Fish Bulletin No. 7. The Life-History and Growth of the Pismo Clam (Tivela stultorum Mawe)

Weymouth, Frank W

1922-10-07

STATE OF CALIFORNIA
FISH AND GAME COMMISSION
FISH BULLETIN No. 7
The Life-History and Growth of the Pismo Clam[*]
(Tivela stultorum Mawe)

BY

FRANK W. WEYMOUTH

Stanford University, California

October 7, 1922

TABLE OF CONTENTS.

1. INTRODUCTION

1.1. Importance of edible mollusks

On the coast of California are found six or eight species of mollusks which are commercially important. of these, the amounts marketed are shown in the following table, and to this considerable total must be added those used locally, regarding which no data are available, although the number, in some localities, is known to be large. These animals thus represent a valuable economic asset and there is good reason to believe that their importance can be materially increased.

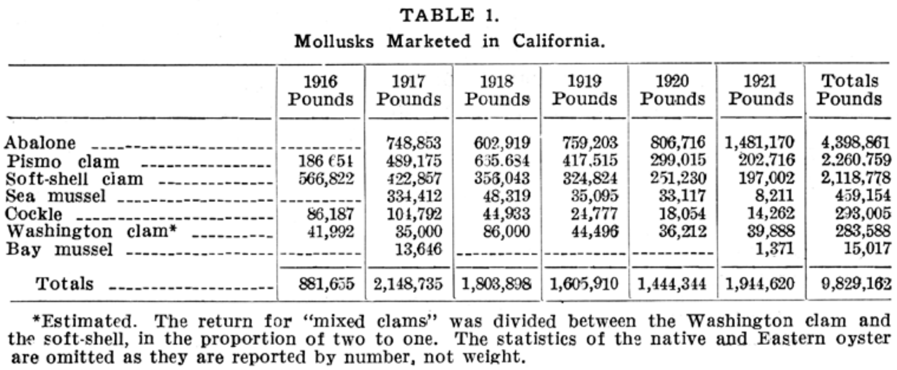


TABLE 1.

Mollusks Marketed in California.

	1916 Pounds	1917 Pounds	1918 Pounds	1919 Pounds	1920 Pounds	1921 Pounds	Totals Pounds
Abalone	----------	748,853	602,919	759,203	806,716	1,481,170	4,398,861
Pismo clam	186 651	489,175	635.684	417.515	299,015	202.716	2.260.759
Soft-shell clam	566,822	422,857	356,043	324,824	251,230	197,002	2,118,778
Sea mussel	----------	334,412	48,319	35,095	33,117	8,211	459,154
Cockle	86,187	104,792	44,933	24,777	18,054	14,262	293,005
Washington clam*	41,992	35,000	86,000	44,496	36,212	39,888	283,588
Bay mussel	----------	13,646	----------	----------	----------	1,371	15,017
Totals	881,655	2,148,735	1,803,898	1,605,910	1,444,344	1,944,620	9,829,162

*Estimated. The return for "mixed clams" was divided between the Washington clam and the soft-shell, in the proportion of two to one. The statistics of the native and Eastern oyster are omitted as they are reported by number, not weight.

Table 1. Mollusks Marketed in California

1.2. Absence of life history data

Yet of their life histories—the rate of growth, the age reached, the age of spawning, the productivity and many related problems—we know next to nothing. The introduced soft-shell (Mya) and the eastern oyster have been studied on the Atlantic coast; the native oyster is being investigated (Scofield, 1921: Stafford, 1913, 1918),[*] but for the other native species there exists no body of known facts and only a few scattered observations.

1.3. Why the Pismo clam was selected for study

While making a survey of the edible bivalves of the State (Weymouth, 1921), this lack was so strikingly apparent that it was thought profitable to work out the life history of at least one important and representative species. The species chosen was the Pismo clam (Tivela stultorum) Commercially the Pismo clam ranks first in importance in California among the clams and third among all the mollusks, being exceeded only by the oyster and the abalone. A second reason for considering this species is that there has been such evidence of depletion as to lead to increasingly more stringent protective laws, all of which have been urged by the residents of the county in which the

---

[*] This and other papers referred to will be found in the bibliography, p. 102.

clam is most abundant. In 1911 the legal size, below which no clam might be taken, was fixed at 13 inches in circumference and the bag. limit, or maximum number permitted to one person, at 200 per day. In 1915 the legal size was reduced to 12 inches in circumference and the bag limit to 50. In 1917 the legal size was changed to 4¾ inches in greatest length (a slight reduction). In 1919 the bag limit was further reduced to 36 per day. In 1921 the bag limit became 15.

An accurate study of the cause and extent of this apparent diminution must await knowledge of at least the fundamental facts of the life history of this clam. This lack the present study attempts to supply. The more important features are considered to be: the habits, enemies and mortality of the adult; the rate of growth and the factors affecting it; the age at certain significant periods, particularly at sexual maturity and at the time when the legal size is reached; the most common age of clams forming the commercial catch; the season of spawning and the productivity; and the habits, enemies and mortality of the young. Some answer to each of these questions will be attempted.

1.4. Importance of problems involved

While the problems selected for attack are those believed to be of the most immediate importance for the conservationist in maintaining the economic value of the species, it will be evident that they are also problems of fundamental biological significance. The writer wishes to record his hearty agreement on this point with the attitude expressed by his friend, Will F. Thompson, in formulating the aims of the State Fisheries Laboratory (1920).

The problem of growth has received much attention, but the material has generally, in fact, almost exclusively; been drawn from terrestrial organisms—man, such domestic animals as the horse and cow, the white rat, cultivated plants, forest trees—while a detailed knowledge of growth in aquatic plants or animals, aside from certain phases of the life-history in fish, is scarce and fragmentary. In the sea the conditions of life are so different from those on land that a study of growth in aquatic organisms can hardly fail to throw light on the fundamental conceptions of that process. Certain of these differences will be considered in detail later. One other point may be emphasized here. Before the effect of differences in environment can be evaluated, a sound and accurate knowledge of the normal progress of growth in many species must be available. Such growth norms have been worked out for but a very few organisms, and these mostly mammals; it is in part as an addition to this type of important and neglected knowledge that this paper is offered.

1.5. Order of treatment

The general order of treatment will be: (1) a short account of the natural history of the adult Pismo clam; (2) a detailed study of its growth; (3) a presentation of the data available on the breeding habits; (4) a study of the habits and mortality of the young; (5) a consideration of the problem of the conservation of the species.

2. NATURAL HISTORY OF THE ADULT

2.1. Range and relationships

Both in appearance and in habits the Pismo clam is strikingly distinct. It belongs to a family (the Veneridae) characteristic of tropical seas, and though the Pismo clam is not tropical in its distribution, it prefers the warmer waters, being recorded from Socorro Island, off Mexico, north to Santa Cruz. A few individuals have been taken at Half Moon Bay, just south of San Francisco, but as far as I am aware this is the extreme northern range, and though introduced at other points as far north as Oregon it has not established itself. It does not reach any considerable abundance north of the beaches of San Luis Obispo County. No reliable information is at hand concerning its abundance in Mexico, but it is apparently found in considerable numbers as it has been shipped to California on several occasions from the south. It seems fair, therefore, to consider it a subtropical form. The Pismo clam is not typical of the genus Tivela, but belongs to a group (subgenus Pachydesma) characterized by a larger size, valves less deep and triangular and far heavier, and a more northerly distribution. Its nearest relative on the Atlantic coast is the quahaug (Venus mercenaria).

