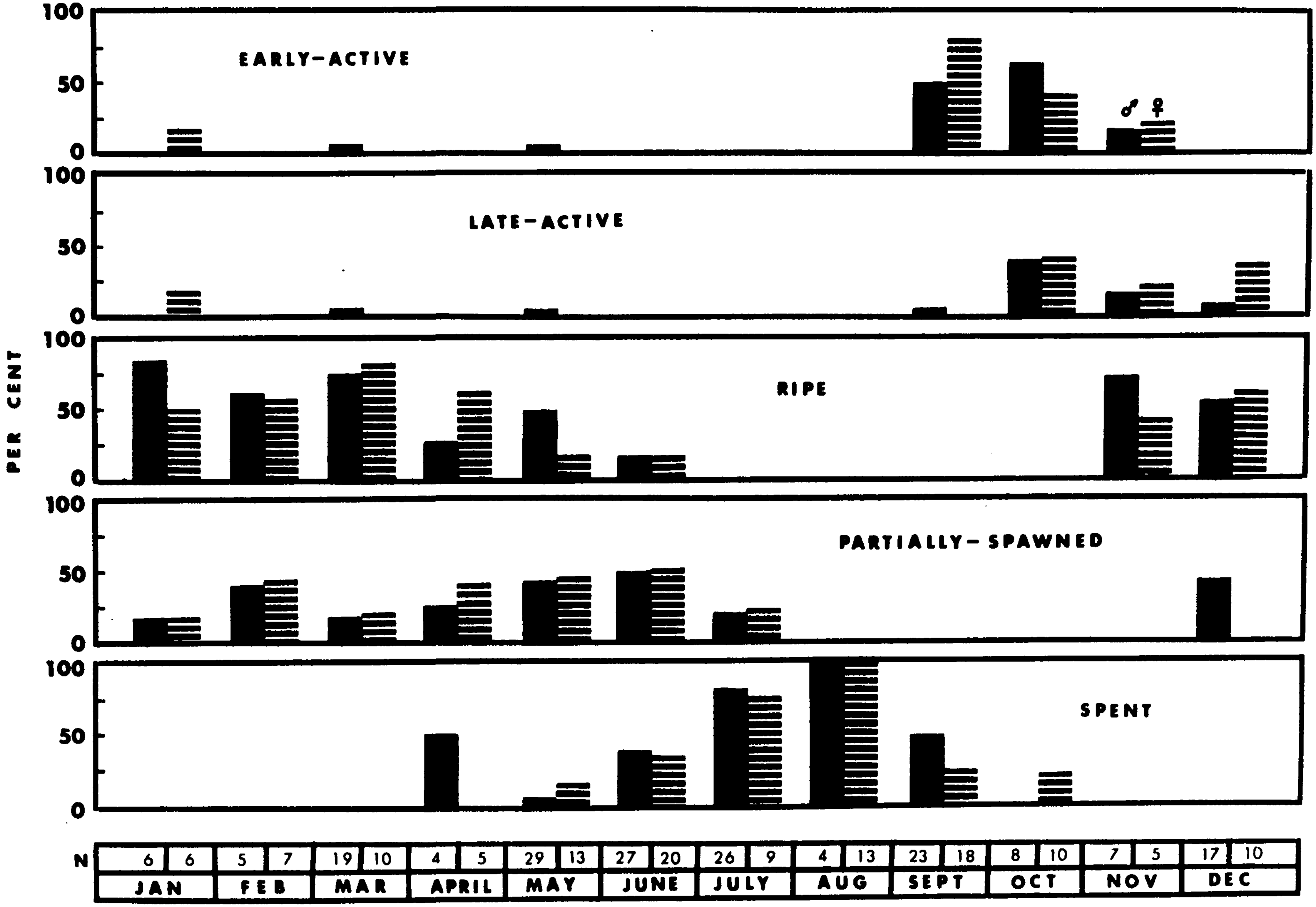

Figure 22. The annual cycle of reproduction in geoducks. The solid histograms are males, the hatched histograms are females.

Spent gonads first appeared in April. Here "spent" includes Stages 5 and 6, since the distinction between the two was the presence of phagocytes in Stage 6. The percentage of spent gonads in the samples reached a peak in August when 100% were spent. In September, early developmental stages started replacing the spent stages, and the annual cycle began again.

The sections also indicated that although males ripen earlier than the females both sexes finish spawning in June.

Variation between individuals within the population is also apparent, even with the small samples. In May, for example, the gonads of 29 males range from early development to spent. These five stages, incidentally, all appeared in the May 1969 sample.

Variation in the timing of the annual reproductive cycle probably occurs, as it does in other species. During this study yearly variation in the reproductive cycle appeared insignificant.

COMPARISONS OF RESULTS

Goodwin (1970) found that geoducks from Quilcene Bay (about 12 miles by water from Big Beef Creek) would spawn in the laboratory at temperatures from 9 to 16°C, and that above 20°C the larvae suffered heavy mortalities. My histological study revealed that geoducks spawned in 1967, 1968, and 1969, years with air temperatures about average (U.S. Weather Bureau, 1965-1970). Furthermore, Goodwin and I showed that geoducks spawn before the high summer temperatures are reached, and Lindsay (1966) stated that Geoducks spawned in the spring. It is unlikely, then, that unusually warmer years are necessary for a significant geoduck spawning.

The histological studies indicated that gametogenesis was an uninterrupted process. Goodwin, however, mentions a "period of inactivity" following spawning. In the Big Beef geoducks, even as the last gametes were being discharged or resorbed, new gametes were developing. Moreover, the connective tissue surrounding the follicles was proliferating, probably storing up nourishment to be transferred later to the developing gametes. Although a "resting" or "inactive" stage has been recorded for a number of bivalves, I agree with Ropes (1968a) that an inactive period, per se, does not occur.

Goodwin states that only the females showed a definite annual reproductive cycle. At Big Beef, however, although not all males were in the same stage of gametogenesis at the same time, males as well as females showed a definite annual cycle of reproduction.

My study and Goodwin's agreed on the size of the ova. Goodwin reported that newly-released ova averaged 80μ in diameter. In my study, the primary ovocytes within the follicles ranged from 40 to 150μ and averaged 62μ in diameter. Considering that the discharged ova are spherical and mature whereas the primary ovocytes are irregularly-shaped and immature, the sizes compare favorably.

Goodwin showed that at 14 to 17°C geoduck larvae lose their swimming ability in about one month. Thus, with geoducks spawning from March to July, the larvae probably set from April to August.

SUMMARY

1. The annual cycle of reproduction of geoducks was studied by examining 398 permanent histological preparations of gonads. These gonads came from geoducks ranging from 2.8 to 19.7 cm in shell length, and were collected from June 1967 through January 1970 at Dosewallips and Big Beef.

2. Geoducks are gonochoristic. No hermaphrodites were found. In fact, mature males were found to possess distinctive sperm ducts enabling

3. During the first year of their lives (when their shells are shorter than 4.0 cm) geoducks are immature. Most remain immature during their second year.

4. Most males spawn for the first time in their third year, when they have shells between 6.0 and 10.0 cm long.

5. Most females spawn for the first time in their fourth year, when they have shells between 10.0 and 12.0 cm long.

6. Primary ovocytes in ripe ovaries average 62μ in diameter. Each ovocyte is surrounded by a gelatinous layer.

7. Spawning occurs each year from March to July. Gametogenesis begins in September, the gonads are ripe by February, and by August all are spent.

8. Residual gametes are resorbed by phagocytic blood corpuscles.

9. Setting probably occurs from April to August.

10. These results agree, generally, with the two published notes on geoduck reproduction.

AGE AND GROWTH

The growth rate of geoducks was estimated by examining the growth lines on shells, by studying length-frequency distributions of geoducks collected from Dosewallips and Big Beef, and by planting and recovering tagged geoducks at Big Beef. In addition, the mathematical relationships between various body parts were determined.

GROWTH LINES ON SHELLS

Attempts to determine the ages of molluscs from growth lines on their shells have met with various degrees of success. The theory and technique are reviewed by Segerstråle (1960), Weymouth (1923), and Wilbur and Owen (1964). For many species annual marks have definitely been shown to occur (Ansell, 1961; Kenny, 1968; Lammens, 1967; Merrill, Posgay, and Nichy, 1966). Daily growth lines have even been recognized (Clark, 1968; Millar, 1968). In some species, however, annual marks either do not occur or are confused with other marks on the shells (MacKenzie, 1960; Olsen, 1968; Quayle, 1952; Tegelberg, 1964).

In this study, geoduck shells were examined to determine when the major growth lines occurred and to see if they could be used to estimate ages.

Methods

Several hundred shells collected during this project were examined. For each shell the collection location and date were known. Big Beef and Dosewallips shells were treated separately and then combined and reexamined.

To determine when the major growth lines occurred, shells dug at different times within one year were compared. Then shells dug in different years were compared to see if similar marks were laid down each year.

To test the value of the major growth lines as indicators of seasons, attempts were made to predict when the clams were dug.

For recovered tagged geoducks attempts were made to estimate how many months had elapsed between planting and recovery.

No attempts were made to age geoducks by examining cross sections of shells or hinge ligaments because of time limitations, although this method worked with sea scallops (Merrill, Posgay, and Nichy, 1966).

Results

After two-and-a-half weeks of trying to age geoducks from the markings on their shell, I gave up without success. More intensive studies with more frequent and larger samples, however, might have produced satisfactory results. In general, Big Beef and Dosewallips geoducks of the same size and dug at the same time showed similar markings. Yet geoducks of the same size but dug in different seasons, especially if they were dug in different years, could not be separated. Many geoducks apparently laid down two major growth lines each year, once in the spring and once in the fall. Significant marks, however, were also laid down at other times, often during early summer. The use of markings on the shells of tagged geoducks for predicting the time from planting to recovery often gave meaningless results.

LENGTH-FREQUENCY DISTRIBUTIONS

Length-frequency distributions were examined to detect age groups, and to determine the average lengths for the various age groups at different times. The data were then used to construct a theoretical curve for geoduck growth.

Methods

Usually the length-frequency distributions necessary for a growth study are developed from random samples systematically collected from the population.

In this study, however, the time available for work precluded regular sampling specifically for a study of growth. Instead, the length frequencies were developed from composites of samples dug for other purposes on the assumption that the resulting length-frequency distributions would be adequate for determining the rate of growth. For the Dosewallips, the large geoducks were dug by recreational diggers for their own use (experienced recreational diggers seek out large geoducks, inexperienced diggers are less particular). The small geoducks are the result of much effort by my assistants and me to collect small geoducks. For Big Beef, the length-frequency distributions included not only the recreationally-dug and small geoducks from the intertidal beach, but also random samples of subtidal geoducks collected for studies on the reproductive cycle. Thus, although the length-frequency distributions have wide ranges in lengths, they are not necessarily representative of the true abundance of the different sizes on these beaches.

Since comparisons showed the left and right lengths to be equivalent (Appendix 2) the length-frequency distributions are comprised of left lengths when they were available, otherwise right lengths were used.

Results

Dosewallips Geoducks

Dosewallips geoducks were collected during the spring and summer from 1967 to 1969, and once in January 1970. The length frequencies summarized by month are shown in Figure 23. The growth of three distinct year classes can be followed for several months. A summary of the lengths for each age group is contained in Table 2.

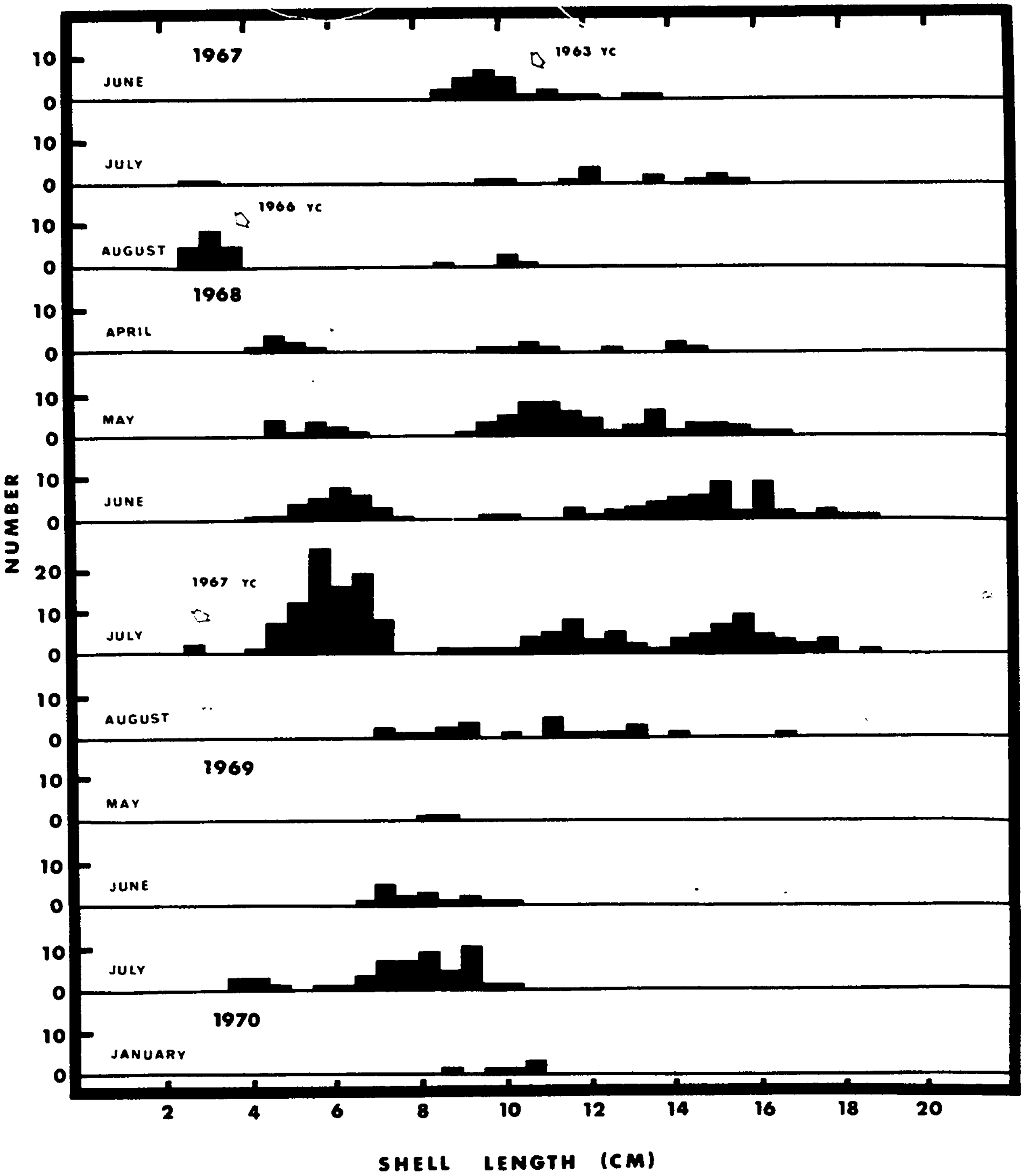

Figure 23. Length-frequency distributions of Dosewallips geoducks.

Table 2. Shell lengths of geoducks one to five years old, based on length-frequency distributions. Lengths in centimeters.

Area	Age in Years				
	1	2	3	4	5
Dosewallips					
Mean	3.22	6.00	8.16	9.92	11.90
Range	2.50-3.83	3.70-7.68	5.94-10.38	8.70-11.35	9.79-13.90
Number	24	127	60	30	49
Big Beef					
Mean	3.13	5.31	8.46	10.47	12.46
Range	3.07-3.21	4.19-6.74	7.11-10.00	8.84-11.83	11.46-13.85
Number	3	20	9	10	14
Combined					
Mean	3.21	5.90	8.20	10.06	12.03
Range	2.50-3.83	3.70-7.68	5.94-10.38	8.70-11.83	9.79-13.90
Number	27	147	69	40	63

The growth of the 1966 year class is the most obvious. Clams of this year class were first taken in 1967, at an average length of 3.0 cm in July and 3.25 cm in August. Samples of this year class were collected again in 1968, averaging 4.97 cm in April, 5.52 cm in May, 6.16 cm in June, 6.02 cm in July and 7.42 cm in August. In 1969, they occurred in the May, June, and July samples, with an average length of 8.11 cm in July. The last time this year class was sampled was in January 1970 when the average length was 10.16 cm. The assumption that these groups of clams are of one year class, the 1966 year class, is supported by: 1) the absence of other groups of small clams during 1967, 2) the regular progression of the histograms with time, 3) the occurrence of a new group of small clams in July 1968, and 4) the knowledge that geoducks spawn from March to July with the prediction that setting occurs from April through August. One further assumption is still necessary, that is, geoducks grow at least 2.0 cm and as much as 3.0 cm during their first year, say from June 1966 to June 1967. With the above assumptions, the 1966 year class had attained an average length of 3.0 cm at the start of its second year in July 1967, 6.02 cm by the start of its third year, 8.11 cm by the start of its fourth year and 10.16 cm in the middle of its fourth year.

A second group of small geoducks, represented by two individuals with lengths of 2.80 and 2.94 cm, appeared in the July 1968 samples. This group was apparently the 1967 year class. It appeared again in the July 1969 samples at an average length of 4.10 cm.

Finally, another distinct group, apparently the 1963 year class, was first noted in the recreational fishery in June 1967 at lengths averaging 9.70 cm and ranging between 8.50 and 11.0 cm. A few of this group were also taken in July and August of 1967. The 1963 year class showed up next in

April 1968 at an average length of 10.55 cm. In May, the average length had increased to 11.05 cm, and by July to 11.73 cm. The presumption that these clams were 4 years old when first taken is based on their lengths, and the relations between these lengths and the lengths the 1966 year class would have attained by its fourth year. Under the assumption these clams were, in fact, a single year class, their average length had increased 2.03 cm during their fifth year of life.

Big Beef Geoducks

Length-frequency distributions of Big Beef geoducks (Figure 24) support the inferences about growth rates drawn from the length-frequency distributions of Dosewallips geoducks. A summary of the lengths for each age group is contained in Table 2.