2.2. General description

The shell is easily identified from its extremely massive valves which are far heavier than in any other non-attached species north of Mexico on the Pacific coast. In the young, the shell is covered with a heavy, glossy periostracum which gives it the appearance of being varnished. In the older shells. though well marked on the newer parts of the valves, this periostracum weathers off to a considerable extent about the umbo. The characteristic color is what might be called a pale buckskin, with occasional deposits of darker color, tending towards purplish, which are particularly characteristic of the siphonate end of the shell and occur in concentric bands which we shall have occasion to consider later in connection with the rate of growth. Occasional individuals are met with, which are strikingly marked with radiating lines of chocolate brown on the ground of buckskin. These lines begin at the umbo and radiate out to the margin, increasing in width with the distance from the umbo, and occur in irregular widths, those of the two valves of the single shell often differing markedly. Still less common, among the adults at least, are individuals entirely of the chocolate brown color found in the stripes just mentioned. The percentage of these individuals may be indicated by the following tabulation of one lot of young:

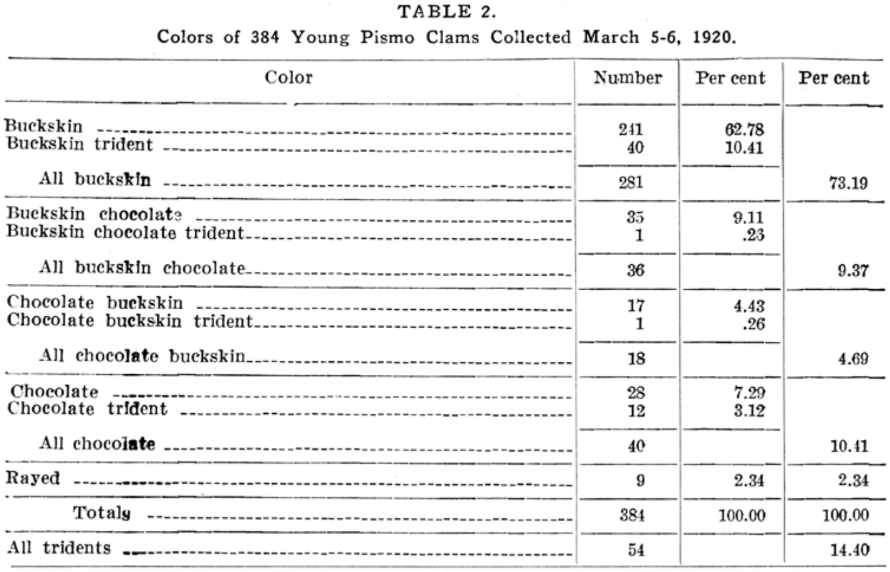


TABLE 2.

Colors of 384 Young Pismo Clams Collected March 5-6, 1920.

Color	Number	Per cent	Per cent
Buckskin	241	62.78	
Buckskin trident	40	10.41	
All buckskin	281		73.19
Buckskin chocolate	35	9.11	
Buckskin chocolate trident	1	.23	
All buckskin chocolate	36		9.37
Chocolate buckskin	17	4.43	
Chocolate buckskin trident	1	.26	
All chocolate buckskin	18		4.69
Chocolate	28	7.29	
Chocolate trident	12	3.12	
All chocolate	40		10.41
Rayed	9	2.34	2.34
Totals	384	100.00	100.00
All tridents	54		14.40

Table 2. Colors of 384 Young Pismo Clams Collected March 5–6, 1920

The terms buckskin-chocolate and chocolate-buckskin are self explanatory, indicating intermediate forms between the common and the dark phase. "Trident" refers to the presence of three light marks radiating from the umbo, less frequently seen in the adult and much less distinct, especially toward the margin, than the "stripes". It will be seen that nearly seventy-five per cent are classed as buckskin, about fourteen per cent as intermediate and ten per cent chocolate. The latter percentage

centage is lower in the adult. of all these color forms about fourteen per cent show the "trident" which is seldom shown by the adult, perhaps due in part to erosion near the umbo. It will be noted that the "trident" is most common in the dark phase. The significance of this is not known. Between two and three per cent are striped, a figure which would hold equally well in the adult.

The pigment responsible for both the bluish and brown color is deposited in the superficial portion of the shell, immediately beneath the periostracum, by the margin of the mantle which secretes the edge of the shell (see section on structure of shell, page 40). If in a fresh specimen the mantle is turned back from the valve the dark line of pigment-forming cells may easily be seen. This is much darker in dark-colored individuals than in light ones and in the striped cases it is easy to see that opposite the brown stripes the pigment-forming tissue is much heavier than opposite the light interspaces. There seems to be no good reason for viewing these banded or striped specimens as other than a color variation of the single species.

A similar striped color-variety of Mytilus galloprovincialis is recorded by List (1902) who denied it the specific rank conferred upon it by some of the earlier authors. The pigment forming the stripes lies in the same position as in Tivela, though its origin is not discussed.

2.3. Habitat

In habitat Tivela is sharply restricted to beaches of pure sand directly exposed to the ocean. Where active surf is absent as in sheltered bays and in lagoons this species does not occur; and fishermen claim that clams transferred to such bays, in order to be available for shipment during periods when tides are unsuitable for digging, seldom live more than a few days. This would indicate that complete aeration, due to the constant surf, is essential to the Pismo clam. It has been noticed, however, that adults in aquaria, even though the water is well aerated, soon die. This would seem to suggest that aeration is not the only factor; possibly some food organism characteristic only of the open beaches may be necessary. No further analysis of this interesting question is possible without more extensive experiments.

On suitable beaches the clam is found from a point on the beach twenty or thirty yards below high water mark to a depth of at least several fathoms. Its normal distribution through this region is now very difficult to determine. Under the present conditions the upper or intertidal zone is chiefly occupied by the young as will be discussed more in detail in a later section of this paper (see page 79). The commercial digger operates from a little below low tide to the greatest depths which he can reach, perhaps four or five feet, and the clams of marketable size are most abundant at the outer limit of this zone as shown by the dependence of the catch on the lowness of the tides. Only an occasional adult is met with above low tide. This condition is, however, chiefly the result of intensive fishing as indicated by the fact that it was formerly possible to turn out immense numbers of Pismo clams by running a plow along the beach at low tide. Many different competent observers have told the writer of the wagon loads of clams obtained in this way on various southern beaches. Sufficient clams have been taken on fishermen's lines or in other ways to show their presence in waters of a few fathoms, but how abundant they are can not be stated.

2.4. Habits

During ordinary weather the clam is found buried in the sand at a depth roughly equal to the length of its own shell. During stormy weather the clams are usually found at a greater depth. The siphons are not long, but serve to establish connection with the water at the depths at which the clam is commonly found. Under ordinary conditions the clams show a constant orientation to the direction of wave action, being found with the hinge or dorsal side turned toward the sea and the open margin of the shell pointing up the beach. The uniformity of this position is illustrated by the following data. of 91 consecutive specimens in which the position was carefully observed before they were turned completely out of the sand, 90 lay with hinge pointing within 20 degrees of the ocean and one was turned inward and toward the north. Many others were observed on this and other occasions and all amply confirmed these observations.

How this orientation is accomplished and maintained is not known. It is possible, since the dorsal or exhalent siphon lies nearer the ocean and the inhalant nearer the land that this position bears some relation to the nature of the food, oxygen or other features of the water supply, but no direct evidence of this is at hand. It is perhaps more probable that the orientation is the result of mechanical factors and represents the most stable position in relation to wave wash. Some experiments which were tried tend to confirm this view.

Experiment No. 1. Nine clams were placed in each of three positions (*a*) with the hinge away from the sea, (*b*) with the hinge toward the sea, (*c*) "broadside on," all at the same depth, the top flush with the surface of the sand. This was done at a level covered perhaps half the time, on a day with fairly heavy surf (April 10, 1920) and many were soon washed out again. (At this time the clams found *in situ* were all deeper in the sand.) In fact, after a few trials the experiment had to be abandoned as part were washed out before those in the other positions could be placed, and often after a wave the entire set would have disappeared. On this occasion the numbers counted in position after a wave were (*a*) hinge away from the sea, 1 (*b*) hinge toward sea (normal position) 4, and (*c*) "broadside on" none.

Experiment No. 2. With ten in each position the following remained, (*a*) hinge away from the sea 10, (*b*) hinge toward sea (normal position) 10, (*c*) "broadside on" 7.

Experiment No. 3. Twenty-eight clams were thrown into a wave and their position on the sand when the wave had receded was noted. Twenty-five lay on the side with the hinge toward the sea and the long axis parallel with the coast, and three with the hinge away from the sea.

Opportunity was not offered for the repetition and elaboration of these interesting experiments but the last clearly shows that the mechanical effect of the form leads to an assorting of position in the water above the sand, and the previous experiments indicate that all positions in the sand are not equally stable; in all cases clams "broadside on" were most quickly washed out.

Though far from conclusive these observations suggest that the question may be one of physical selection. Those in the most stable position, with the hinge toward the sea, maintain their position; those in other positions are washed out and in burrowing again, part assume the stable position and remain in place until by repeated selection all come to have the same orientation. This would be independent of sensory stimuli. The question deserves further attention. It might be noted in passing that a definite orientation has also been observed in the razor clam and in the wedge shell clam. (Weymouth 1921, pp. 31, 47 and 51.) It is possible that such orientation is characteristic of many of the forms found on open beaches.

Since the position occupied by this species is one in which the sand is constantly shifting to an extent seldom realized, it is necessary that the clam be surprisingly active in order to maintain its position, since according to the type of wave action there is either a deposition or an erosion of sand going on at nearly all times. During stormy weather this is often very extensive and very rapid. It occasionally occurs in some of the severest of winter storms that considerable numbers of clams are washed out and are found lying at higher levels on the beach. Presumably burying of the clams also occurs at times, but this would not be as easily noted. However, these accidents are of comparatively infrequent occurrence and under ordinary circumstances the clam is active enough to maintain its feeding position, which is near the surface of the sand. The situation is a very different one from that confronting the clams living in sheltered bays, where the adult usually shows little power of burrowing. In the Pismo clam the foot is broad and thin, and, in the young, can be protruded to a considerable distance. This ordinary action of the foot in burrowing appears to be supplemented in the Pismo clam by the ejection of the water within the mantle cavity. After the foot has been extended and fixed, it is powerfully contracted. The return of the foot to the mantle cavity would displace a portion of the water, and this is accompanied by a partial closure of the shell which forces out a still greater amount of water. The details of the process can not be made out, since it occurs below the sand, but the ejected water causes the sand to "boil" near the foot and it is apparent that this action, recalling the method of "jetting" a pile, is an important factor in moving such a bulky shell through the sand. The young will burrow from sight in a few moments if placed on wet sand, and though the adult is less active, those turned out usually regain their position if wave action is not too violent and the clam is undisturbed long enough to get a "foothold."

The water from which the Pismo clam draws its supply usually contains sand and the siphons show a very nice adaptation to this condition. The siphons are of moderate size, roughly equalling the shell in length, and the two tubes are united except for a short distance at the tip. The exhalent or anal siphon is slightly the shorter and its delicate, thin-walled tip, rimmed with a few short tentacles, closes in a line parallel with the margins of the shell when no current is passing out. At other times the exhalent current prevents the entrance of sand. The inhalent or branchial siphon is somewhat enlarged at the tip and ends in a broad flat surface which to the first glance shows no opening. If the undisturbed animal, buried in the sand of some small pool, is examined with a low power lens, it will be seen that the opening of this siphon is guarded by a system of delicate pinnately branched papillae which form so fine a screen that sand grains falling upon it do not find entrance while at the same time the water and the microscopic food organisms have free access to the mantle cavity through this living filter. As the water flowing over this clam always contains some sand and is often filled with whirling clouds of it, in contrast to the water of bays which is clear or contains only fine sediment, the value of this arrangement is obvious since the water supply bears both oxygen and food to the animal.

It is interesting to compare the siphons of Tivela with those of certain species described by Morse (1919), the only writer who gives adequate data on these structures. Venus mercenaria, the nearest relative of Tivela which he figures (p. 177), is very different, having short siphons devoid of any elaborate screen. Its habits apparently explain this difference, as it is found almost entirely in sheltered bays where the water contains no sand. In general appearance and length, though they lack as complete a screen, the siphons figured for Mactra solidissima (p. 188) most closely approach those of Tivela, a fact probably correlated with the similarity of habitat of the two species, both of which are found on exposed sand beaches. Mya arenaria, a widespread and hardy form usually found within bays, in both mud and sand, is figured as having an inhalent siphon resembling the Pismo clam though the papillae are far less richly branched. Many of the bivalves, probably from their plant-like restriction to a single spot for most of their life, show extremely close adaptations of which the siphons may serve as an example, but unfortunately these have received comparatively little attention and even the "soft parts" are too often regarded merely as food or as an encumbrance to be removed before the "shell" is ready to appear in the "collection." The careful observations of Morse, for this reason, deserve special commendation.

In a number of specimens examined, the contents of the alimentary canal consisted largely of one kind of small unicellular plant, an undetermined flagellate species. In these cases no diatoms were observed, although these form an important part of the food of most bivalves.

2.5. Fishing methods

Commercial fishing is almost entirely confined to the beaches at Morro and at Pismo-Oceano. Two methods are in use for obtaining the clams. In one a six-tined potato fork is used in working in water which is from one to four or five feet deep at low tide. The digger "feels" for the clams with the fork and when one is encountered turns it out and transfers it to a "drag" which is usually fastened to the waist. (See Fig. 1). On account of the position of the clams, already mentioned, fishermen find it more advantageous to work along a line parallel with the edge of the water, since in this way the "broadside" of the clam is more likely to be encountered. In the second method a "rake" formed by bending the tines of a heavy pitch-fork is used, usually with a considerable extension of the handle. A rope attached to the fork is looped around the waist and with the long handle resting on his shoulder the clammer walks backward dragging the tines through the sand. When a clam is struck, it is turned out by tilting the handle of the rake upright. This is a laborious method of digging but, with it, more ground can be covered than by using a fork.