The first group of small Big Beef geoducks, probably the 1966 year class, was sampled the first time in May 1967. One clam, measuring 3.75 cm in length was taken. Two more, 3.07 and 3.11 cm were collected in June. Another, 3.90 cm, was collected in December 1967. During 1968, clams of this group were taken in May ($\overline{X}$ = 5.01 cm), June ($\overline{X}$ = 5.43 cm), and July ($\overline{X}$ = 4.94 cm). The decrease in average length between June and July is probably due to the small July sample. In 1969, this group appeared in the March sample ($\overline{X}$ = 7.62 cm), in May ($\overline{X}$ = 7.77 cm), in June ($\overline{X}$ = 8.35 cm), and in July ($\overline{X}$ = 8.62 cm). Thus, this group had increased in average length by 2.34 cm during its second year, and by 2.92 cm during its third year.

A second group of small geoducks, probably the 1968 year class, appeared in the samples collected during the spring of 1969. In May, two small clams, 2.08 and 2.62 cm in length, were dug from the intertidal beach at Big Beef. Another, 3.21 cm long was taken in June, and two more, 4.04 and 4.51 cm, were

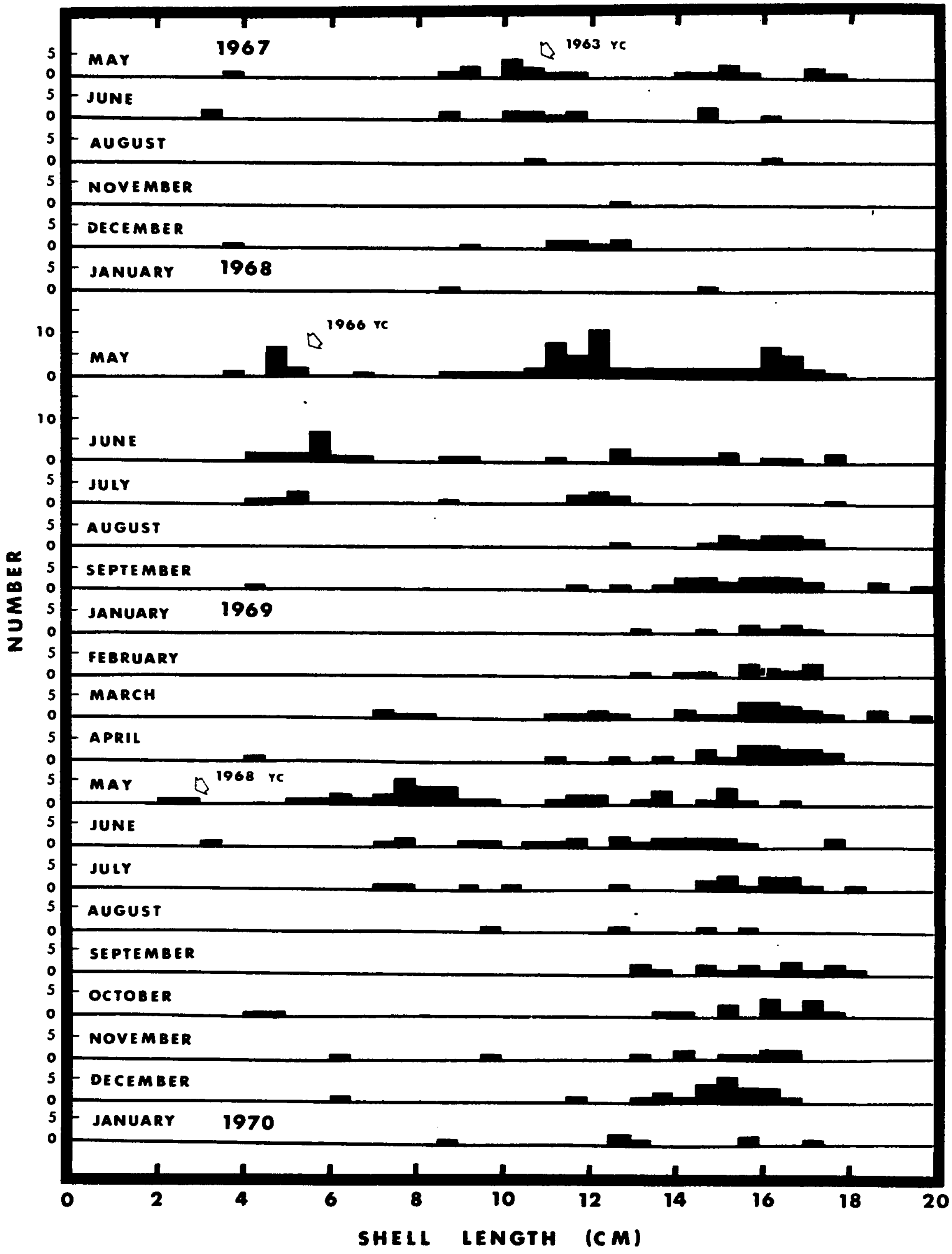

Figure 24. Length-frequency distributions of Big Beef geoducks.

collected in October. These clams follow the growth trend of the 1966 year class and conform with samples taken from the Dosewallips.

And, as with the Dosewallips clams, the growth of a third group of somewhat larger clams can be followed for a few months. This group, apparently the 1963 year class, first appeared in the samples from Big Beef in May 1967 with an average length of 10.20 cm. In June, the average length had increased to 10.25 cm, and by December to 11.62 cm. During 1968, this group appeared in the May sample, and although an average length is difficult to determine, the mode is about 12 cm. In July, this year class again appeared, this time as six clams having an average length of 12.25 cm. Thus, during their fifth year, the 1963 year class had grown from 10.25 cm to 12.25 cm, an increase of 2.00 cm.

Growth Curve

Growth data from the foregoing length-frequency distributions were fitted to a von Bertalanffy growth curve, $l_t = L_\infty(1-e^{-K(t-t_0)})$, where:

l_t is the length at any age, t,

L_∞ is the theoretical average maximum length attainable,

K is a constant determining the growth rate,

e is the base of Naperian logarithms, a constant, 2.718. . .,

and t_0 is the hypothetical age when a geoduck would have had zero length if it had always grown in the manner described in the equation.

Growth data from other molluscs have fitted this curve well (Hancock, 1965; Newman, 1968; Tomlinson, 1968; Wolfe and Petteway, 1968).

Using the prediction that setting occurs mostly during June, July, and August, the length-frequency distributions for the three months were pooled for each year to determine the mean length and range in lengths for each age group. To simplify analyses and presentation of the data, the start of a geoduck's life was assumed to be 15 July, the midpoint of the predicted period of setting. Thus, for example, the 1966 year class is assumed to have become one year old on 15 July 1967. Table 2 contains the resulting pooled means, ranges, and sample sizes for geoducks one to five years old.

Following the usual methods (Beverton and Holt, 1957; Ricker, 1958), the mean lengths in Table 2 of the combined Big Beef and Dosewallips geoducks were used to estimate the three parameters of the von Bertalanffy growth equation. Trial estimates of L_∞ and K were obtained from a Walford plot (Figure 25). These trial estimates were then used as data in a computer program[2] to find better estimates for L_∞, K, and an estimate of t_0. When the sample sizes were used as statistical weights the final estimates were: $L_\infty = 22.7$, $K = 0.15$, and $t_0 = -0.01$. When statistical weights were set equal to 1.0, the estimates became: $L_\infty = 22.9$, $K = 0.15$, and $t_0 = 0.05$.

For a comparison, the three parameters were estimated using only data from Dosewallips geoducks. When the sample sizes were used as statistical weights the final estimates were: $L_\infty = 22.34$, $K = 0.15$, and $t_0 = -0.05$

All the above estimates of L_∞ are realistic, being somewhat larger than the observed maximum length (20 cm) measured in this study.

The estimates of t_0 are all near zero, indicating that the growth of geoducks follows the von Bertalanffy growth curve from time of setting, when they are about one month old.

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[2] Weighted nonlinear least squares parameter estimation, FRG 709 programmed by Lawrence E. Gales, Fisheries Research Institute, University of Washington, 1964.

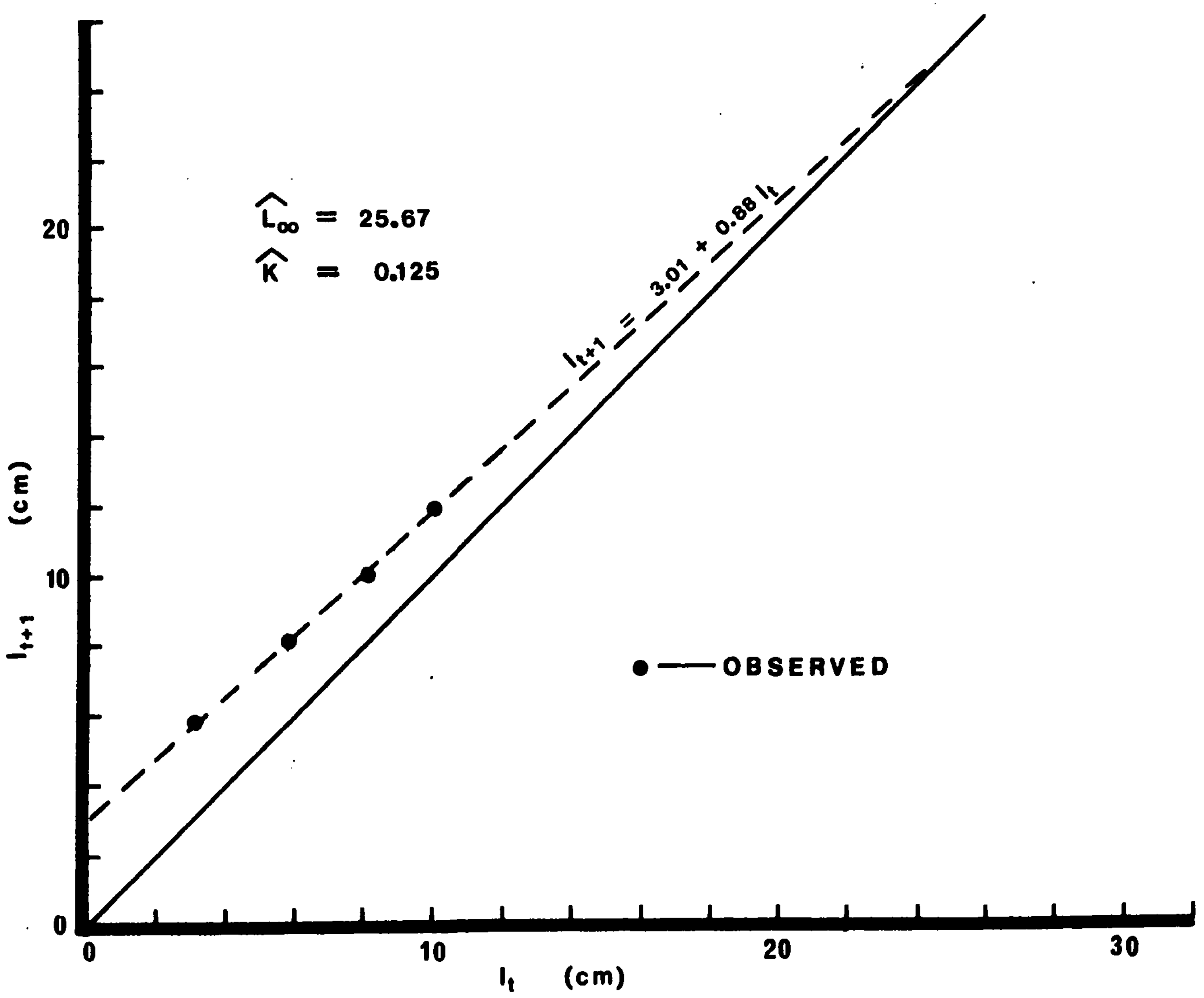

Figure 25. Walford plot, of valve length (in cm) at year t + 1 against valve length at year t, for combined Big Beef and Dosewallips geoducks (Table 2).

The exact values for the estimates of L_{∞}, K, and t_0 are unimportant, however, since the growth data used to obtain them was derived from four year classes from two beaches during three years. A specific year class could have parameters quite different from these estimates, depending upon the specific growing conditions (e.g., temperature, food, population densities, etc.) it encountered. A curve based on the estimates obtained from the data used, nevertheless, represents a general growth pattern for Dosewallips and Big Beef geoducks.

In constructing the theoretical growth curve shown in Figure 26, therefore, rounded values of the parameter estimates were used, with L_{∞} = 22.5 cm, K = 0.15, and t_0 = 0 years. The plot of the observed lengths for geoducks aged one to five in Figure 26 shows how well the theoretical curve based on these estimates fits the observed data. There are dangers, of course, extrapolating a curve past the observed data, but geoducks much larger, and obviously much older than those used to determine the curve were collected. I feel confident that the curve in Figure 26 represents the growth of geoducks up to age 20. Whether a geoduck will live to age 40 is unknown; some clams will (Comfort, 1957).

The main shortcoming of this curve is that it reaches an asymptote, L_{∞}. As will be shown later, geoducks apparently grow in length until they are about 20 years old, then they begin to shrink. Thus, the real growth curve for geoducks would begin to decline around age 20. But since the age of geoducks could not be told from their shell markings, the age when geoducks begin to decrease in length and the rate of decrease are unknown.

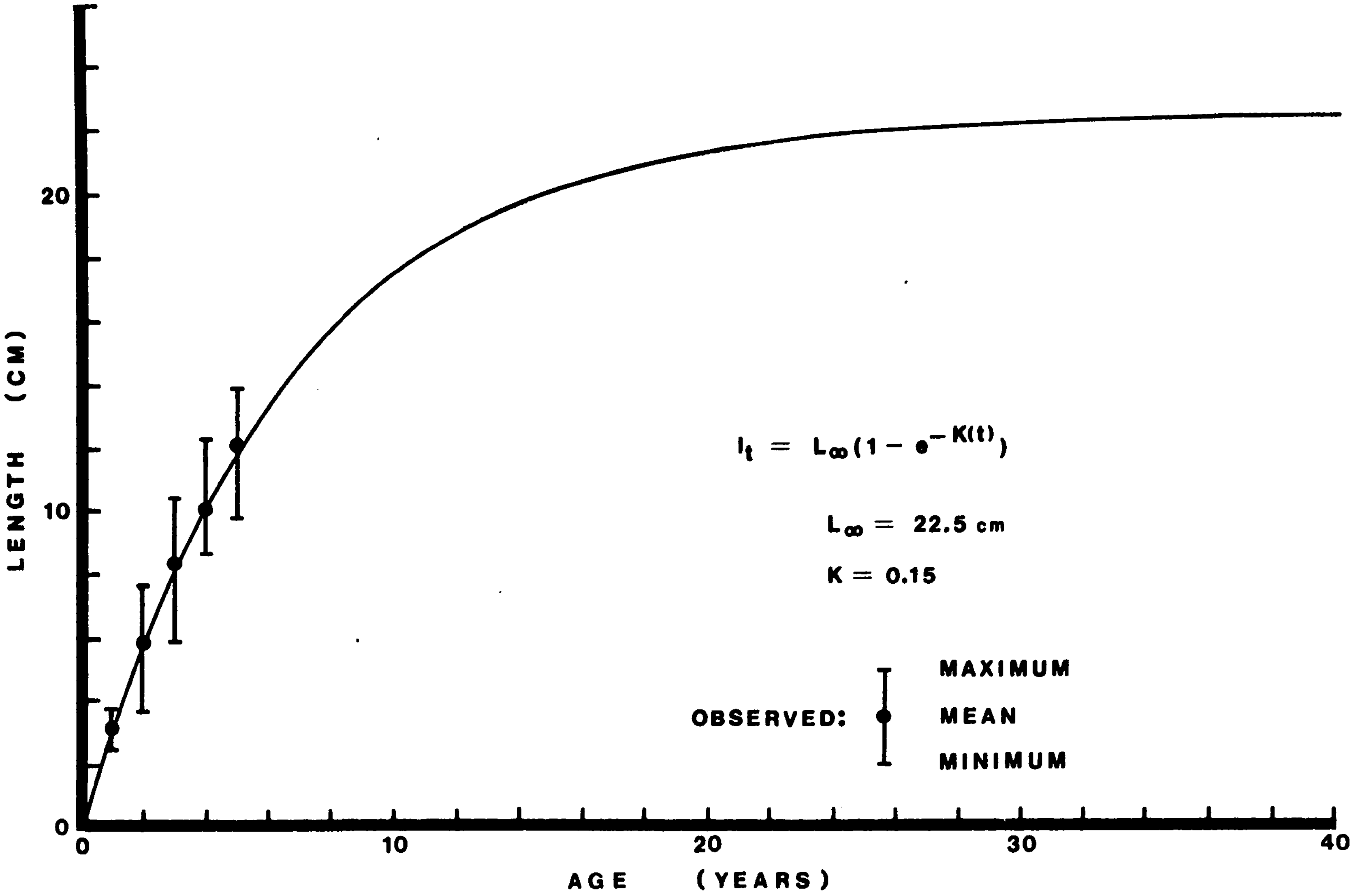

Figure 26. The von Bertalanffy growth curve for geoducks, growth in terms of valve length.

TAGGING

Geoducks were tagged, planted, and recovered in an attempt to fulfill four objectives: first, to determine if geoducks could be tagged, planted, and recovered successfully, since previous attempts had met with little success (C. E. Lindsay, personal communications); secondly, to determine seasonal rates of growth; thirdly, to determine the rate of growth at various beach levels; and finally, to provide a check on the growth rate estimated from the length-frequency distributions.

Overall, 215 geoducks were tagged. Of these, 24 died or were accidentally killed before they could be planted. Of the 191 planted, 56 (29%) were unaccounted for, 14 (7%) died, and 121 (63%) were recovered alive at least once.

Effects of Tagging and Planting

Geoducks generally tolerated the tagging and planting process well, although they were susceptible to breaking, poisoning, and freezing. They could live out of water for at least 24 hours if they were kept cool and damp, and they could withstand a change from 10 to 18°C in water temperature without noticeable ill effects.