For several years the Pismo clam has ranked next to the abalone in commercial importance in California but the catch during the past two years has shown a considerable decline, the significance of which will be

FIG. 1. Gear used in digging Pismo clams. Rake with extension handle and rope by which it is pulled through sand, fork and "drag" with snap and belt

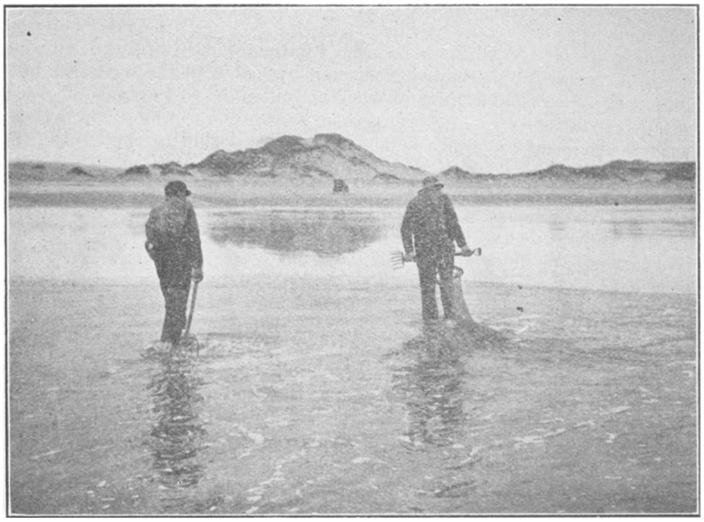


FIG. 2. Diggers returning with clams, Oceano. Note, the wide level beach

considered in another section. The clams, taken in San Luis Obispo County are sent chiefly to Los Angeles or San Francisco and other bay cities where they are used almost wholly in cafes and restaurants, few being retailed. In the southern part of the state large numbers of clams are used for bait in surf fishing. (See Table 1) .

3. GROWTH

3.1. Nature and importance of problem

of the questions above outlined the growth of the Pismo clam is, as I purpose to show, by far the most important. Growth has always attracted the attention of biologists but the present trend of investigation in this problem is comparatively recent. Quetelet, in the early part of the nineteenth century, applied quantitative methods to the study of growth in man (among a variety of other subjects) and laid the foundation of modern statistics. The present period of the problem dates, however, more properly from the work of Minot who less than forty years ago applied these methods to laboratory animals. Since this, there have been many studies attempting to supply accurate values for age and size throughout the life of a particular species while other workers, as Robertson and Ostwald have sought to find in known chemical or physical processes an explanation of the course of growth thus expressed.

Although both lines of effort have served to clarify certain phases of growth it seems increasingly clear that more basic data rather than more speculations are needed. Comparatively few of the many diverse types of animals have been studied quantitatively and these have often been under special uncontrolled or unrecorded conditions which were neither typical of the species in nature nor adequate for experimental study. The most complete data are on the most complex group—mammals.

The study of the Pismo clam under natural conditions and with adequate material for statistical treatment appealed to the writer as offering an excellent opportunity of working out in detail the facts of growth in an organism representative of a large group—the mollusks. It was with the hope of making a substantial contribution to this most interesting of biological problems that the writer undertook the present work.

A most significant step would be accomplished if the main factors, external and internal, involved in growth could be identified, their relative importance determined, and their mode of action discovered. The most effective method of analysis would be to compare the normal growth in one locality with that in a second locality, known to differ markedly in some external factor, or to compare, in the same locality, the normal growth with the growth observed in a particular season notable for its unusual conditions. Such comparisons would indicate the factors involved and these could then be studied by controlling them experimentally and noting the results. Without reliable norms any such program is impossible. From this point of view the purpose of the present work is twofold; first, by furnishing a method of determining age to facilitate the working out of such standards for the bivalves and, secondly, to establish by this method one such norm, that for Tivela on the San Luis Obispo coast. Such a norm would be available when from animals living under natural conditions, reliable averages of the weights or lengths or both at all ages were obtained. Such information could be represented in the form of a growth curve or graph in which the age in years or months would be plotted against the weight or length and would show the size at any age, the growth during any year, the relative rapidty of growth at different ages or sizes, and similar features.

3.2. Importance to conservation

The importance of such knowledge of the course of growth to the conservationist will be evident from a few applications. What age is represented by the legal size of 4 ¾ inches? There is a widespread belief among the clam diggers that this size is reached in three years. Careful study of the soft shell (Mya arenaria) on the Atlantic coast has shown that a marketable size may be reached in two years, or, under favorable conditions, even less. If the Pismo clam should mature in two years, a short time would suffice to restock depleted areas and the effect of a successful spawning season would soon be felt. But if the Pismo clam should require two, three or four times this period, restocking would be a slow process and the natural fluctuations due to marked differences in the success of spawning years or unusual destruction of animals, for example from storms, would cover a long period and the phase of decline could not easily be distinguished from the decline due to over-fishing. Much the same thing would be true of the question of total age. The problem of protection would be very different in a species in which a complete turnover of the entire population occurred in three years from one in which twenty years was required for the process, and both these periods of total life are known in the mollusks.

If we have a complete knowledge of the course of growth we can analyze the composition of the commercial catch, and by a study of the changes in numbers of the different year-groups determine what changes in abundance are due to over-fishing and what to natural fluctuations. When this is possible, the productivity of a species in nature may be as intelligently utilized as the productivity of an animal or plant under cultivation.

One more special and easily recognized example may be cited. When the breeding size or age has been determined, the protection of an adequate supply of breeding animals will cease to be a matter of guess work and become a simple and potent method of protection.

Having thus defined what is considered the most urgent problem of growth and pointed out its importance, we will proceed, after a brief survey of what has been done along this line in the mollusks, to a consideration of the methods available for the analysis of this question and their detailed application in the present case.

3.3. Previous data on growth in mollusks

Though certain species of bivalves, notably the oyster and some clams and mussels, have long been cultivated with distinct success, accurate knowledge of the normal course of growth is surprisingly small. Only a brief statement will be given here of those studies furnishing data for a normal growth curve or methods of estimating age; a detailed analysis will be postponed to the following sections on the methods of determining age and the results of the present study of the Pismo clam.

The oyster, first in economic importance, has naturally received the most attention; the list of publications dealing with it is now a formidable one. The irregular form characteristic of an attached species does not, however, lend itself to accurate measurement, and though there are numerous figures showing growth of particular lots in particular localities, general results for growth over a series of years under natural conditions seem not to be available, nor, as we shall see later has a reliable method been developed for determining the age of "wild" oysters. For instance Stafford (1913, p. 86) is able to make only a very guarded statement of the size for each of the first four or five years.

In the case of the soft clam (Mya arenaria), though also extensively studied by several workers (for example, Kellogg, 1910, and Belding, 1916), no methods of determining age or satisfactory results on the general rate of growth have appeared. The work of Belding on the scallop (1910) and the quahaug (1912) is much more complete and furnishes data not only for a curve of growth but for an adequate comparison of growth in different localities. It deserves high commendation. Mention might also be made of the work of Crozier (1918) on Chiton.

3.4. Methods of determining age.

Age-group method

In the study of the rate of growth two main methods are available where direct knowledge of age, as in man and domesticated animals, is not at hand. The first is what may be called the age-group method. If at any one time a large number of animals of all sizes are measured or weighted it is usually possible to identify by a comparison of these sizes, certain of the age-groups, that is, groups of animals of the same age. In the present case the young clams in their first year form a distinct group, easily told from those in their second year, since the largest of the one-year-olds is obviously smaller than the smallest of the two-year-olds. The difference in size between those in their second and those in their third year is less but still sufficient to distinguish the groups. With each successive year the difference becomes less marked though by careful measurements of a large number of individuals the modes corresponding to the various age groups may be identified with varying success in different species; with the Pismo clam this method might serve for the first four or five years. Beyond this point the method ceases to be decisive without confirmatory evidence from some other source.

3.5. "Annual ring" method

The second method is one that has been used extensively in other groups, notably with fish. Here, as is well known, the evidence of unequal rates of growth at different times in the scales, otoliths, vertebrae or other hard parts has been interpreted in terms of years. According to some observers similar zones resulting from alternate rapid and slow growth may be identified at the base of the horns of cattle (D'A. W. Thompson, 1917, p. 614) and the age thus determined. In the molluscan shell the presence of similar rings has been both affirmed and denied. The validity of this method, which from the term applied to its first recognized occurrence in the wood of trees may be called the "annual ring" method, has recently been attacked on the ground that it may be an entirely physical phenomenon. (D'A. W. Thompson, 1917, p. 432.) Since this is the chief method employed in the present work, it will be necessary to examine the evidence bearing on the annual nature of such markings critically and in some detail.

3.6. In trees

The conception of records in permanent structures of alternating periods of rapid and slow growth, corresponding to the yearly rhythms of temperature or other external conditions, undoubtedly had its origin in the now well established fact that the "annual rings" in the wood of trees indicate their age. The growth of a tree is not continuous but shows fluctuations with the season due to variations in the temperature, rainfall, or other features of its environment, the rate falling to a slow ebb or ceasing altogether in the winter and rising to a maximum in the summer.[*] Corresponding to this variation in the rate of growth, the tissue deposited varies in texture and in appearance giving rise to the "rings" which are truly "annual" because one is formed each year. In other organisms showing a similar intermittent growth, or a great seasonal variation in the rate of growth, similar "annual" marks might be expected.

3.7. In fish

In the case of fish we have definite though not abundant evidence of variations in the rate of growth at different seasons; examples of such evidence are found in the work of Fraser (1917) and of Rich (1920). Many competent observers have recorded annual marks in the scales, otoliths, vertebrae and other hard parts of fish. In the scales these take the form of a local crowding of the numerous fine, usually concentric markings or circuli. Examples may be seen in the figures of Gilbert (1913) or the writers just quoted. In the otoliths they appear as concentric zones of differing degrees of translucency. For such marks to be of service in the determination of age it would have to be proved:

1. That the marks in question were distinctive in appearance and could be identified by a competent observer in the great majority of cases;
2. That they were annual—i. e., that one and only one is formed each year. This might be established in three ways:
   a. By a definite seasonal relation of the marks to the forming mrgin;
   b. By the correspondence of the number of the marks to the known age of animals either kept in captivity or distinctively marked and recaptured;
   c. By the agreement in number of the marks with the evidence from the modes of age-groups.

3.8. Criticism of annual ring theory

One of the more prominent critics of the reliability of these marks in fish has justly remarked "that we have no right to *assume* that an appearance of rhythm and periodicity in structure and growth is necessarily bound up with, and indubitably brought about by, a periodic recurrence of particular *external conditions*." (D'A. W. Thompson, 1917, p. 433.)

He points out that a similar appearance of regularity and periodicity may be due to purely physical causes as certain conditions may lead to

---

[*] See D'A. W. Thompson, 1917, p. 120, for an excellent example of such a curve of rate of growth in trees; although unconvinced of the annual nature of the "zones of growth" in the fish scale or otolith he accepts the "annual ring" in the tree without question.

the rhythmic deposition of the silver chromate in Liesegang's rings or the banded structure of agate or onyx. Such rings might also conceivably arise from a rhythm of external conditions the period of which was not the year but the day, month, or decade. These objections are not valid, however, in the case of a number of species of fish, where the annual nature of the marks rests on no assumption of any kind but on direct observation. In some a study of the scales throughout the year has clearly shown that the ring is formed during the winter and only once each year. In others it has been shown that the number of rings agrees with the known age of fish kept in captivity or of marked fish recaptured after known periods (Snyder, 1921, 1922; Calderwood, 1908, p. 99 *et seq.*). The soundness of these conclusions is not affected by the fact that in certain species the rings are less distinct and hence in these cases may be an unreliable guide to age, nor that incompetent or hasty workers may have reached incorrect conclusions in any species.

3.9. Growth in young.

Methods of collecting

The first data on the Pismo clam to be presented will be those on growth in the young. In order to understand their significance it will be necessary to point out the method of collection and some of the precautions that must be observed to make the specimens representative. During 1919 and 1920 the young of the first two years were systematically collected. Tivela is far more abundant on the beaches of San Luis Obispo County than elsewhere in California, and in consequence this is the center of the commercial fishery. For this reason it was decided to collect here, and because of its accessibility the Pismo-Oceano beach was chosen instead of that at Morro. The probability of local races was anticipated from the writer's previous experience with Cancer magister, the edible crab, (Weymouth, 1918) and this was further indicated by the claim of the fishermen that the clams from different localities could be recognized by their shape. To avoid error from this source, collection was restricted to the above locality with the exception of some data designedly taken for comparison. It was not known, however, until brought out in the course of the work, how great was the variation between different parts of the same beach. The majority of the collecting was done on a few hundred yards of beach about a quarter of a mile north of the old wharf at Oceano. From this point to the town of Pismo is only two and one-half miles along an open and straight coast without obvious differences, yet the young collected at these two places on the same day differed widely as may be seen from the following figures:

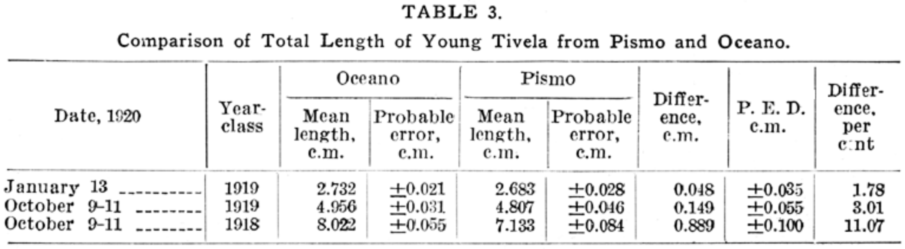


TABLE 3.

Comparison of Total Length of Young Tivela from Pismo and Oceano.

Date, 1920	Year-class	Oceano		Pismo		Difference, c.m.	P. E. D. c.m.	Difference, per cent
		Mean length, c.m.	Probable error, c.m.	Mean length, c.m.	Probable error, c.m.			
January 13	1919	2.732	±0.021	2.683	±0.028	0.048	±0.035	1.78
October 9-11	1919	4.956	±0.031	4.807	±0.046	0.149	±0.055	3.01
October 9-11	1918	8.022	±0.055	7.133	±0.084	0.889	±0.100	11.07

Table 3. Comparison of Total Length of Young Tivela from Pismo and Oceano

The percentile difference in length is thus a constant and significant difference, exceeding at times the growth to be expected (as it proved) from the interval between collections. Still later it was found in making a "cross section" of the beach that the clams from different levels showed distinct differences in size, as shown in the following table. The possible significance of this will be considered in a later section.