Breaking was a primary source of mortality for tagged geoducks. Their shells, especially those of small geoducks, are easily cracked. Thus several were killed before they could be planted and eleven more were killed or injured as they were being planted. Yet even injured geoducks survived and grew (Figure 27).

Several also apprently died from poisoning. In one instance, small geoducks held overnight in a plastic bucket filled with sea water died while others held in another type of plastic bucket showed no ill effects. Three factors point to poisoning by heavy metals. First, many plastics are

Figure 27a, b, c. Photographs showing repaired breaks in the shells of tagged geoducks; a (X 0.49), b (X 0.92), c (X 0.35).

Figure 28a, b, c. Photographs showing marking checks on tagged geoducks; a (X 0.69), b (X0.35), c (X0.78).

a. Planted 9 July 1968 (6.04 cm)
Recovered 28 August 1969 (7.50 cm)
Recovered 30 December 1969 (9.71 cm)

b. Planted 11 July 1968 (5.86 cm)
Recovered 17 December 1969 (10.52 cm)

c. Planted 29 July 1969 (4.21 cm)
Recovered 17 January 1960 (5.10 cm)

Clam "c" shows only a slight marking check in comparison with those on clams "a" and "b." It also shows an autumn growth check, the heavy growth line appearing between the time it was planted and 6 months later when it was recovered.

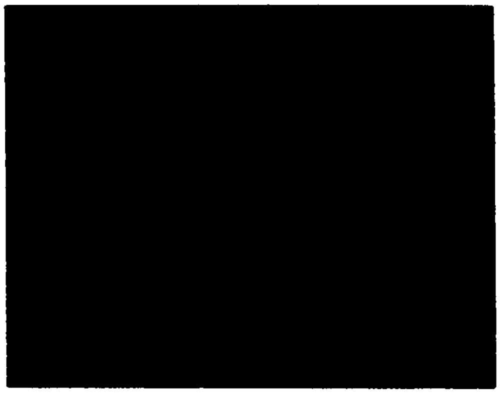

Figure 27a

Figure 27b

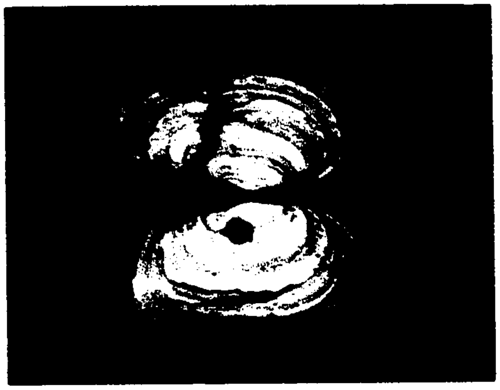

Figure 27c

Figure 28a

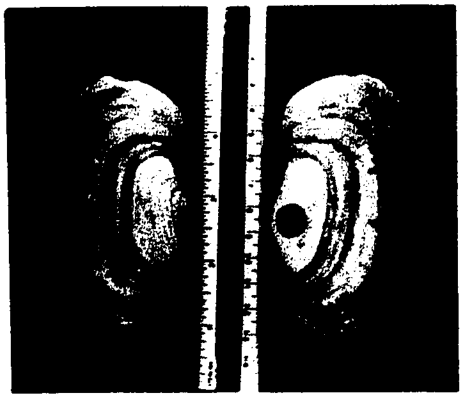

Figure 28b

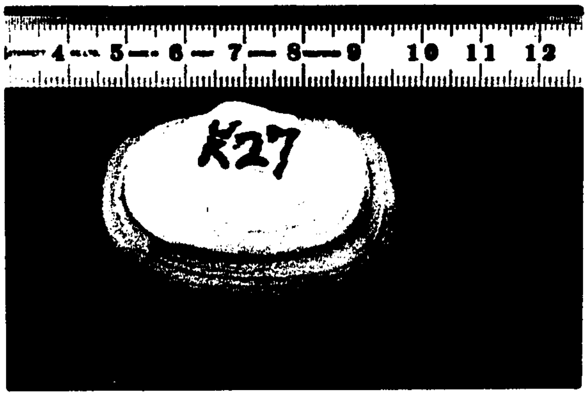

Figure 28c

known to contain heavy metals (e.g., Ba, Cd, Pb) from plasticizers, mold releases, and so on, whereas other plastics are relatively free of heavy metals (Autian, 1963a, 1963b, 1964). Secondly, small salmon (fry and fingerlings) survived in both types of plastic buckets before and after the buckets had held the geoducks. Finally, molluscs are apparently sensitive to heavy metals at concentrations unnoticed by fish. Geoducks also apparently died from poisoning on several occasions when they were held in aquaria supplied by the recirculating sea water system of the College of Fisheries, yet on other occasions they survived well. On those occasions when geoducks died, other shellfish in adjacent aquaria also died. The cause of these mortalities is unknown, but cannot be ascribed to low dissolved oxygen levels or temperature extremes.

A few geoducks died when they were exposed for several days to near-freezing temperatures, even though they were kept in aquaria with aerated and frequently-changed sea water. The exact cause of death is unknown, but the low temperature is suspected.

Overall, 24 (11%) of the 215 geoducks tagged, died or were accidentally killed before they could be planted.

Once planted, though, only 14 (7%) of 191 tagged geoducks were known to have died, although another 56 (29%) were unaccounted for. Nine of the known dead were in poor condition when planted, most having cracked or broken valves, but for none is the exact cause of death known. Those unaccounted for just disappeared; whether they died is unknown. Twelve (10 of these were less than 3.5 cm long) of those missing were among the first 19 tagged clams planted. Postplanting checks revealed that the first 19 tagged clams were not planted deeply enough, thus predators might have pulled out the missing clams soon after they were planted. There is some evidence, however, that small tagged geoducks could have worked their way out of the sand. On seven occasions small geoducks were found lying on the beach. Two were tagged. Of these, one was being eaten by several Searlesia dira snails, the other was whole and alive. The other five were untagged and were also found at Big Beef, one in the winter and four in the summer. All seven of these clams apparently came to the surface by their own activity. One of the tagged clams might have surfaced to avoid suffocating (see p. 90). Armstrong (1965), however, contends that geoducks are unable to surface. But it is unlikely that anything can pull a naturally-set geoduck out of the ground uninjured, if at all. The important point is that two tagged and five untagged geoducks were found lying free on the beach. If seven got to the surface, others--including the missing tagged clams--could have too.

Regardless of how well most geoducks tolerated the tagging and planting processes, the shock of being dug, handled, and having to adjust to a new burrow stopped growth temporarily and usually caused a marking check on the shells (Figure 28). Marking checks usually occur when bivalve molluscs are handled (Orton, 1926; Quayle, 1952; Tegelberg, 1964; Weymouth, 1923; Wilbur and Owen, 1964). Young geoducks held in aquaria for several days before being planted exhibited the most pronounced marking checks, whereas some large, old clams showed no marking checks.

Growth by Initial Size and Elapsed Time

After adjusting to their new burrows the tagged geoducks grew well. Some nearly doubled in size after 1.5 years. One, for example, grew from 5.16 to 10.27 cm, an increase of 5.11 cm (99%) in 524 days. In contrast, the clam out the longest time (587 days, decreased from 17.18 to 16.78 cm, the greatest decrease shown by any clam. In general, the amount of growth was inversely related to the length of the geoduck when it was planted and directly related to the amount of time between planting and recovery.

The inverse relationship between growth and length at planting can be seen in Table 3 . These data are taken from Appendix 3 , linear regressions of length change, Δl, on weeks elapsed from planting to recovery, Δt. The regressions predicted that geoducks less than 6.0 cm will grow about 2.81 cm in one year, whereas those 8.00 to 9.99 cm will grow about 0.99 cm, and those greater than 14 cm will shrink by 0.01 cm. The confidence intervals for the mean annual increases reflect the variation in growth of individual clams caused by inherent differences, and variation in growing conditions between years and between beach levels. As an example of variation in growth by individuals, two clams (4.76 and 4.84 cm long) were planted at the -1-foot beach level on the same day. In 18 weeks the first had grown 0.3 cm while the second had grown 1.7 cm.

Table 3. Predicted annual increase in length for geoducks of various sizes. Lengths in centimeters.

Original lengths	Predicted mean annual increase in length, Y	95% confidence intervals for mean annual increase in length
3.70 to 5.99	2.81	$2.55 \leq Y \leq 3.07$
6.00 to 7.99	2.45	$2.20 \leq Y \leq 2.70$
8.00 to 9.99	0.99	$0.49 \leq Y \leq 1.49$
10.00 to 11.99	0.61	$0.20 \leq Y \leq 1.02$
12.00 to 13.99	0.17	$-0.01 \leq Y \leq 0.35$
14.00 to 17.18	-0.01	$-0.16 \leq Y \leq 0.14$

The positive relationship between growth and growing time is evident in the linear regressions of recovery lengths on planting lengths (Table 4). For estimating the regression parameters, tagged geoducks, irrespective of their size or planting site, were grouped into the four growing periods of about 10 weeks each. The number of tagged clams that were recovered made smaller time intervals impractical; even so, too few were recovered in less than 18 weeks or between 26 and 54 weeks to be considered (Appendix 4 contains the vital statistics of recovered tagged geoducks. In the regressions, the intercepts are directly related and the slopes are inversely related to the growing periods. The intercepts indicate that the longer the growing periods the greater the change in length. The slopes show that as growing time increases growth approaches a maximum. Thus, as would be expected, the longer the clams had to grow the more they grew. This relationship, however, also indicates that geoducks grew throughout the year.

Table 4. Growth rates of tagged geoducks shown by the linear regressions of recovery lengths on planting lengths, by the number of weeks elapsed. (Tagged geoducks of all lengths and from all planting sites were used. Lengths were in centimeters.)

Weeks from planting to recovery	Number of geoducks	Regression coefficients		
		Intercept, a	Slope, b	Standard deviation, $S_{y.x}$
18 - 29	36	1.60	0.878	0.446
50 - 59	21	5.14	0.637	1.330
60 - 69	17	5.39	0.627	2.465
70 - 81	29	7.03	0.490	1.414

Growth by Season

The tagging study, through plantings and recoveries at different seasons and repeated recoveries of individual clams, was intended to provide information on seasonal rates of growth. Geoducks did grow throughout the year, even in the winter. For example, one tagged clam planted at the minus 2-ft beach level on 28 December 1967 grew from 3.90 to 4.83 cm by 15 May 1968, an increase in length of 24%. But the small number of plantings and recoveries during winter and spring and the cessation of growth caused by handling precluded an analysis of seasonal growth rates on the basis of first recoveries. Repeated plantings and recoveries of individual tagged clams also failed to provide good information on seasonal growth rates. Thirty-seven tagged geoducks were recovered a second time. Most of these showed little new growth. Many, in fact, shrank. Three were recovered a third time; each was longer than 10 cm when first planted and each had become shorter at each recovery. Thus, neither first recoveries nor repeated recoveries provided usable information on seasonal growth.

Growth by Beach Level

Of the 125 tagged geoducks recovered once, 68 with initial shell lengths between 3.70 and 7.99 cm were suitable for an analysis of growth at the four beach levels. These clams had been recovered from all four plots and had been planted long enough to resume growing. Data from larger clams and clams recovered a second or a third time were unsuitable (for reasons already given).

Comparisons of growth by beach level were made by analysis of covariance on the linear regressions of length on time, where length is the shell length either at planting or at recovery and time is the number of days since planting (t = 0 for initial lengths). Appendix 5 contains the statistics for the four regression lines.

The analysis of covariance (Table 5) shows that the linear regressions are parallel ($F = 0.732$, $p > 0.25$) but are at different elevations ($F = 8.674$, $p < 0.005$). A plot of the regression lines (Figure 29) shows that most of the difference in elevations is contributed by one group of clams. Those at the -1-ft level were shorter on the average when planted than those planted in other plots. The important result, however, is that the slopes--the growth rates--were not significantly different between the four beach levels.

Tagged Geoducks and the Theoretical Growth Curve

In general, the growth of tagged geoducks supports the growth curve derived from the length-frequency distributions of Big Beef and Dosewallips geoducks, Annual differences in growing conditions and temporary stunting of the tagged clams probably account for the differences.

In Table 6 the growth of tagged clams is compared with the predicted and observed lengths for geoducks up to age four. Clams greater than 10 cm were tagged but they grew little, some even became smaller (Appendix 4), so they are not included here. Considering the amount of variation about the mean lengths (Appendix 6), the tagged clams grew about as predicted by the growth curve. For example, those planted in June-August 1968 at an average length of 6.10 cm ($S_x = 0.64$ cm) grew to an average length of 9.09 cm ($S_x = 0.80$ cm) by June-August of 1969.

In contrast, the estimates of L_∞ and K derived from the tagged clams differ considerably from the estimates derived from the length-frequency distributions of the wild Big Beef and Dosewallips clams (Table 7).

For the combined Big Beef and Dosewallips clams the estimates were 0.125 for K and 25.67 cm for L_∞. Since the von Bertalanffy growth curve based on these estimates fits the observed data well and the estimate for L_∞ is

Table 5. Analysis of covariance of shell length (Y) on time (X) by four beach levels.

Source	df	$\sum x^2$	$\sum xy$	$\sum y^2$	Deviations from regression		
					df	Sum of squares	Mean square
-1-ft level	11	607515.7	4005.24	36.31	10	9.904	0.990
-2-ft level	31	680160.7	4669.47	74.69	30	42.633	1.421
-4-ft level	29	1791849.6	12093.62	94.45	28	12.827	0.458
-10-ft level	61	3413862.1	26799.44	261.91	60	51.530	0.859
Within					128	116.894	0.913
Difference between slopes					3	2.005	0.668
Common	132	6493388.1	47567.77	467.36	131	118.899	0.908
Difference from adjusted means					3	23.628	7.876
Total	135	6769149.2	50629.01	521.20	134	142.527	

Comparison of slopes: $F = 0.668/0.913 = 0.732$, $p > 0.25$. Hypothesis of parallel lines is not rejected.

Comparison of levels: $F = 7.876/0.908 = 8.674$, $p < 0.005$. Hypothesis of equal levels is rejected.

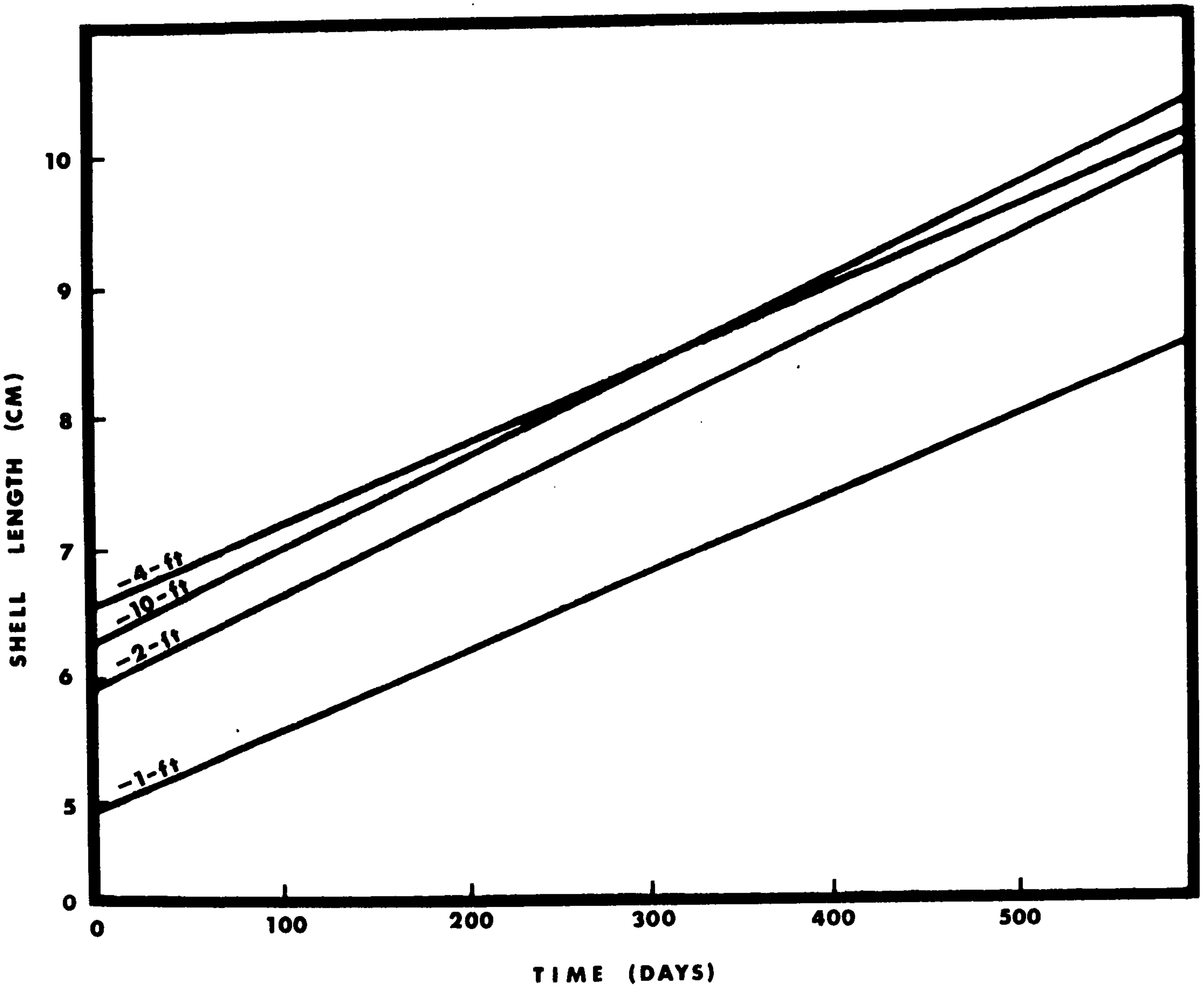

Figure 29. Growth of tagged geoducks at four beach levels. The slopes do not differ significantly; but the elevations do, because of the clams at the -1-foot level.

Table 6. Comparison of geoduck shell lengths predicted by the growth curve with observed lengths and the growth of tagged clams. Lengths are means, except where noted, and are in centimeters.

Source	Age in years[a]								
	0.0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0
Predicted lengths (from growth curve)	0.0	1.4	3.1	3.8	5.8	7.0	8.1	9.2	10.1
Observed lengths (length frequencies)			3.2		5.9		8.3		10.1
Growth of tagged geoducks, planted:									
December 1967				3.9[b,c]	4.8				
June-August 1968			3.6[b]			6.4			
do					6.1		9.1	10.0	
June-August 1969			3.7[b]	5.0					
do					6.6	7.5			
do							8.9	9.3	

[a] Based on 15 July as the start of a geoduck's year.

[b] Growth of single clams.

[c] Underlined values are lengths of tagged clams when planted.

realistic these estimates can be taken as the expected values of the real growth parameters. If the tagged clams grew as the wild Big Beef and Dosewallips clams did, the estimates of K and L_∞ obtained from them should be equivalent to the expected values.

The estimates of K and L_∞ were obtained from the tagged clams by two methods. First, the parameters were estimated from the four groups of clams that grew for different lengths of time (Table 4). These estimates were obtained by the Manzer and Taylor adaptation of the Walford technique (Ricker, 1958). The estimates of the asymptotic length, L_∞, were derived by solving for the points of intersection between the computed regression lines and the one-to-one line, $Y = X$. The estimates of K were obtained from the slopes of the regression lines. The slopes are estimates of $e^{-K(t)}$, and K(t) was easily determined. Then for each group of tagged clams the average growing time, expressed as a fraction of a year, was computed and divided into the estimate of K(t) to find K. The resulting K's, therefore, are yearly rates. The second set of estimates was obtained by using Gulland and Holt's method of estimating growth parameters from recoveries with unequal growing periods (Gulland and Holt, 1959; Hancock, 1965). Here all tagged clams regardless of planting site or growing times were pooled. All resulting estimates for K are higher and those for L_∞ are lower than the expected values. The estimates of L_∞ derived from the tagged clams are smaller than the size of some of the clams measured in this study. Obviously, tagging and planting stunted the clams.

Nevertheless, some tagged geoducks grew well. In Figure 30 the length changes of 20 tagged geoducks are superimposed on the theoretical growth curve. The tagged geoducks selected for this figure not only showed good growth but represented the range in lengths and grew during different seasons.

The point of Figure 30 is that the growth of at least some of the tagged geoducks followed the theoretical growth curve.

In conclusion, although some tagged clams grew as well as the wild ones, many did not. Thus, the average growth rate of tagged geoducks will underestimate the average growth rate of wild geoducks.

Table 7. Estimates of the growth parameters K and L_∞ obtained from wild and tagged geoducks.

Source	K	L_∞ (cm)
Length-frequency distributions of wild geoducks.	0.15	22.5
Tagged geoducks		
Manzer and Taylor method, by length of growing period.		
18 to 29 weeks	0.32[a]	13.1
55 to 59 weeks	0.40[a]	14.2
60 to 69 weeks	0.37[a]	14.5
70 to 81 weeks	0.48[a]	13.6
Gulland and Holt method for recoveries with unequal growing times.	0.31	14.8

[a] Estimates of K are adjusted to a common base of 52 weeks.

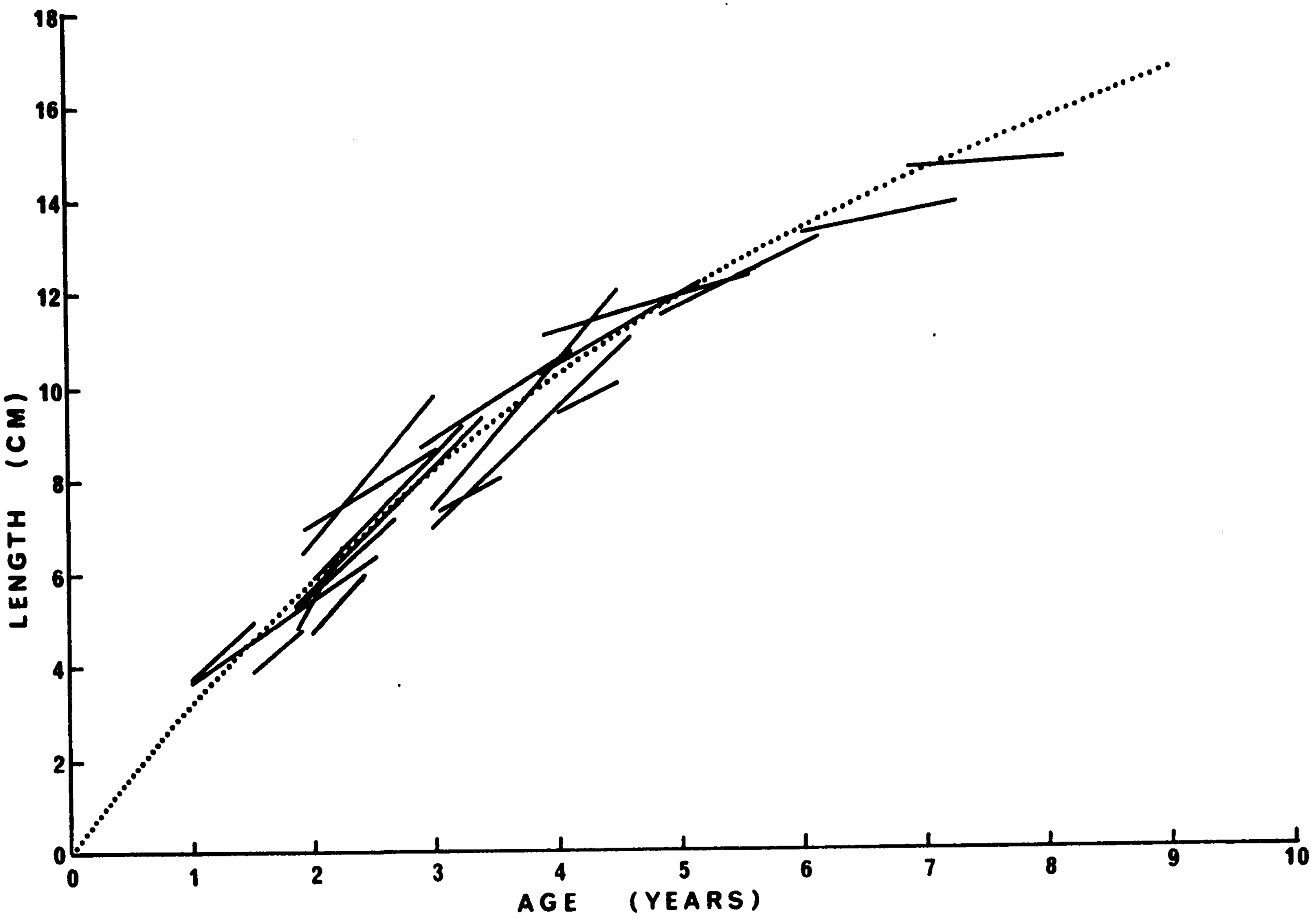

Figure 30. The growth of 20 selected tagged geoducks compared to a von Bertalanffy growth curve derived from wild geoducks.

MORPHOMETRIC RELATIONSHIPS

Since geoducks vary in size and shape, one aspect of this project was to determine the amount of variation in several morphometric characteristics and to establish the relationships between them.

Preliminary studies showed the right and left valves of a pair to be equivalent with respect to lengths, widths, and weights (Appendix 2), and that in the relationship between valve width and valve length (the only relationship with suitable data) there was no evidence of sexual dimorphism (Appendix 7). Therefore, the morphometric relationships were developed from the pooled measurements of males, females, immature, and unsexed geoducks taken throughout this study.

For purposes of determining relationships with valve measurements, it was immaterial whether the right or left valve was used, since in pairs they were equivalent. But frequently one of the valves would be broken and it couldn't be measured. Thus, a relationship was developed with the left valve measurements when possible, otherwise it was developed with the right valve measurements. The two separate relationships were then combined to form a general relationship.

In all of the relationships, lengths are in centimeters (cm), weights are in grams (g), and logarithms are Naperian (Ln).

The Relationship Between Total Weight and Valve Length

The weight-length relationship is curvilinear, with the variation about the line proportional to valve length (Figure 31). Using logarithms to straighten the line and to stabilize the variance (Snedecor and Cochran, 1967), a linear regression for 1417 pairs of weight (W) and length (L)

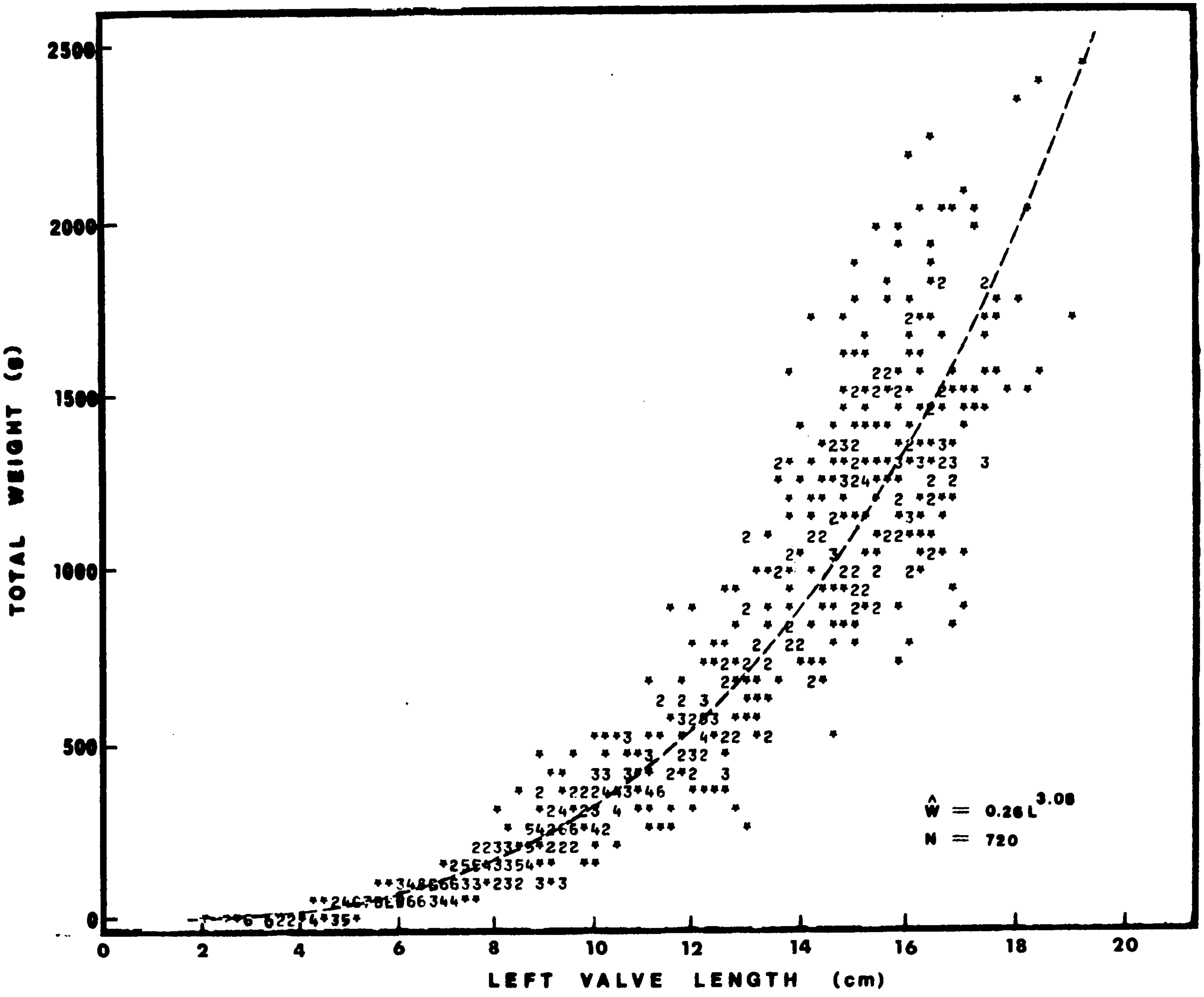

Figure 31. The relationship between total weight and shell length.

measurements was computed to be:

$$\mathrm{Ln}(\widehat{W}) = -1.324 + (3.064)\mathrm{Ln}(L),$$

with $r = 0.977$ and $S_{y.x} = 0.2847$. Thus, the curvilinear relationship is:

$$\widehat{W} = 0.266(L)^{3.064}.$$

For the left valve only (Figure 31), the curvilinear relationship for 720 pairs of measurements is:

$$\widehat{W} = 0.259(L)^{3.079}.$$

The Relationship Between Meat Weight and Total Weight

The meat weight-total weight relationship is linear with the variation proportional to total weight (Figure 32), where the meat (M, as defined earlier) consists of the siphon and the thick part of the mantle. By using logarithms to standardize the variation, a linear regression for 246 pairs of weights was computed to be:

$$\mathrm{Ln}(\widehat{M}) = 0.048 + (0.868)\mathrm{Ln}(W),$$

with $r = 0.983$ and $S_{y.x} = 0.2337$.

If the untransformed data are used instead, and the assumption is made that the best-fitting straight line will pass through the origin (an expectation, actually), then the relationship becomes:

$$\widehat{M} = b(W),$$

where $b = \Sigma M/\Sigma W$. For 246 pairs of weights, $b = 0.425$. In other words, the meat, on the average, makes up about 42.5% of the total weight.

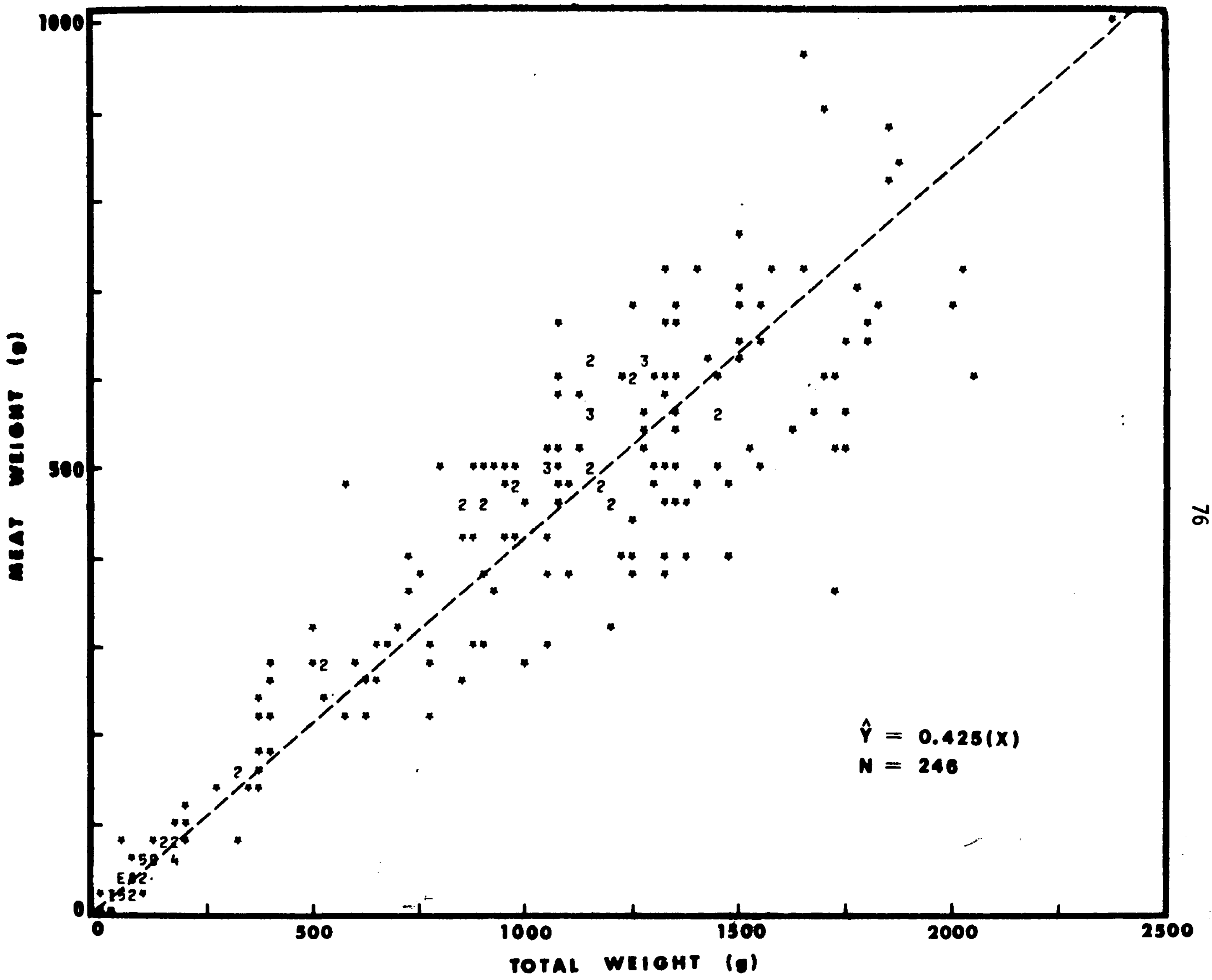

Figure 32. The relationship between meat weight and total weight.

The Relationship Between Visceral Weight and Total Weight

The visceral weight-total weight relationship is linear, with the variation about the line proportional to total weight. When logarithms of the weights are used to standardize the variance, the linear regression for 211 pairs of transformed weights is:

$$\mathrm{Ln}(\widehat{V}) = -1.372 + (0.891)\mathrm{Ln}(W),$$

with $r = 0.968$ and $S_{y.x} = 0.2540$.

If untransformed weights are used with the assumption that the line passes through the origin, the relationship becomes: $\widehat{V} = b(W)$, where b is defined to be $\Sigma V/\Sigma W$. For 211 pairs of weights, $b = 0.119$. Thus, on the average, the viscera make up about 12% of the total weight.