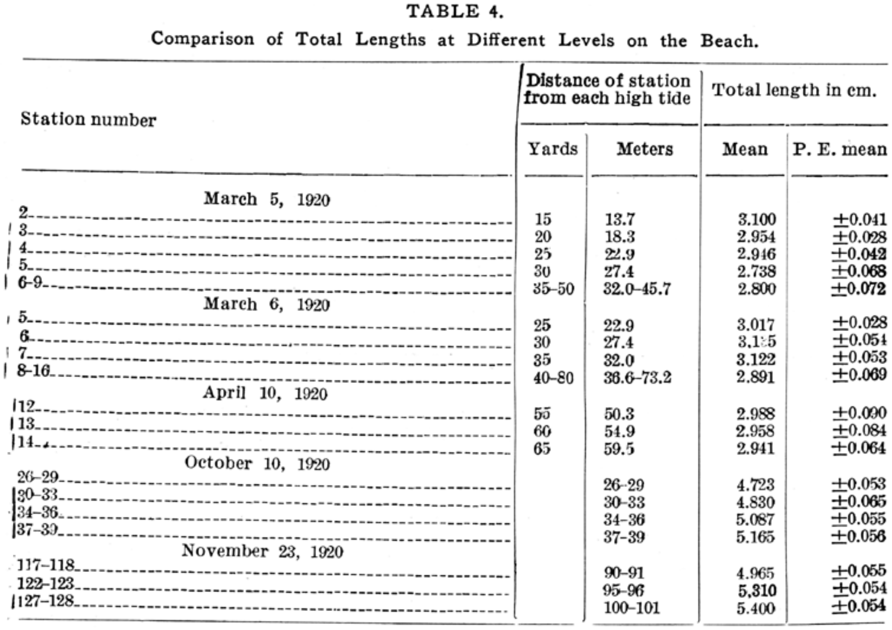


TABLE 4.

Comparison of Total Lengths at Different Levels on the Beach.

Station number	Distance of station from each high tide		Total length in cm.	
	Yards	Meters	Mean	P. E. mean
March 5, 1920				
2	15	13.7	3.100	±0.041
3	20	18.3	2.954	±0.028
4	25	22.9	2.946	±0.042
5	30	27.4	2.738	±0.068
6-9	35-50	32.0-45.7	2.800	±0.072
March 6, 1920				
5	25	22.9	3.017	±0.028
6	30	27.4	3,135	±0.054
7	35	32.0	3.122	±0.053
8-16	40-80	36.6-73.2	2.891	±0.069
April 10, 1920				
12	55	50.3	2.988	±0.090
13	60	54.9	2.958	±0.084
14	65	59.5	2.941	±0.064
October 10, 1920				
26-29		26-29	4.723	±0.053
30-33		30-33	4.830	±0.065
34-36		34-36	5.087	±0.055
37-39		37-39	5.165	±0.056
November 23, 1920				
117-118		90-91	4.965	±0.055
122-123		95-96	5,310	±0.054
127-128		100-101	5.400	±0.054

Table 4. Comparison of Total Lengths at Different Levels on the Beach

To obtain a strictly representative sample of Tivela, therefore, it would be necessary to collect at a single point on the beach and to take equal numbers from all levels of the beach or the entire population of a "cross section." In the later collections all of these precautions were observed. The difficulties of sexual differences in size, troublesome in some species because the sexes can not easily be identified in bivalves, are obviated in the present case by the fact that the Pismo clam is hermaphroditic.

3.10. Methods of measurement

All measurements were made by one person, the writer, with a sliding caliper reading directly to millimeters and by a vernier to to 0.1 mm. The nearest 0.1 mm. was recorded, though not used in all the calculations. The length (greatest antero-posterior dimension) was measured in all specimens; when time and facilities were available certain other measurements were made and the weight taken. The measurements most often taken were those of height (greatest dorso-ventral dimension) which would perhaps be most naturally called "width" in a separated valve, and the thickness of the tightly closed animal. (See Fig. 3) The young were weighed on a balance sensitive to .01 g., the weight being recorded to the nearest 0.05 g. or 0.1 g. according to size.

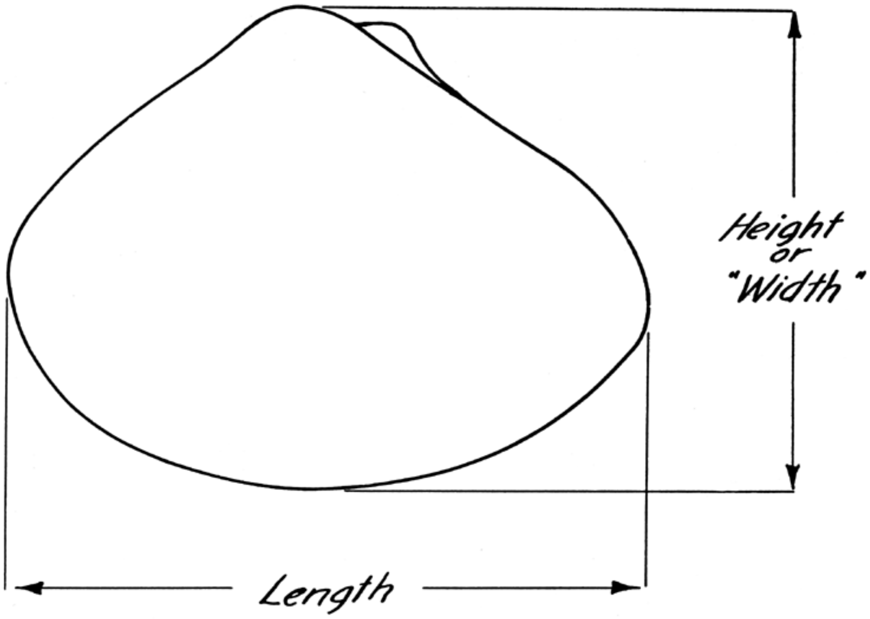


FIG. 3. Outline of *Tivela* shell showing method of measuring.

FIG. 3. Outline of Tivela shell showing method of measuring

3.11. Length versus weight as a criterion of size

Studies of growth have been based, sometimes on length, and sometimes of weight. In the case of man both have been used; with small mammals, such as rats, mice and guinea pigs, weight has usually been employed, chiefly for the practical reason that it is much easier to determine in active animals. On the other hand, work with marine animals has usually been based on length. Accurate measurements may be made with a tape or calipers in the field where a delicate balance could not easily be carried and where the time necessary for its use is not available. The sources of error in the weight of a form like a clam are greater than in the length, for the shell is firm while the amount of water in the mantle cavity may vary widely. Practical considerations have therefore forced, in this as in most similar work, the adoption of length as a standard.