The Relationship Between Shell Weight and Total Weight

The shell weight-total weight relationship is also linear, with the variation about the line proportional to total weight. A linear regression for 208 pairs of transformed weights is:

$$\mathrm{Ln}(\widehat{S}) = -2.932 + (1.158)\mathrm{Ln}(W),$$

with $r = 0.960$ and $S_{y.x} = 0.3516$.

For the untransformed weights and the assumption that the line goes through the origin, $b = 0.174$. Thus, on the average, the shell makes up about 17.4% of the total weight.

The Relationship of Burrow Depth to Shell Length

The depths of 168 geoduck burrows were measured so that the tagged geoducks could be planted to the proper depths. Burrow depths ranged from 18 to 86 cm, with an average of 51.7 cm. Although the shallowest burrow was inhabited by the smallest geoduck for which a burrow was measured, the largest did not inhabit the deepest burrow. Generally, though, the depth of the burrow was related to the shell length of the geoduck (Figure 33).

The relationship between burrow depth and age can be derived by referring to the growth curve (Figure 26). Geoducks in their first year may be as deep as 30 cm, those in their second year as deep as 65 cm, and those in their third year are nearly as deep as they will burrow (80 to 90 cm).

The Orientation of the Hinge with Respect to the Shoreline

To determine whether tagged geoducks should be oriented one particular way when planted, the orientation of 79 geoducks was classified subjectively, when they were dug, as to whether the hinge was pointing towards, parallel with, or away from the shoreline.

Of the 79 examined, 28 pointed toward, 28 parallel with, and 23 pointed away from the shoreline. If the clams were randomly oriented, they should be parallel with the shoreline twice as often as they would be pointed either toward it or away from it, since by being parallel they could face either left or right.

A test of the hypothesis that the clams were randomly oriented yielded a Chi-square value of 10.68 ($p < 0.01$, with 2 degrees of freedom); thus, fewer than expected were parallel with the shoreline. This test, however, may be meaningless because the orientations were not measured accurately, but were determined subjectively. In another study, Armstrong (1965) examined the orientation of 50 geoducks and concluded that they were randomly oriented. The important point, however, is that the hinges are not all pointing seaward as in razor clams (Pohlo, 1963) or Pismo clams (Weymouth, 1923).

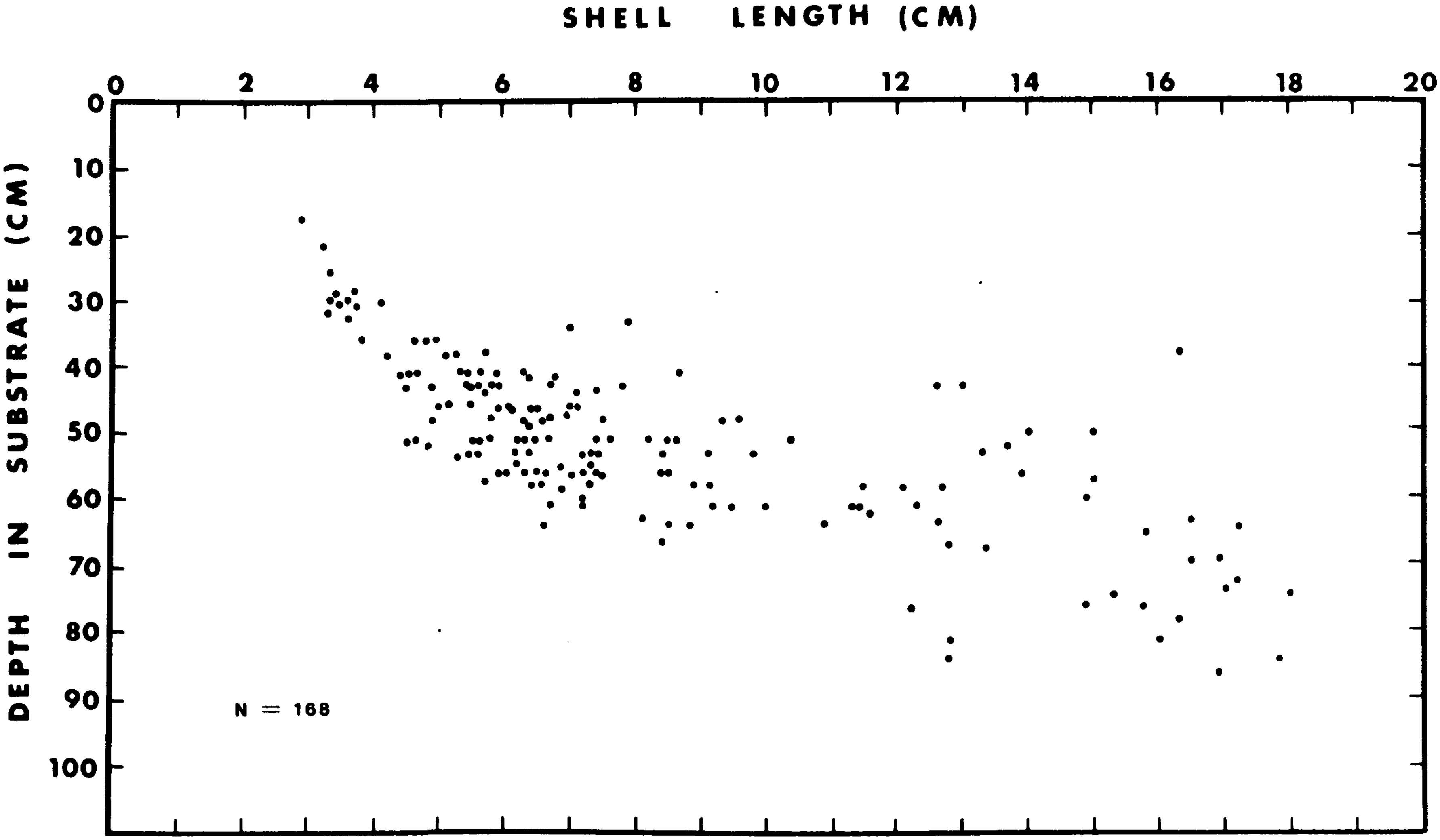

Figure 33. The relationship between burrow depth and shell length.

Discussion

The foregoing relationships are probably representative of Hood Canal geoducks. They are based on the combined collections of 1135 geoducks taken from intertidal and subtidal beds at Big Beef and from intertidal beds at Dosewallips over a period of 32 months. The geoducks ranged from 2 to 20 cm in shell length and from 2 to 2625 g in total weight.

On the other hand, using the entire collection to establish the relationships probably accounts for some of the variation in the relationships. The time and place effects are confounded with other sources of variation. For example, the probable seasonal changes in gonads and meats are unaccounted for in the relationship between viscera weight and total weight, or between total weight and valve length. Also, possible differences between the Dosewallips geoducks and those from Big Beef are ignored, as are those between the subtidal and intertidal geoducks. Small and irregular samples, however, prevented separate analyses.

Additional variation in the relationships can be explained by remembering that clams grow by adding new layers to the insides of their shells. In young clams these new layers extend beyond the borders of the previous layers; thus, the valves increase in length and width as well as in weight. In older clams, though, the new layers are often smaller than the former ones; in fact, the body cavities become smaller (Figure 34). When this happens the edges of the valves wear away and the clams are said to be undergoing shell recession. Valves of the oldest clams, then, are not the longest but the thickest and the heaviest. A second source of variation comes from valves that have been broken or cracked and have healed. These valves are heavier than expected on the basis of their lengths.

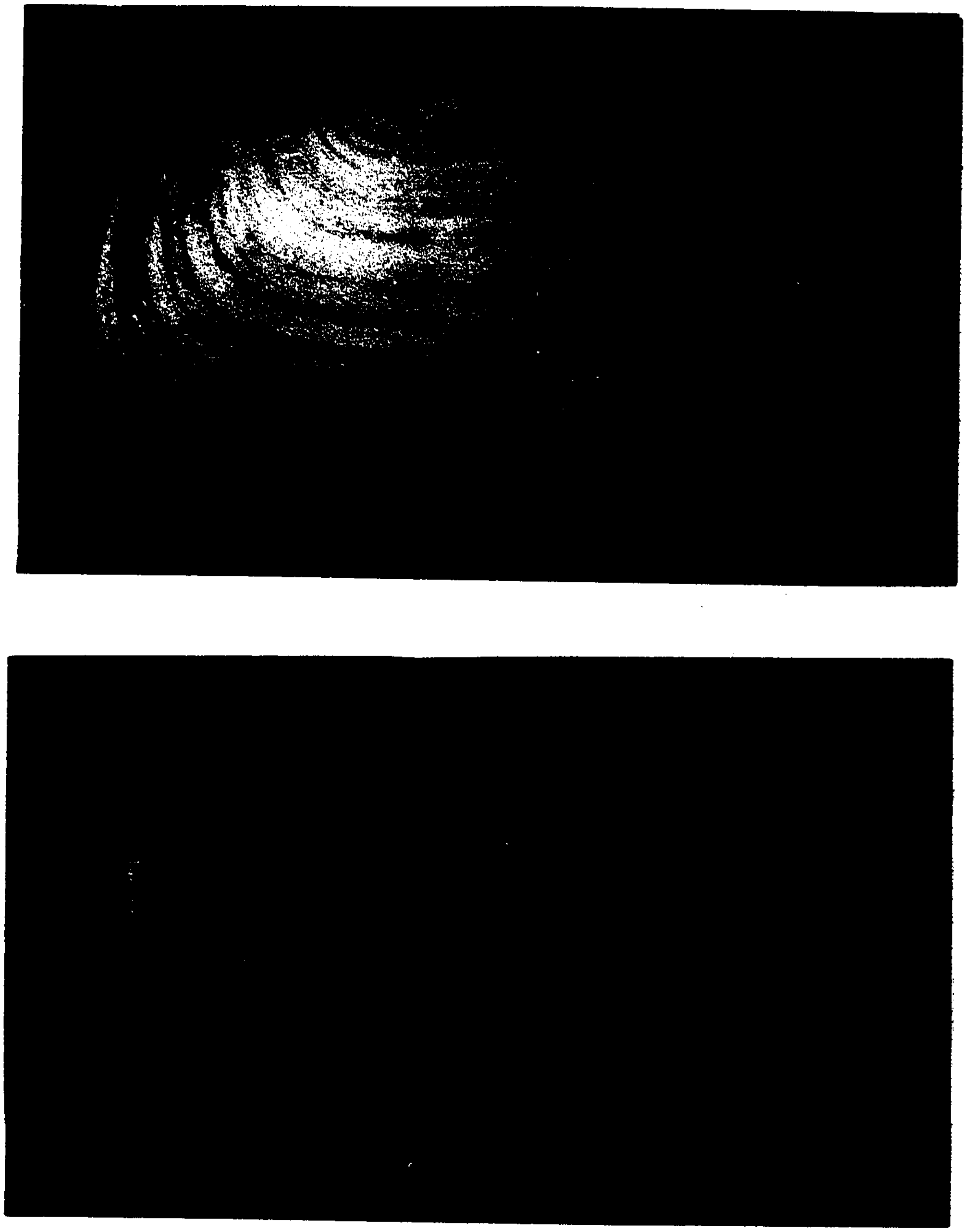

Figure 34. Photographs of the left valve of an old geoduck (negative reversed in printing). The whole geoduck weighed 1325 grams. This valve weighed 186 grams and was 17 centimeters long.

The upper picture shows the lines of growth on the outside of the shell.

The lower picture shows shell recession on the inside of the shell. The recent shell layers are smaller than the previous ones, thus reducing the size of the body cavity and, as the outer margins of the shell wear off, the overall size of the shell.

Few morphometric data are available for making comparisons with the relationships developed here. Lindsay (1966, 1969) states that geoducks average 3 pounds (1362 g) in total weight and attain a maximum of 13 pounds (5902 g). Because of the emphasis on small geoducks in this study a comparison of average weights would be meaningless, but the maximum weights can be compared. Lindsay's maximum is more than twice as heavy as the largest clam taken in this study (2625 g). But few large clams were weighed, and besides, conditions for molluscan growth are not as favorable in Hood Canal as they are in other parts of Puget Sound (Westley, 1967). Undoubtedly, geoducks larger than the largest measured in this study exist. Westley and Goodwin (1970) give the average meat weight of geoducks as 1.4 pounds (636 g). With this average meat weight and Lindsay's average total weight the meat would make up 47% of the total weight. This value is close to the average of 42.5% I obtained.

The weight of geoducks at various ages can be determined from the age-length relationship (Figure 26) and the length-weight relationship (Figure 31). Thus, a geoduck one year old will have shells about 3 cm long and will weigh about 10 grams, when it is three years old it will be about 10 cm long and weigh about 300 g, and by the time it is ten years old it will be about 17 cm long and weigh about 1600 g.

The total weights varied greatly because the geoducks contained variable amounts of sand and water within their body cavities. The relationships of meat weight, viscera weight, and shell weight to total weight indicate that the average whole geoduck consists of by weight: 42.5% meat, 12.0% viscera, and 17.4% shell. The amount of sand and water account for the rest of the total weight. Thus, the average whole geoduck is 28.1% sand and water.

SUMMARY

1. A growth curve was developed for geoducks on the basis of length-frequency distributions and was tested with the growth of tagged clams. The inability to age geoducks from markings on their shells hindered development of the growth curve.

2. Length-frequency distributions for geoducks collected at Dosewallips and Big Beef over 3 years were studied separately. Three distinct year classes could be followed in both distributions. A Walford plot of the mean lengths at each age provided estimates of parameters for the von Bertalanffy growth curve, $L_t = 22.5(1 - e^{-0.15t})$. This curve fitted the observed lengths well and predicts the shell lengths of geoducks from the time they set until age 40 (although for geoducks older than about 20 years the prediction may be too high).

3. A total of 191 geoducks ranging from 3.08 to 17.18 cm in shell length were tagged and planted into plots at four beach levels at Big Beef. After being out from 28 to 587 days, 125 (65%) were recovered at least once. Individuals varied greatly, but growth was inversely related to length at planting and directly related to time elapsed between planting and recovery. Geoducks grew throughout the year, but data were insufficient to quantify seasonal growth rates. The growth rates for tagged clams planted at the four beach levels did not differ significantly, but only data from 68 clams were suitable for the analysis. Tagging, and planting temporarily stopped growth and caused marking checks on the shells. Although the growth of some tagged clams supported the growth curve developed from the length-frequency distribution, the growth of tagged geoducks generally is less than that of undisturbed geoducks.

4. Morphometric relationships for geoducks were determined with data from 1135 geoducks dug at Dosewallips and Big Beef. The geoducks ranged from 2 to 20 cm in valve length and from 2 to 2625 g in total weight. A maximum of 12 measurements were possible for each geoduck: weights of the whole geoduck; weights of the meat, viscera, shell, and dried right and left valves; and the lengths, widths, and breadths of the left and right valves. Usually, though, only a few of these characteristics were measured for any one geoduck.

5. Geoducks vary in size and shape, but paired right and left valves are equivalent in length, width, and weight. Also geoducks apparently lack sexual dimorphism; males and females did not differ significantly in the relationship between valve length and valve width.

6. The hinges of geoducks, in contrast to those of the Pismo clam and the Pacific razor clam, are orientated without respect to the surfline.

7. A 1-year-old geoduck lives in a burrow about 20 cm deep, has shells about 3 cm long, and weighs about 10 g. A 3-year-old geoduck lives about 60 cm deep, has shells about 10 cm long, and weighs about 300 g. A 10-year-old geoduck is nearly full-grown, lives in a burrow about 80 cm deep, has shells about 17 cm long, and weighs about 1600 g.

8. The average whole, freshly-dug geoduck consists of, by weight: 28.1% sand and water, 17.4% shell, 12.0% viscera, and 42.5% meat.

ABUNDANCE, DISTRIBUTION, AND NATURAL MORTALITY

Although the goals of this part of the study were to determine a) spatial distribution patterns, b) abundance, c) recruitment, and d) natural mortality rates, a number of errors and misfortunes (including vandalism) made only the data on abundance and spatial distribution meaningful and worthwhile.

ABUNDANCE AND DISTRIBUTION

Geoduck positions were marked and mapped during 1968, but neither job was thorough and the results have been discarded. Using the experience gained during 1968, the efforts in 1969 were more successful. Still, the northern study strip had to be abandoned because of vandalism. Lack of time and favorable tides prevented repeating the work. The results presented here, then, are those from the seven plots in the southern study strip (see Figure 2).

The abundance of geoducks was inversely related to beach level. The number of geoducks in the 100-by-100-foot plots ranged from 19 at the +0.5-foot level to 264 at the -2.5-foot level (Table 8). The number counted in the -3.5-foot plot is probably low because the drainage from much of the beach flowed across the northwest corner of this plot. The flowing water made it difficult to find any geoducks that might have been there, and none was found.

Table 8. Abundance of geoducks by beach level in 100-by-100-foot plots.

Approximate beach level	+0.5-ft	0.0-ft	-0.5-ft	-1.0-ft	-1.5-ft	-2.5-ft	-3.5-ft
Geoducks per plot	19	59	100	105	110	264	190
Geoducks per 1000 m^2	20	63	110	113	118	284	204

Lindsay (1966, 1969) reported geoducks in densities up to one geoduck per square foot. The high count of 264 in the -2.5-foot plot gives an average of 0.026 geoducks per square foot (or 0.28 geoducks per square meter). Occasionally in a 10-by-10-foot square within a plot the density was as high as 0.08 geoducks per square foot, and frequently two or three geoducks could be found side by side. But over a large area the average density never approached one per square foot, and Big Beef is a good geoduck beach.

To determine whether geoducks were randomly distributed within a plot, a grid of 100 squares (each 10 feet by 10 feet) was superimposed over the map of each plot and the number of geoducks in each square counted. The maps of the plots, made with an alidade and plane table, were drawn at a scale of one inch to ten feet. The hypothesis that the clams were randomly distributed was tested by comparing how well the counts fitted a Poisson distribution (Snedecor and Cochran, 1967). If the resulting Chi-square exceeded the 5% level of significance the hypothesis of randomness was rejected.