There is logic in the use of weight if increase in mass is taken as the criterion of growth. It is usually claimed, however, that weight is more variable than length or height. Such a condition is shown in the case of man by the figures quoted by D'A. W. Thompson (1917, p. 79) from the work of Bowditch, Boas and Wissler where the coefficient of variability (percentile variability) for the ages of five to eighteen years ranges from 9.92 to 16.80 for weight whereas that for height is but 3.69 to 5.79. This has been claimed to result from the fact that although the skeletal features which determine height, once formed can not easily be altered, the weight may fluctuate from the gain or loss of fat or muscular tissue and must therefore be less stable. For instance, after the age of twenty years in man there is no change in height beyond a slight loss in extreme old age, but there may be, according to everyone's experience, great fluctuations in weight. The comparison implied in the above figures is, however, not entirely just, as I shall attempt to show, although the following relationship is apparently seldom appreciated by those presenting such data. It is clear on the face of the data that the weight shows a percentile variability between two and three times as great as that of height, but this results in part from a simple mathematical relation and does not prove that the form of the children measured varies more widely than does the height.

This may be made clearer by an example. Suppose we were to measure a series of cubes (or other regular solids) of different sizes. Though each cube were to have its three dimensions of length, breadth, and thickness exactly equal, their volumes (or if they were equally dense, their weights) would show a far greater percentile variability than their heights—in fact, exactly three times as great. While it is clear that the "variability" of weight in this case is greater than height, it is equally clear that this is not because of variability in form but is a simple mathematical result involved in a comparison of a series of numbers with their cubes. If there were, in addition, an actual variability in form—if the three dimensions of part or all of the "cubes" were not equal—the coefficient of variability of the volumes would of course exceed three times that of the heights.

A collection furnishing two homogeneous series of clams of the same age and from the same locality on the same date was examined with this point in mind, and the results are presented in Table 5. For each year-class it will be seen that the coefficient of variability of the lengths and of the lengths cubed follow the above mathematical relation almost exactly. A similar comparison of the coefficient of variability of lengths and weights shows a not significantly different result, so we are not justified in assuming any material difference of form. It still remains true that in the handling of results the three-fold greater proportional dispersion of the weights makes them less distinctive, for instance, as a measure for comparison of different year-classes or other natural groups with. which we must deal. Thus, though we have clear proof in the present case that in a mathematical sense length is just as good as, but no better a measure of size than weight, it remains that in comparison of results length is more workable and its use, while enforced by practical questions of field working conditions, is theoretically on an exact par with weight and in practice more serviceable.

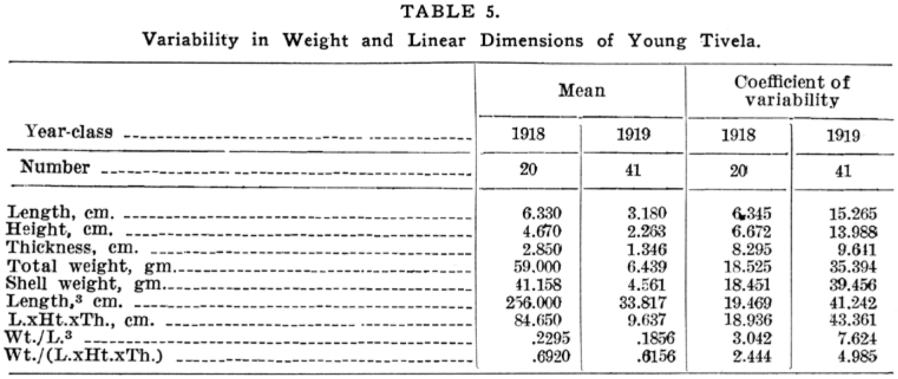


TABLE 5.

Variability in Weight and Linear Dimensions of Young Tivela.

	Mean		Coefficient of variability	
Year-class	1918	1919	1918	1919
Number	20	41	20	41
Length, cm.	6.330	3.180	6.345	15.265
Height, cm.	4.670	2.263	6.672	13.988
Thickness, cm.	2.850	1.346	8.295	9.641
Total weight, gm.	59.000	6.439	18.525	35.394
Shell weight, gm.	41.158	4.561	18.451	39.456
Length,^{3} cm.	256.000	33.817	19.469	41.242
L.xHt.xTh., cm.	84.650	9.637	18.936	43.361
Wt./L.^{3}	.2295	.1856	3.042	7.624
Wt./(L.xHt.xTh.)	.6920	.6156	2.444	4.985

Table 5. Variability in Weight and Linear Dimensions of Young Tivela

There are indications that in man growth in height is not equivalent to growth in weight but is a more conservative and significant phenomenon; this, for example, is the attitude of Porter (1922). In the absence of adequate data it is impossible to decide whether such a distinction may be expected outside the vertebrates.

Length, then, will be used as the basis of the study of growth in Tivela; where it is desired to translate length into weight for comparison with other work or for any purpose, this is made possible by the use of formulae discussed in the section on the relation of length to weight.

Having discussed the method of collecting data we may turn to the results obtained by comparison of the young, with particular regard to the question of age-groups.

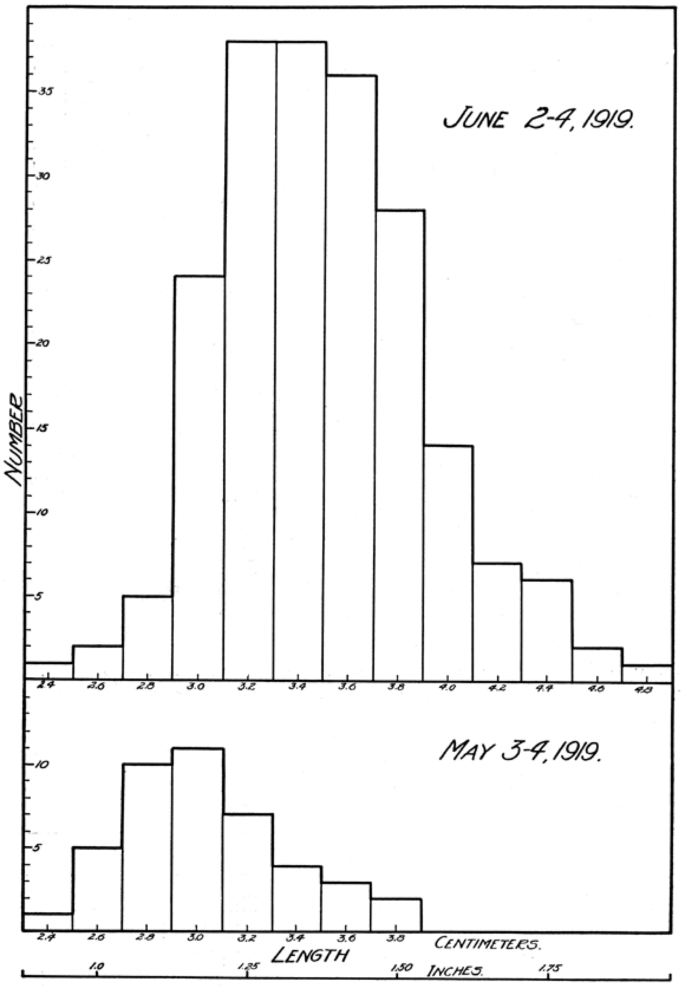
3.12. Identification of age-groups

The first collections were made on May 3 and 4, 1919. These gave a group averaging 3.04 cm. in length. Material collected on June 2 and 4, 1919, furnished similar results; the clams averaged 3.5 cm., thus being slightly larger than those of the previous month. To give a clear picture of the composition of these collections of young, Graph 1 is presented, showing the frequency of the different sizes found at these times. The upper frequency polygon (June 2–4) since it represents more specimens will be the more satisfactory for examination, though the previous collection gives essentially the same picture. It will be seen that they are compactly grouped, none measuring less than 2.4 cm. and none more than 4.8 cm. Although a careful search was made and, as may be seen from the tables, over two hundred clams obtained, no smaller specimens were found and the next larger clams, too few and scattered to permit analysis, began with specimens 8.1 and 9.1 cm. in length.