Geoducks were distributed either randomly or clumped within the plots (Figure 35, Table 9). The distribution patterns are unrelated to either the number of geoducks in a plot or to the beach level. A number of factors may be responsible (setting, survival, nonuniform substrate) but the differences are real. Connell (1955) examined the distributions of two clams, *Mya arenaria* and *Petricola pholadiformis*, on an intertidal beach and found their distributions to be clumped because of variations in substrate. With geoducks, survival may be more important than substrate. The relations between survival and spatial distribution will be discussed in the following section on mortality.

Table 9. Distribution patterns for geoducks in 100-by-100-foot plots at seven beach levels (see Appendix 8).

Approximate beach level	+0.5-ft	0.0-ft	-0.5-ft	-1.0-ft	-1.5-ft	-2.5-ft	-3.5-ft
Chi-square for goodness-of-fit to Poisson	1.44	4.59	12.50	17.83	16.55	9.76	53.32
Pattern of distribution	Random	Random	Clumped	Clumped	Clumped	Random	Clumped

Even though geoducks are plentiful in the lower intertidal zone, the center of geoduck abundance may be subtidal. Densities of geoducks from subtidal beds at Big Beef are not available for comparison with the densities of geoducks from the intertidal beach, but subtidal geoducks were numerous. The increasing abundance of geoducks with depth indicates a trend that

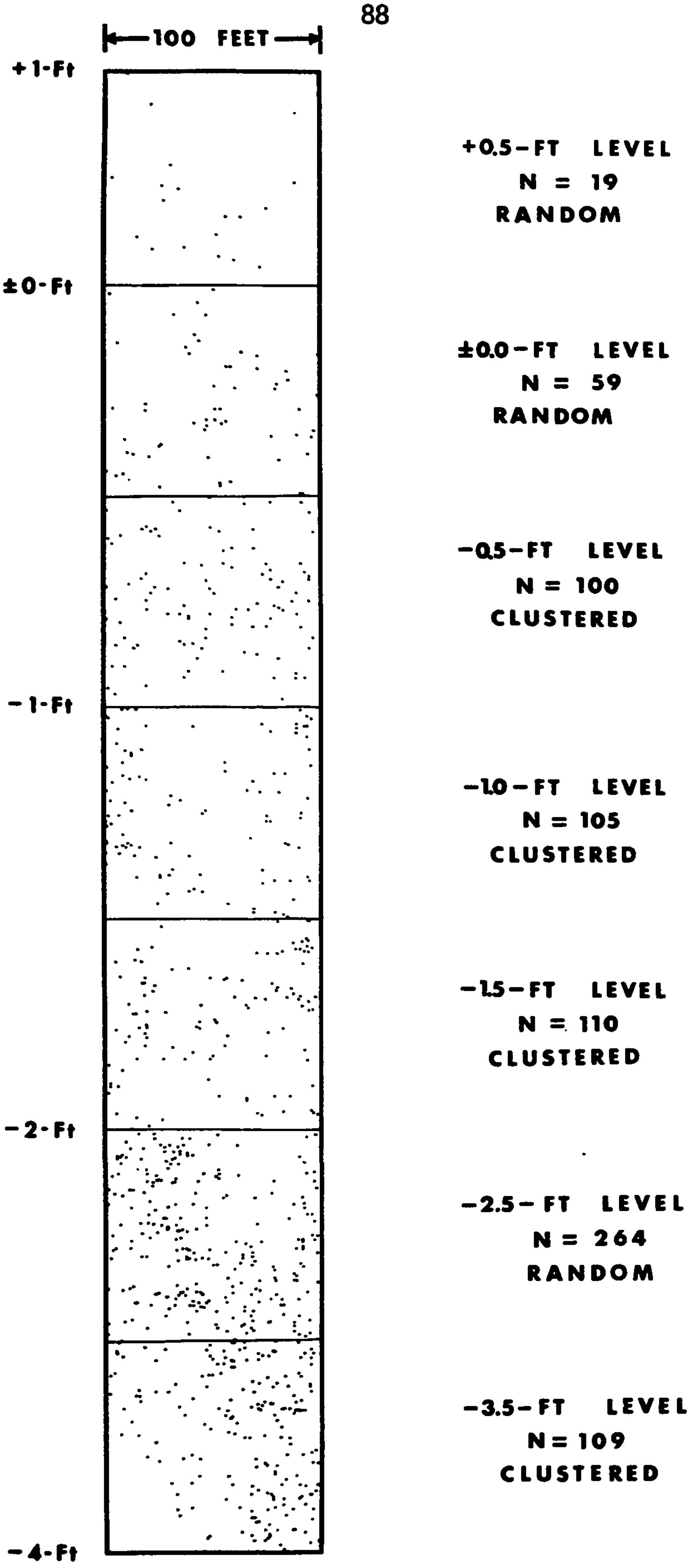

Figure 35. Spatial distribution of geoducks in a 100-foot-wide by 700-foot-long study area at Big Beef Creek.

probably continues. Also some geoducks have been reported from as deep as 150 feet below low water. Considering the range in depths where geoducks occur, from above the +1-foot level to at least the -150-foot level, geoducks living in the intertidal zone may be living in a marginal habitat.

The data on abundance and distribution of geoducks permit calculations of biomass (standing crop). For the intertidal beach below the 0-foot level, the average density is 154 geoducks per plot, or 671 geoducks per acre. At an average weight of 3 pounds per geoduck, that density gives 2013 pounds of geoducks per acre (or 226 g/m^2). Then, since on the average 42.5% of a whole geoduck is edible meat, there would be 855 pounds of edible geoduck meat per acre (or 96 g/m^2). If the maximum density of geoducks per plot (264) is used, rather than the average (154), the standing crop would be 3450 pounds of whole geoducks per acre (344 g/m^2), or 1466 pounds of edible meat per acre (142 g/m^2).

NATURAL MORTALITY

Although the attempts to measure rates of natural mortality were abandoned, some observations relating to natural mortality are worth mentioning here.

Vegetation

Accumulations of vegetation probably kill geoducks and may partially account for the clumped distributions. During the summer of 1968, vegetation (various sorts of algae and eel grass) accumulated in piles, sometimes a foot or two high, on the intertidal beach. As this vegetation decayed, the area beneath it became anaerobic and many small clams (mostly butter clams, Saxidomus nuttalli; macoma, Gastrana irus; and horse clams, Tresus spp.) died. Geoducks might also have died, but dead geoducks are rarely observed; their shells are so deeply buried that they rarely come to the surface. Often, though, geoduck siphons extended through to the top of the vegetation; and once when a pile of vegetation was removed from over a plot of tagged geoducks, one of the tagged geoducks (5.45 cm in shell length) was found completely out of the ground. Apparently this geoduck had come to the surface to avoid being smothered.

In a laboratory experiment, Armstrong (1965) buried 10 species of clams, including geoducks, at several depths. He could detect no evidence of surfacing ability. Most of the clams suffocated. None surfaced. Armstrong felt that if the clams had the ability to surface they would have. Yet, somehow, small geoducks do come to the surface (p. 62).

At any rate, the accumulated vegetation could have either killed the geoducks in place or have forced them to the surface where they would be susceptible to predators. The result would be the same either way--a clumped distribution of the survivors.

Cracked Shells

A number of the geoducks collected during this study at Big Beef, from subtidal as well as intertidal areas, had healed cracks in their shells (Figure 36). The cracks apparently occurred naturally. The subtidal clams, for example, were taken from beds around the minus 10-foot level, and with their shells buried two to three feet in the substrate it is unlikely that any predator (including man) broke them. A probable explanation is that movements of the substrate, by earthquakes or by the normal settling and slumping, cracked the shells.

How serious shell breakage is as a source of natural mortality is unknown. My experience in planting tagged geoducks, however, showed that cracked ones survived poorly. Probably many of those that are cracked die.

Figure 36a,b,c,d. Photographs of healed cracks in shells from live subtidal geoducks. The causes of the cracks are unknown; a(X 0.27), b(X 0.43), c(X 0.50), d(X 0.47).

Figure 37. Photograph of egg capsules from an unknown gastropod on the tip of a geoduck siphon (X 2.3).

Figure 36a

Figure 36b

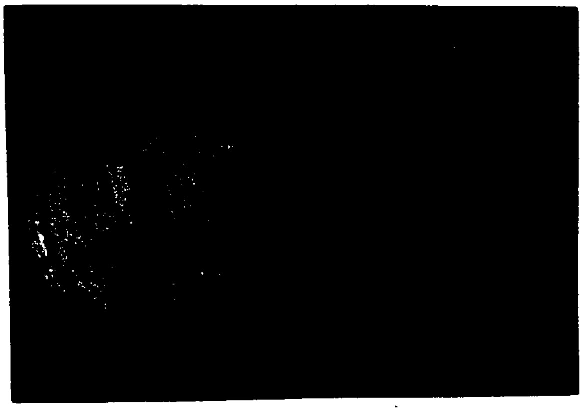

Figure 36c

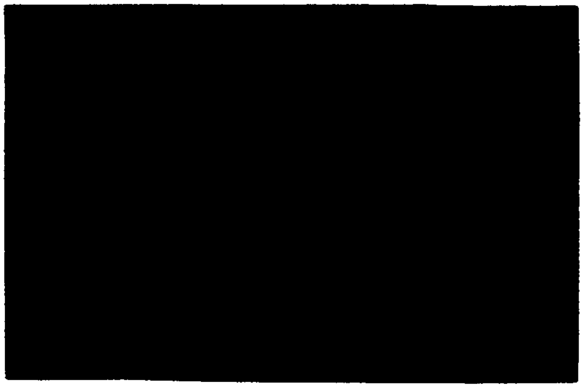

Figure 36d

Figure 37

Predators

Predators, other than man, appear to be of little importance. Only once during this project did I see any evidence of active predation. A starry flounder, *Platichthys stellatus*, tried for several minutes to eat the tip of a geoduck siphon; finally it gave up, unsuccessful.

Other predators, though, have been more successful. Sheats (1970) reported that spiny dogfish, *Squalus acanthias*, have been found with as many as seven geoduck necks in their stomachs, and that seastars eat geoducks. Cabezon, *Scorpaenichthys marmoratus*, also eat siphon tips; the stomach of one contained 14 (Charles A. Simenstad, 1970, personal communication). Whether the loss of part of its siphon will kill a geoduck is unknown. Occasionally live geoducks were collected with pieces of their siphons missing. Fitch (1965) believes that "siphon nipping by fishes probably seldom contributes to adult clam mortality."

Besides the fish and seastars, moon snails, *Lunatia lewisi*, might also prey on geoducks. Geoducks less than two years old live shallow enough to be susceptible to moon snails, and moon snails are abundant on geoduck beds. Moon snails do prey on other deep-burrowing clams (*Macoma spp*., *Phacoides annulatus*, *Protothaca tenerrima*, and *Tresus spp*.), so they probably eat small geoducks, too.

In summary, predators appear to be a minor source of adult geoduck mortalities.

Parasites and Commensals

Pea Crabs: Pea crabs (Pinnotheridae) have been reported from a wide variety of marine invertebrate hosts (Christensen and McDermott, 1958; Hopkins and Scanland, 1964; Pearce, 1966a, b; Wells, 1928), even in fossils (Zullo and Chivers, 1969), but they have never been reported from geoducks.

In this study, pea crabs were found in 15 (3.8%) of the 398 geoducks examined. One contained two crabs. Eleven of the 16 crabs were preserved and saved. Pea crabs were found only in geoducks having a shell length greater than 13 cm, although some as small as 3 cm were examined.

The 11 pea crabs saved for detailed study were all early instar males of the genus Pinnixa. The species and even the sex are difficult to determine on early instars of pinnixids (Pearce, 1966b). These were classified as males on the basis of the shape of their abdomens, and as P. faba or P. littoralis on the shape of their carapaces, shape of the dactylus of their third pereiopods, and whether or not the dactyli of their chelipeds were toothed. Eye shape, the usual characteristic for separating the adults of these two species, is valueless since early instars of both species have rounded eyes (Pearce, 1966b). The carapace widths indicate that these crabs were in the 6th to 11th instar (Pearce, 1966b). The identity of each crab, date discovered, and carapace dimensions (length and width, measured on the preserved crabs) are given in Table 10.

The seasonal distribution of pea crabs in geoducks is puzzling. Most were found in the fall, 11 of the 16 were found in September (7 in 1968 and 4 in 1969). The others were found in the summer or winter. None was found in the spring. Since the examination procedures were standardized and only 10% of the geoducks examined were collected in September, sampling does not account for the results. The possibility that males were searching for mates inside geoducks can also be dismissed. No adult females were found in the geoducks, and Pearce (1962a, 1966a,b) showed that pinnotherids copulate precociously at an early, free-swimming stage. Pearce (1966b) gives evidence, however, that early instars of pinnixids can be found throughout the year. He found them in the horse clam, Tresus capax, in all seasons,

Table 10. Pea crabs from geoducks (measurements in millimeters).

Date collected	Species	Sex	Carapace (length & width)	Shell length of host
22 June 1967	*Pinnixa faba*	male	3 x 5	146
20 Sept. 1968	(2 lost)			166
20 Sept. 1968	*P. littoralis*	male	4 x 6	188
20 Sept. 1968	*P. littoralis*	male	5 x 8	157
20 Sept. 1968	*P. littoralis*	male	4 x 7	162
26 Sept. 1968	*P. littoralis*	male	4 x 7	156
26 Sept. 1968	*P. faba*	male	4 x 6	160
23 Feb. 1969	(lost)			172
12 July 1969	*P. littoralis*	male	4 x 5	183
12 July 1969	*P. faba*	male	3 x 4	164
11 Sept. 1969	*P. faba*	male	4 x 6	147
11 Sept. 1969	*P. littoralis*	male	4 x 7	180
11 Sept. 1969	(lost)			159
11 Sept. 1969	(lost)			136
22 Dec. 1969	*P. faba*	male	4 x 6	164

although there was much monthly and yearly variation in occurrences. The explanation for the high frequency of young pea crabs in geoducks during September will have to await further study.

The finding of pea crabs only in geoducks larger than 13 cm is also puzzling. Juveniles of these two pinnixids have been found in many smaller hosts (Pearce, 1966b; Rathbun, 1918; Wells, 1928), so geoducks less than 13 cm are large enough to contain pinnixids. Pearce (1962b) reports that in two similar species of horse clams, *Tresus capax* is almost always infested with adult pea crabs, whereas *T. nuttalli* never contains an adult and rarely contains a juvenile pea crab. The difference between the two species, he says, is that *T. capax* has a "visceral skirt," and *T. nuttalli* does not. Geoducks lack the visceral skirt. Perhaps that is why they also lack adult pea crabs and rarely contain juveniles. A "host-factor," however, may also be important. Johnson (1952) discovered that the pinnotherid, *Dissodactylus mellitae*, was associated only with the sand dollar, *Mellita quinquesperforta*, because of a chemical substance, a host-factor, produced by the sand dollar. In contrast, Pearce (1966a) found larger crabs in larger mussels, *Modiolus modiolus*, until the mussels were 8.5 cm long. Mussels longer than 8.5 cm seldom contained a crab. Pearce suggested that perhaps only the young mussels produce a host-factor and that, as the mussels have a long life span, they outlive their guests and are not reinfested. Perhaps if geoducks produce a host-factor, only larger ones do.

Although pea crabs are known to cause minor damage in some hosts, they are too infrequent in geoducks to be a significant cause of mortality.

Parasitic Copepods: In 1949, Illg reported on a previously undescribed copepod, *Paranthessius panopea*, that he found in the mantle cavity of a geoduck dug at Tomales Bay, California. He later found this copepod in geoducks from the San Juan Islands in Washington, and he expected that they would be found in geoducks from Hood Canal (Illg, personal communication).

Although I examined each geoduck I butchered during this study for parasites and commensals, I found neither Illg's copepod nor any other. They may have been overlooked. Adults of P. panopea are small, attaining a length of about 2 mm, and no attempts were made to collect them with $MgSO_4$ or by examining each geoduck with a microscope. Yet it is unlikely that they could have been abundant and not been noticed. Paranthessius might require water of higher salinity than that of Hood Canal; waters of Tomales Bay and the San Juan Islands are nearly oceanic.

I doubt that P. panopea, if present, is a significant cause of mortality in Hood Canal geoducks.

Gastropod Egg Capsules: Egg capsules of unknown gastropods were attached to the tips of several geoduck siphons. Figure 37 shows a typical cluster. Egg capsules were recorded on six geoducks, but occurred and were not recorded on several others. The egg capsules were small, about 2 mm long; and were found throughout the year--April (twice), July, September, October, and December. Whether or not these egg capsules were all from the same species of gastropod is unknown, the adult gastropods were never observed depositing the capsules. The capsules are unlikely to cause mortalities in geoducks.

Diseases

About 10% of the geoducks examined in this study had abnormal growths on their bodies. One type occurred externally on the siphons as white or black pustules (Figure 38). Frequently, scars showed where pustules had been. The second type, apparently unrelated to the first, occurred internally on the visceral mass as one or more small "swellings" dorsad to

Figure 38a,b. Photographs of external blisters or pustules on siphons of geoducks.

Figure 39a,b,c,d. Photographs of abnormal growths on visceral masses.

Figure 38a

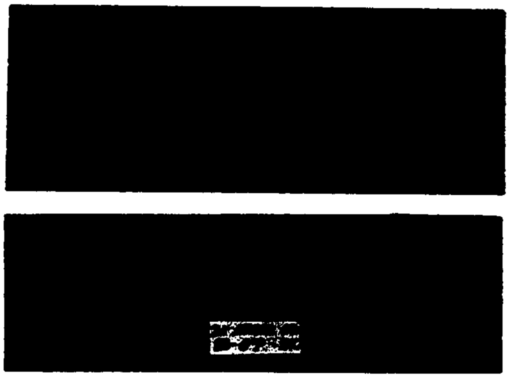

Figure 38b

Figure 39a

Figure 39b

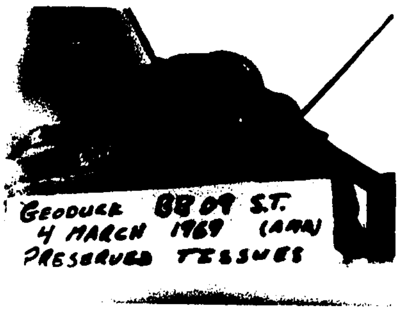

Figure 39c

Figure 39d

the ctenidia (Figure 39). Microscopic examinations of two of the internal swellings revealed an infestation of an unidentified fungus.

The causes and consequences of these diseases are unknown. Neither of the two diseases reported here nor similar diseases have been reported from other molluscs (for example, Sinderman and Rosenfield, 1967).

Discussion

Once they set, geoducks probably have a low rate of natural mortality, with most deaths occurring within a year or two after setting and at old age. During their first two years, the young geoducks are shallow enough to be eaten by moon snails and possibly by fish, and their fragile shells are highly susceptible to being crushed by movements of the substrate. The small geoducks may also be smothered or forced out of the ground by decaying algae and eelgrass. Should they surface, they would be easy prey for crabs, fish, and other predators. Adult geoducks, on the other hand, appear to have a low rate of natural mortality until they finally die of old age. The adults have few obvious causes of death, and the geoduck's apparent potential for a long life indicates a low rate of natural mortality (Comfort, 1957).

MANAGEMENT IMPLICATIONS

The Recreational Fishery

Judging from the facts turned up in this study and elsewhere, the public recreational geoduck fishery in Washington is in trouble.

In the first place, Washington has little public beach with geoducks; and those beaches, such as the Dosewallips, that do have geoducks receive heavy digging pressure.

In the second place, the fishing pressure is bound to increase. Not only is the human population increasing at an exponential rate, but the amount of leisure time for outdoor recreation is increasing and travel is becoming easier and faster. The Outdoor Recreation Resources Review Commission, for example, predicts twice as many residents for Washington by the year 2000 as there were in 1960 (O.R.R.R.C., 1962b). The Commission further predicts that the average workweek will decrease from 38.5 hours in 1960 to 30.5 hours in the year 2000. The increase in leisure time will be partially spent on outdoor recreation, and most outdoor recreation, says the Commission, is associated with water areas (O.R.R.R.C., 1962a). The Commission goes on to predict that individuals, citizens and foreigners, will travel farther and more often. Where in 1960 an average U.S. citizen traveled a total of 4,170 miles, by 2000 he is expected to travel 11,000 miles, a 161% increase in total travel. And while noting that total travel is a good index for recreational travel, the Commission predicts that recreational travel will increase at a greater rate than that for total travel (O.R.R.R.C., 1962b). In summary, more people are going to travel farther more often for outdoor recreation, and digging geoducks will be one of their goals.

In the third place, even though geoducks spawned and set every year during this study, thus indicating that recruitment might not be a problem, other aspects of the geoduck's life history show that geoducks can easily be overfished. Geoducks are not abundant. The highest average density measured in this study comes out to 1150 adult geoducks per acre. With the present limit of three geoducks per digger per day, 40 diggers could harvest the entire geoduck population from an acre of beach in 10 days. During each of the good daylight low tides, more than a hundred geoduck diggers are on the Dosewallips alone. The rate of growth is another factor to consider. Since geoducks require 10 or more years to reach full size, with the heavy digging pressures, few geoducks on public beaches will ever reach their potential full size. The average geoduck taken in the fishery will soon be about two or three years old and will weigh about one-half pound.

Not only will the average size decrease, but the average catch per unit of effort will also decline as more people dig fewer geoducks. Similar fates have already befallen the Pismo clam in California (Rickets, Calvin, and Hedgpeth, 1968), and the Pacific razor clam in Washington (Tegelberg, 1970). Adult Pismo clams, once removed by the wagonload, are now almost unobtainable in the intertidal zone. The recreational razor clam fishery is nearly as badly off; it has recently been closed during the most popular digging seasons because the catch consisted of clams too small to be used.

Harvesting might have slight beneficial effects on geoduck populations by increasing recruitment and speeding up the growth rate. The large, old geoducks grow little but take up space and eat food. If the old clams were removed there would be more space for new set and, possibly, more food for the fast-growing young. But more set and a slight increase in the growth rate will be futile unless some way is found to limit the number of diggers.

A limit on the number of diggers would give everyone an equal chance to get a reasonable-sized geoduck for a reasonable amount of effort, and would prevent the stocks from being overfished. Other approaches at management are impractical or unappealing. A legal size limit for geoducks is impractical because the shells are too easily broken. Prohibiting digging for several years until the stocks rebuild and then reopening the beach for digging is unappealing, because without a limit on the number of diggers the stocks would be fished out within a day or two after digging was permitted. A catch quota for individual beaches is unappealing for the same reason. One approach for limiting the number of diggers would be to issue a limited number of geoduck permits by lottery for each public beach each year, as is already done for goat hunting permits.

Regardless of how the number of diggers is regulated, the regulations enacted in 1931 for managing the recreational geoduck fishery are no longer doing the job they were designed to do; they must be revised.

The Commercial Fishery

The commercial fishery got off to a good start. The act authorizing the fishery (State of Washington, 1969) limited entry into the fishery, thus making this act a unique and significant contribution to fishery legislation.

But the act has its shortcoming. Ideally, a fishery should be managed to maximize the long-term benefits to society (Beverton and Holt, 1957; Christy and Scott, 1965). One of the requirements for an ideal fishery is that the fishermen be professional and be employed full-time. Crutchfield (1965) excellently expresses the cultural benefits of having full-time professional fishermen in a fishery. The geoduck bill, however, tends to encourage part-time fishermen, especially SCUBA divers, who plan to make a few extra dollars harvesting geoducks when they are away from their regular jobs. As the fishery matures, the state will probably amend the original act so that the fishery will come closer to maximizing the benefits of this resource. The limited-entry provision of the act, however, outweighs this slight shortcoming.

Evidence presented in this dissertation, that geoducks spawn every year and that they grow to a usable size in five years or so, indicates that a plot of ground could yield a crop of geoducks every five years, perhaps in less. Controlled harvesting will probably enhance geoduck production by increasing the set and the growth rate.

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APPENDIX 1. Means ($\bar{X}$) and standard deviations (S_x) in microns of ovocytes nuclei, nucleoli, and follicles, listed by gonad number within stage of maturity. Twenty-five measurements were made of each item in every gonad sample, giving a total of 125 for each stage.

State of maturity	Ovocytes		Nuclei		Nucleoli		Follicles	
	$\bar{X}$	S_x	$\bar{X}$	S_x	$\bar{X}$	S_x	$\bar{X}$	S_x
Early active								
033	17.02	3.60	10.04	1.69	3.73	1.21	104.09	45.52
074	24.57	5.04	12.33	1.91	4.49	0.79	214.47	126.79
083	23.14	3.29	13.19	1.84	4.78	0.00	214.86	119.80
119	24.57	3.68	13.86	2.18	4.97	0.65	171.26	131.92
236	22.18	4.16	13.19	1.40	4.78	0.00	182.65	106.03
Average	22.30	3.95	12.52	1.80	4.55	0.53	177.47	106.01
Late active								
246	19.22	5.93	11.95	2.17	4.02	1.08	234.50	183.54
248	25.33	4.73	13.38	1.19	4.78	0.00	139.44	81.39
266	61.85	10.40	34.70	6.17	9.27	1.86	552.28	347.76
269	27.53	3.97	16.16	1.86	4.97	0.65	211.33	197.31
272	52.48	12.56	26.48	2.92	8.32	1.40	327.99	217.59
Average	37.28	7.52	20.53	2.86	6.27	1.00	293.11	205.52
Ripe								
095	58.70	7.67	33.94	2.06	10.23	2.41	604.13	439.74
138	61.76	10.20	36.90	4.36	12.24	1.05	401.05	193.58
183	64.24	14.51	32.70	4.37	11.57	2.22	462.72	265.24
273	59.56	9.60	37.95	2.42	11.95	0.95	968.25	577.44
295	63.76	7.46	37.38	4.61	12.52	1.41	935.26	864.16
Average	61.60	9.89	35.77	3.56	11.70	1.61	674.28	468.03
Partially spawned								
001	64.43	13.56	27.25	4.97	10.42	2.37	257.84	106.42
037	65.87	26.24	32.03	4.61	9.94	1.89	289.49	229.00
129	65.29	10.52	36.04	4.13	11.84	1.77	353.13	196.98
170	59.46	11.40	30.78	5.35	10.99	1.69	389.52	275.18
185	64.15	7.19	36.42	4.42	11.57	2.22	676.40	431.49
Average	63.84	13.78	32.50	4.70	10.95	1.99	393.28	247.81

APPENDIX 2. Comparisons of paired right and left valves.

Hypothesis Tested: Comparable measurements of the right and left valves are equal.

Test: $t = \frac{\overline{D} - 0}{S_{\overline{D}}}$

Results:

A) Lengths

$N = 714$
$\mathrm{Sum}(D) = -1424$
$\overline{D} = -1.99$
$\mathrm{Sum}(d^2) = 348488$

$t = -2.415$
$p > 0.01$

Do not reject the hypothesis.

B) Widths

$N = 671$
$\mathrm{Sum}(D) = -457$
$\overline{D} = -0.68$
$\mathrm{Sum}(d^2) = 218705$

$t = -0.976$
$p > 0.20$

Do not reject the hypothesis.

C) Weights

$N = 286$
$\mathrm{Sum}(D) = 33$
$\overline{D} = 0.12$
$\mathrm{Sum}(d^2) = 1045401$

$t = 0.032$
$p > 0.50$

Do not reject the hypothesis.

Conclusion:

The paired right and left valves do not differ significantly with respect to length, width, or weight. Accept the hypothesis.

Appendix 3. Linear regressions of length change (Y) on weeks elapsed between planting and recovery (X) for tagged geoducks, by lengths at planting. Clams from all beach levels are pooled. Lengths are in centimeters.

Lengths when planted	Number of geoducks	Regression coefficients: Intercept	Slope	Standard error from regression, Sy.x	Correlation coefficient, r	Predicted increase in length after 52 weeks
3.70 to 5.99	35	+0.05	+0.053	0.736	0.87	2.81
6.00 to 7.99	34	-0.77	+0.062	0.710	0.87	2.45
8.00 to 9.99	12	-0.05	+0.020	0.525	0.61	0.99
10.00 to 11.99	10	-0.38	+0.019	0.553	0.69	0.61
12.00 to 13.99	10	-0.14	+0.006	0.240	0.48	0.17
14.00 to 17.18	9	-0.12	+0.002	0.170	0.25	-0.01

Appendix 4A. Vital statistics of recovered tagged geoducks planted at the -1-foot beach level (weights in grams, lengths in centimeters).

Tag number	Date[a]	Total weight	Valve lengths left	Valve lengths right	Valve widths left	Valve widths right
329	13 May 1968	550.0	12.27	11.92	7.59	7.72
	1 Sept 1969	520.1	12.15	11.86	7.50	7.67
	23 Dec 1969	622.9	12.10	11.78	7.51	7.67
330	13 May 1968	400.0	11.57	11.26	6.04	6.08
	1 Sept 1969	557.0	13.13	12.95	6.72	6.87
331	13 May 1968	350.0	10.34	10.36	6.60	6.38
	1 Sept 1969	529.4	12.09	11.96	7.39	6.98
	22 Dec 1969	871.5	11.88	12.00	7.40	7.13
332	13 May 1968	250.0	8.73	8.95	5.12	5.34
	1 Sept 1969	373.6	10.66	11.00	6.06	6.17
	23 Dec 1969		10.57	11.16	6.14	6.13
336	14 May 1968	2025.0	17.18	16.90	10.66	10.80
	22 Dec 1969	2260.0	16.79	16.63	10.59	10.62
337	14 May 1968	1825.0	16.93	16.86	9.45	9.63
	5 Oct 1968	1375.0	17.00	16.84	9.38	9.60
339	14 May 1968	750.0	12.96	12.92	8.06	8.32
	1 Sept 1969	742.9	13.45	13.42	8.21	8.52
	22 Dec 1969	880.0	13.32	13.46	8.22	8.43
340	14 May 1968	1100.0	15.74	15.86	9.03	9.16
	5 Oct 1968	900.0	15.64	15.77	8.97	9.13
342	14 May 1968	575.0	11.45	11.15	7.53	7.56
	1 Sept 1969	594.8	11.95	11.78	7.79	7.84
	22 Dec 1969	760.0	11.94	11.76	7.83	7.82
343	14 May 1968	800.0	12.28	12.38	8.00	8.16
	5 Oct 1968	550.0	12.16	12.36	8.01	8.11
344	14 May 1968	475.0	10.80	11.06	6.67	6.53
	5 Oct 1968	325.0	10.75	11.22	6.69	6.56
	1 Sept 1969	405.0	10.65	11.03	6.64	6.68
	23 Dec 1969	536.0	10.62	10.98	6.65	6.58
345	14 May 1968	1000.0	14.92	15.14	9.28	8.92
	1 Sept 1969	1230.0	15.13	15.33	9.43	9.18
	22 Dec 1969	1445.0	15.04	15.21	9.41	9.32
346	14 May 1968	575.0	12.74	12.54	7.76	7.69
	1 Sept 1969	774.3	13.16	13.08	7.95	8.07
	23 Dec 1969	884.6	13.05	13.10	7.96	8.05
358	31 May 1968	28.5		4.86	2.85	2.90
	1 Sept 1969	228.4	8.59	8.66	5.07	5.27
359	31 May 1968	25.1	4.76	4.73	3.15	3.06
	5 Oct 1968	49.2	5.06	5.23	3.37	3.39

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[a] The first date for a given tagged clam is the day that clam was originally planted. Subsequent dates are recovery dates.

Tag number	Date	Total weight	Valve lengths		Valve widths	
			left	right	left	right
360	31 May 1968	26.3	4.84	4.85	2.98	2.91
	5 Oct 1968	81.4	6.55	6.56	3.98	3.94
361	31 May 1968	13.1	3.62	3.69	2.27	2.29
	22 Dec 1969	83.6	6.35	6.44	3.95	3.86
362	31 May 1968	39.5	5.33	5.38	3.34	3.35
	1 Sept 1969	236.1	9.13	9.25	5.66	5.67
364	31 May 1968	550.0	12.09	12.17	7.31	7.30
	5 Oct 1968		12.15	12.21	7.44	7.35
365	31 May 1968	375.0	11.09	10.97	6.60	6.39
	22 Dec 1969	729.7	12.24	12.13	7.39	7.20
376	11 June 1968	69.0	5.64	5.66	3.45	3.46
	9 July 1968				3.34	
388	7 July 1968	64.0	5.30	5.22	3.26	3.22
	22 Dec 1969	257.8	8.52	8.60	5.06	5.18

Appendix 4B. Vital statistics of recovered tagged geoducks planted at the -2-foot beach level (weights in grams, lengths in centimeters).

Tag number	Date	Total weight	Valve lengths		Valve widths	
			left	right	left	right
303	18 Aug 1967	300.0	8.70			
	14 Aug 1968	330.6	9.45	9.43	6.34	6.24
	17 Jan 1970	630.3	11.20	11.31	7.37	7.51
320	28 Dec 1967	496.0	12.30		7.26	
	14 Aug 1968	453.1	12.18	12.16	7.40	7.18
	17 Jan 1970	554.1	12.35	12.32	7.64	7.50
323	15 Jan 1968	1132.0	14.75		8.52	
	14 Aug 1968	790.4	14.72	14.44	8.64	8.34
324	28 Dec 1967	439.0	11.90		7.27	
	14 Aug 1968	468.8	11.58	11.56	7.70	7.24
	9 Jan 1970	789.9	12.63	12.90	8.40	7.93
325	28 Dec 1967	21.2	3.90		2.61	
	15 May 1968		4.83	4.71	3.27	3.29
	14 Aug 1968	31.3		4.86		3.26
326	28 Dec 1967	454.0	11.82		7.58	
	14 Aug 1968	452.2	11.93	11.70	7.56	7.57
	17 Jan 1970	600.0	12.17	12.24	7.78	7.81
347	14 May 1968	925.0	15.40	15.14	9.32	9.36
	20 Aug 1969	925.0	15.20	14.90	9.40	9.61
	9 Jan 1970	902.4	15.27	14.97	9.29	9.44
349	14 May 1968	275.0	9.46	9.61	5.97	5.98
	6 Oct 1968		9.41	9.54	5.93	5.97
	17 Jan 1970	338.0	10.10	9.96	6.54	6.62
350	14 May 1968	375.0	11.04		6.44	
	6 Oct 1968		10.93		6.32	
351	14 May 1968	600.0	11.75	11.78	7.05	6.58
	6 Oct 1968	350.0	12.21	12.15	7.25	6.83
354	14 May 1968	1600.0	16.42	16.37	10.36	10.44
	20 Aug 1969	1375.0	16.42	16.21	10.47	10.46
	9 Jan 1970	1400.0	16.35	16.33	10.38	10.52
356	14 May 1968	850.0	13.79	14.08	8.71	8.56
	20 Aug 1969	1000.0	13.56	13.93	8.52	8.54
	17 Jan 1970	982.5	13.56	13.93	8.57	8.47
357	14 May 1968	1325.0	16.84	16.52	9.57	9.50
	20 Aug 1969	1200.0	16.76	16.57	9.51	9.73
	17 Jan 1970	1029.8	16.70	16.52	9.50	9.62
367	9 June 1968	92.5	6.57	6.64	3.94	3.92
	20 Aug 1969	296.8	9.87	9.88	5.60	5.82
	9 Jan 1970	311.8	9.96	10.10	5.80	5.88
368	9 June 1968	74.0	6.40	6.36	3.69	3.70
	20 Aug 1969	235.3	9.16	9.23	5.16	5.24
	9 Jan 1970	290.7	9.28	9.33	5.51	5.51
370	9 June 1968	53.9	5.28	5.35	3.48	3.45
	6 Oct 1968		6.99	7.06	4.55	4.43

Tag number	Date	Total weight	Valve lengths left	Valve lengths right	Valve widths left	Valve widths right
373	9 June 1968	79.2	6.96	6.88	3.88	3.92
	20 Aug 1969	278.9	8.75	8.79	5.83	6.05
	9 Jan 1970		8.56	8.61	5.95	6.11
374	9 June 1968	46.5	5.42	5.48	3.31	3.33
	20 Aug 1969	214.6	9.28	9.30	5.53	5.56
	9 Jan 1970	226.1	9.50	9.46	5.65	5.82
J03	3 June 1969	134.9	7.40	7.29	4.31	4.45
	17 Jan 1970	152.1	8.07	8.07	4.88	4.91
J05	3 June 1969	732.4	13.36	13.57	7.94	7.41
	17 Jan 1970	856.4	13.51	13.36	8.17	7.63
K03	29 July 1969	324.8	10.38	10.32	6.41	6.32
	9 Jan 1970	376.5	10.30	10.34	6.44	6.55
K09	29 July 1969	143.5	6.88	6.91	3.89	4.19
	9 Jan 1970	148.6	7.34	7.42	4.23	4.49
K14	29 July 1969	177.6	7.77	7.59	4.52	4.69
	9 Jan 1970	213.3	7.99	7.85	4.90	4.94
K15	29 July 1969	165.8	7.34	7.36	4.51	4.45
	17 Jan 1970	108.4	7.97	8.11		4.57
K16	29 July 1969	216.1	7.44	7.54	4.59	4.69
	9 Jan 1970	199.9	7.78	7.87	4.94	4.97
K19	29 July 1969	248.9	9.31	9.54	5.36	5.26
	9 Jan 1970	269.8	9.92	10.28	5.81	5.64
K22	29 July 1969	198.0	8.11	8.36	4.90	5.03
	17 Jan 1970	188.0	8.55	8.61	5.32	5.37
K23	29 July 1969	71.5	5.94	5.96	3.42	3.27
	17 Jan 1970	90.8	6.91	7.03	3.99	4.12
K25	29 July 1969	97.5	6.32	6.33	3.77	3.77
	20 Jan 1970	155.9	7.53	7.50	4.73	4.69
K27	29 July 1969	31.4	4.21	4.19	2.79	2.79
	17 Jan 1970	40.0	5.10	5.24	3.45	3.46
K29	29 July 1969	19.9	3.70	3.64	2.30	2.22
	9 Jan 1970		5.00		3.00	
M12	4 May 1969	53.7	5.41	5.64	3.38	3.26
	9 Jan 1970	101.6	6.66	6.77	4.15	4.11

Appendix 4C. Vital statistics of recovered tagged geoducks planted at the -4-foot beach level (weights in grams, lengths in centimeters).

Tag number	Date	Total weight	Valve lengths left	Valve lengths right	Valve widths left	Valve widths right
392	9 July 1968	117.2	6.55	6.78	4.04	3.96
	28 Aug 1969	280.0	8.99	9.11	5.40	5.33
	16 Jan 1970	263.9	9.18	9.20	5.63	5.54
393	9 July 1968	68.1	6.04	6.06	3.70	3.76
	28 Aug 1969	133.4	7.50	7.61	4.56	4.67
	30 Dec 1969		9.71	10.09	6.46	6.37
396	9 July 1968	92.2	6.09	6.12	4.09	4.05
	28 Aug 1969	236.2	8.90	8.70	5.68	5.71
	8 Jan 1970	308.5	9.05	8.90	5.91	5.91
704	10 July 1968	65.8	5.80	5.77	3.71	3.96
	7 Jan 1970	381.7	9.37	8.55	5.39	5.80
706	10 July 1968	73.7	6.84	6.72	3.95	3.90
	8 Jan 1970	437.4	11.37	11.36	6.42	6.42
707	10 July 1968	83.2	6.56	6.72	4.07	4.06
	28 Aug 1969	266.0	9.10	9.28	5.70	5.65
	7 Jan 1970	378.1	9.35	9.40	5.92	5.74
718	10 July 1968	100.2	7.09	6.98	3.90	4.10
	16 Jan 1970	376.4	10.92	10.99	6.13	6.33
720	10 July 1968	96.9	6.63	6.62	3.88	3.92
	28 Aug 1969	284.8	10.03	10.00	5.68	5.66
	8 Jan 1970	326.1	10.43	10.56	6.10	6.00
723	10 July 1968	75.3	5.87	5.78	4.04	4.04
	28 Aug 1969	240.9		8.82		5.84
724	10 July 1968	1111.2	13.33	13.02	7.72	7.88
	28 Aug 1969	965.0	13.86	13.54	8.42	8.37
	8 Jan 1970	856.2	13.86	13.61	8.38	8.32
730	11 July 1968	111.0	6.74	6.89	4.11	4.13
	28 Aug 1969	251.8	8.61	8.94	5.41	5.39
	22 Jan 1970	230.0	8.64	8.84	5.45	5.45
731	11 July 1968	71.0	5.84	5.87	3.76	3.82
	16 Jan 1970	317.2	9.77	9.88	6.29	6.30
740	11 July 1968	127.9	7.08	6.94	4.18	4.16
	16 Jan 1970	401.1	11.03	10.98	6.38	6.31
743	11 July 1968	86.8	6.27	6.40	3.79	3.73
	22 Jan 1970	262.5		10.66		6.00
744	11 July 1968	77.6	5.90	5.90	4.04	3.94
	16 Jan 1970	210.2	8.98	8.82	6.10	6.70
746	11 July 1968	120.0	6.84	6.92	4.38	4.61
	28 Aug 1969	318.0	9.74	9.80	6.22	6.44
	7 Jan 1970	492.9	10.45	10.49	6.84	6.88
K33	28 Aug 1969	270.5	9.81	9.94	5.56	5.71
	8 Jan 1970	365.2	9.95	10.40	5.72	6.00
K34	28 Aug 1969	1200.0	14.99	14.27	8.42	8.63
	8 Jan 1970	1225.0	14.92	15.19	8.37	8.50
K35	28 Aug 1969	659.2	12.76	12.67	7.56	7.63
	7 Jan 1970	708.7	12.80	12.67	7.56	7.58

Appendix 4D. Vital statistics of recovered tagged geoducks planted at the -10-foot beach level (weights in grams, lengths in centimeters).

Tag number	Date	Total weight	Valve lengths		Valve widths	
			left	right	left	right
700	10 July 1968	57.2	5.18	5.18	3.30	3.26
	20 Aug 1969	171.8	7.88	7.89	5.04	5.07
	17 Dec 1969	309.8	7.92	7.86	5.02	5.18
702	10 July 1968	51.3	5.40	5.37	3.08	3.06
	20 Aug 1969	207.9		9.16		5.19
703	10 July 1968	64.6	5.70	5.70	3.66	3.66
	18 Dec 1969	458.9	8.86	8.78	5.86	5.85
705	10 July 1968	96.8	6.92	6.74	4.24	4.14
	20 Aug 1969	224.8	10.24	10.22	6.20	6.21
709	10 July 1968	66.1	5.80	5.70	3.31	3.42
	20 Aug 1969	285.8	9.53	9.79	5.76	5.70
	17 Dec 1969	644.9	11.18	11.14	6.57	6.55
712	10 July 1968	113.1	6.77	6.82	4.08	4.04
	19 Dec 1969	533.7	10.60	10.67	6.44	6.49
713	10 July 1968	86.4	6.22	6.15	3.70	3.72
	30 Dec 1969		10.25	9.78	6.00	5.90
714	10 July 1968	72.0	5.41	5.61	3.29	3.29
	16 Dec 1969	442.4	10.18	10.42	6.04	6.18
715	10 July 1968	84.9	6.52	6.50	4.10	4.05
	17 Dec 1969		10.48	10.35		6.75
716	10 July 1968	85.5	6.52	6.56	3.80	3.78
	20 Aug 1969	208.0	8.97	9.35	5.49	5.55
	16 Dec 1969	304.7	9.20	9.24	5.48	5.53
721	10 July 1968	61.9	5.50	5.48	3.20	3.24
	16 Dec 1969	526.4	9.91	9.87	5.86	5.88
725	10 July 1968	21.8	4.52	4.44	2.56	2.60
	20 Aug 1969	115.8	7.18	7.10	4.13	4.30
727	11 July 1968	60.8	6.20	6.25	3.81	3.74
	20 Aug 1969	250.1	9.86	9.87	5.69	5.81
	30 Dec 1969	363.5	9.85	9.80	5.73	5.78
732	11 July 1968	77.9	6.14	6.10	3.16	3.12
	18 Dec 1969	533.3	12.00	11.72	6.47	6.40
735	11 July 1968	85.2	5.86	5.73	3.46	3.42
	17 Dec 1969		10.52	10.47	6.26	6.18
736	11 July 1968	42.9	5.44	5.39	3.15	3.15
	30 Dec 1969		8.42	8.38	5.10	5.18
737	11 July 1968	143.2	7.38	7.33	4.19	4.02
	17 Dec 1969	748.2	12.03	11.90	7.20	6.85
738	11 July 1968	57.3	5.54	5.50	3.21	3.20
	18 Dec 1969	359.1	10.35	10.11	5.69	5.93
741	11 July 1968	56.6	5.68	5.82	3.26	3.34
	17 Dec 1969		10.69	10.76	6.25	6.22

Tag number	Date	Total weight	Valve lengths left	Valve lengths right	Valve widths left	Valve widths right
742	11 July 1968	50.1	5.16	5.13	3.07	3.02
	20 Aug 1969	175.6	8.29	8.13	5.01	4.90
	6 Jan 1970	212.9	8.09	8.03	4.92	4.88
747	11 July 1968	92.2	6.00	5.88	3.38	3.52
	20 Aug 1969	274.4	9.45	9.30	5.28	5.68
	17 Dec 1969		9.36	9.15	5.45	5.65
748	11 July 1968	109.9	6.62	6.83	3.92	3.91
	17 Dec 1969		9.08	9.52	5.23	5.18
749	11 July 1968	53.0	5.16	5.30	3.18	3.12
	17 Dec 1969	514.8	10.27	10.30	6.05	6.34
750	11 July 1968	63.4	5.78	5.90	3.73	3.78
	6 Jan 1970	287.5	9.20	9.25	5.86	5.81
751	11 July 1968	63.2	5.90	6.00	3.70	3.61
	20 Aug 1969	284.6	9.93	10.05	5.82	5.78
	17 Dec 1969	391.2	9.89	9.90	5.75	5.77
752	11 July 1968	84.0	6.25	6.38	3.64	3.76
	20 Aug 1969	269.4	9.78	9.91	5.63	5.87
	17 Dec 1969	502.2	10.20	10.45	5.86	6.30
753	11 July 1968	72.3	5.68	5.64	3.22	3.23
	18 Dec 1969	657.4	10.93	10.80	6.26	6.37
J07	15 June 1969	164.6	7.30	7.26	4.42	4.52
	19 Dec 1969	276.4	8.79	8.70		5.46
J09	16 June 1969	174.2	8.43	8.52	4.94	4.94
	19 Dec 1969	264.3	10.13	9.82	6.90	6.78
J10	16 June 1969	389.2	10.03	10.12	5.88	5.92
	30 Dec 1969		9.90	10.05		5.77
J11	16 June 1969	192.1	7.81	7.96	4.95	4.91
	16 Dec 1969	404.2	9.12	9.38	5.75	5.90
K04	29 July 1969	213.2	8.16	7.93	5.28	5.12
	16 Dec 1969	282.6	8.15	7.87	5.28	5.09
K05	29 July 1969	263.1	9.38	9.43	5.49	5.56
	16 Dec 1969	341.0	9.33	9.40	5.42	5.58
K06	29 July 1969	269.3	9.20	8.95	5.55	5.58
	17 Dec 1969	469.2	9.54	8.97	6.04	5.92
K08	29 July 1969	169.0	8.24	8.26	4.56	4.66
	16 Dec 1969	214.2		8.78	4.98	5.15
K17	29 July 1969	160.9	7.53	7.52	4.60	4.59
	19 Dec 1969	341.0	8.26	7.97	5.08	5.13
K20	29 July 1969	325.3	9.16	9.20	4.81	4.91
	17 Dec 1969	436.5	9.20	9.24	5.12	5.02
K26	29 July 1969	32.4	4.74	4.77	2.82	2.75
	16 Dec 1969	40.1		6.02		3.66

Appendix 5. Summary of parameters for the linear regressions of shell length (L) on time (T) for four beach levels (lengths in centimeters, time in days).

Statistic	Beach levels			
	-1-ft	-2-ft	-4-ft	-10-ft
Sample size, n^a	12	32	30	62
Mean number of days, $\overline{T}$	186.8	119.7	239.4	218.8
Mean length, $\overline{L}$	6.10	6.75	8.00	7.79
Intercept, a (= $\overline{L}_o$)	4.88	5.93	6.39	6.08
Slope, b	0.0066	0.0068	0.0067	0.0078
Sample standard deviation of b, S_b	0.0013	0.0014	0.0005	0.0005
t, for the test of the hypothesis: B = 0	5.18^b	4.78^b	13.40^b	15.60^b
Mean square deviation from regression, $S_{y.x}$	0.995	1.192	0.677	0.330
Correlation coefficient, r	0.85	0.66	0.93	0.98

[a] Includes lengths at planting ($T_o = o$) as well as lengths at recovery.

[b] $t = (b - B)/S_b$. All slopes are statistically greater than 0; $p < 0.005$.

APPENDIX 6. Number, mean lengths, and standard deviations at planting and at recovery for four groups of tagged geoducks.

Item	Planted	Recovered	Years out
	June-August 1969	December 1969-January 1970	0.5
		Group A	
N	15	15	
$\bar{X}$	6.64	7.50	
S_x	1.60	1.39	
		Group B	
N	9	9	
$\bar{X}$	8.87	9.28	
S_x	0.63	0.68	
	June-August 1968[a]	June-August 1969	1.0
N	23	23	
$\bar{X}$	6.10	9.09	
S_x	0.64	0.80	
	June-August 1968[a]	December 1969-January 1970	1.5
N	25	25	
$\bar{X}$	5.97	10.03	
S_x	0.79	1.24	

[a] From a common planting. The mean lengths of these two groups when planted did not differ significantly, $t = 0.64$, $p > 0.05$.

APPENDIX 7. Covariance analysis of the linear regression of left valve width (y) on left valve length (x) for males and females.

Source	df	Sum x^2	Sum xy	Sum y^2	Slope	Deviations from regression		
						df	Sum of squares	Mean square
Males	147	1786.373	1028.951	611.275	0.576	146	18.5991	0.127
Females	107	596.099	350.029	234.056	0.587	106	28.5192	0.269
Within						252	47.1183	0.187
Common	254	2382.472	1378.980	845.331	0.579	253	47.1744	0.186
Difference between slopes						1	0.0561	0.056
Total	255	2745.844	1609.825	991.978		254	48.1747	
Difference between adjusted means						1	1.0003	1.000

1. Comparison of Residual Mean Squares: $F = 0.127/0.269 = 0.47$ n.s.
   Hypothesis of common variance about the lines is not rejected ($p > 0.25$).

2. Comparison of Slopes: $F = 0.056/0.187 = 0.30$ n.s.
   Hypothesis of parallel lines is not rejected ($p > 0.25$).

3. Comparison of Elevations: $F = 1.000/0.186 = 5.36$
   Hypothesis of equal elevations is not rejected at the 1% level ($0.05 > p > 0.01$).

APPENDIX 8. Tests for randomness in the spatial distribution of adult geoducks.

Beach level	Frequency of occurence	Observed[a]	Expected[b]	Results
+0.5-ft.	0	82	83.5	$\bar{x}$ = 0.19
	1	17	15.0	Chi-square = 1.44
	2	1	1.4	$p > 0.20$
		100	99.9	RANDOM
0.0-ft.	0	61	55.4	$\bar{x}$ = 0.59
	1	24	32.7	Chi-square = 4.59
	2	11	9.6	$p > 0.10$
	3	3 } 4	1.9 } 2.2	RANDOM
	4	1	0.3	
		100	99.9	
-0.5-ft.	0	42	36.8	$\bar{x}$ = 1.0
	1	29	36.8	Chi-square = 12.50
	2	21	18.4	$p < 0.01$
	3	3	6.1	CLUSTERED
	4	5	1.5	
		100	99.6	
-1.0-ft.	0	49	35.0	$\bar{x}$ = 1.05
	1	23	36.7	Chi-square = 17.83
	2	16	19.3	$p < 0.01$
	3	6	6.8	CLUSTERED
	4	2	1.8	
	5	2	0.4	
	6	0	0.1	
	7	2	0.0	
		100	100.1	
-1.5-ft.	0	44	33.3	$\bar{x}$ = 1.10
	1	23	36.6	Chi-square = 16.55
	2	23	20.1	$p < 0.001$
	3	3	7.4	CLUSTERED
	4	5 } 7	2.0 } 2.5	
	5	1	0.4	
	6	0	0.1	
	7	1	0.0	
		100	99.9	
-2.5-ft.	0	12	7.1	$\bar{x}$ = 2.64
	1	19	18.8	Chi-square = 9.76
	2	23	24.9	$p > 0.10$
	3	19	21.9	RANDOM
	4	10	14.4	
	5	7	7.6	
	6	5	3.4	
	7	3 } 5	1.3 } 1.8	
	8	2	0.4	
	9	0	0.1	
		100	99.9	
-3.5 - ft.	0	29	15.0	$\bar{x}$ = 1.90
	1	26	28.4	Chi-square = 53.32[c]
	2	15	27.0	$p < 0.001$
	3	10	17.1	CLUSTERED
	4	8	8.1	
	5	4	3.1	
	6	4 } 8	1.0 } 1.1	
	7	4	0.1	
		100	99.8	

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[a] Observed values are the number of 10-foot by 10-foot subplots containing 0, 1, . . ., n geoducks.

[b] Expected values are the theoretical number of subplots that would contain 0, 1, . . ., n geoducks if the geoducks were randomly distributed, i.e., Poisson.

[c] Accept the observed distribution of geoducks in this plot and the resulting Chi-square test lightly. The NW corner of the plot was always wet, and geoducks may have been present there, even though they were never noticed.