There can be no doubt, therefore, that this represents an age-group in the sense previously defined, that at this time it represents the youngest of such age-groups and, therefore, presumably the young hatched in the previous year, that is to say, 1918.

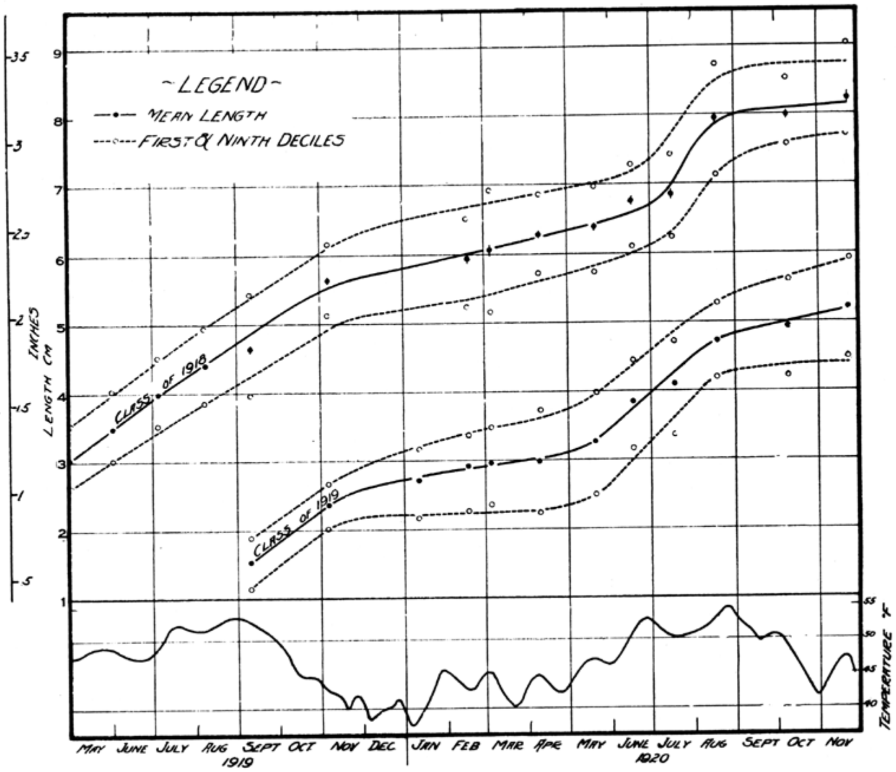
3.13. Method of plotting

The further collections up to September, 1919, present no new features and do not require to be discussed separately. The course of the changes in size are presented in Graph 2. The method adopted will be clear from the figure. The abscissae represent time and the ordinates size (total length) of the clams in centimeters. The mean for the collection of June 2d and 4th is, therefore, recorded above June 3d at 3.5 cm. The extent of the probable error of this mean, when large enough to show with the scale adopted, is represented by the short vertical line extending above and below the mean. In order to present a picture of the extent of variation at this time another value is also recorded. The actual sizes of the largest and smallest individuals are subject to too great irregularity to be satisfactory for this purpose and the values chosen have been the first and ninth decils, or, according to another terminology, the 10th and 90th percentiles. If all the specimens of a collection are sorted and arranged in the order of their length and one-tenth of the total number cut off from either end, we will have as the first decil the smallest individual remaining after discarding 10 per cent of the



GRAPH 1. Frequency polygons showing the numbers of each length of young *Tivela* collected on May 3–4 and on June 2–4, 1919. The increase in average size during approximately one month is clearly shown.

Graph 1. Frequency polygons showing the numbers of each length of young Tivela collected on May 3–4 and on June 2–4, 1919. The increase in average size during approximately one month is clearly shown



GRAPH 2. Growth of young *Tivela*. Graph showing the lengths of young *Tivela* on various dates from May, 1919, to November, 1920. Three values of the length for each collection are plotted; the mean and the first and ninth decils. The first and ninth decils would represent the length of the smallest and largest individuals remaining if all specimens were arranged in their order of size and one-tenth were cut off from either end. Below are shown on the same dates the minimum daily air temperatures at San Luis Obispo (smoothed by a moving average of 21 days to eliminate minor fluctuations).

Graph 2. Growth of young Tivela. Graph showing the lengths of young Tivela on various dates from May, 1919, to November, 1920. Three values of the length for each collection are plotted; the mean and the first and ninth decils. The first and ninth decils would represent the length of the smallest and largest individuals remaining if all specimens were arranged in their order of size and one-tenth were cut off from either end. Below are shown on the same dates the minimum daily air temperatures at San Luis Obispo (smoothed by a moving average of 21 days to eliminate minor fluctuations)

smallest, and in a similar way the ninth decil represents the largest individual remaining after discarding 10 per cent of the largest specimens. Eighty per cent, therefore, of the collection are included between the two decils recorded. A steady rise in all these values will be noted throughout the period under discussion.

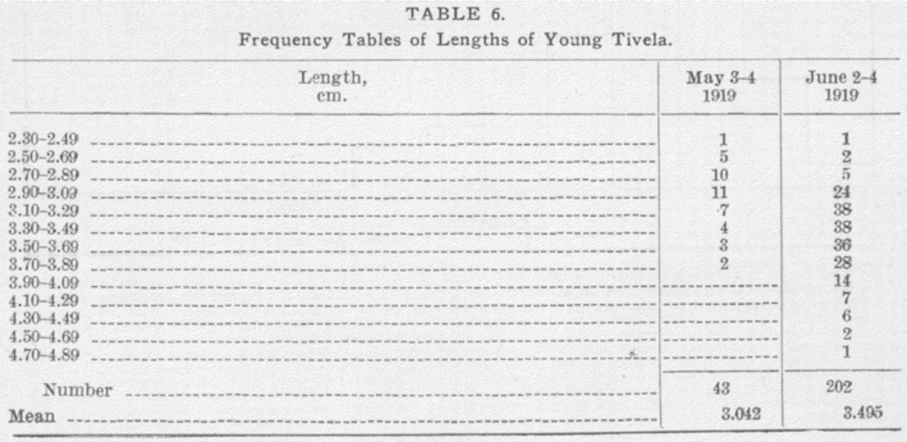


TABLE 6.

Frequency Tables of Lengths of Young Tivela.

Length, cm.	May 3-4 1919	June 2-4 1919
2.30-2.49	1	1
2.50-2.69	5	2
2.70-2.89	10	5
2.90-3.09	11	24
3.10-3.29	7	38
3.30-3.49	4	38
3.50-3.69	3	36
3.70-3.89	2	28
3.90-4.09		14
4.10-4.29		7
4.30-4.49		6
4.50-4.69		2
4.70-4.89		1
Number	43	202
Mean	3.042	3.495

Table 6. Frequency Tables of Lengths of Young Tivela

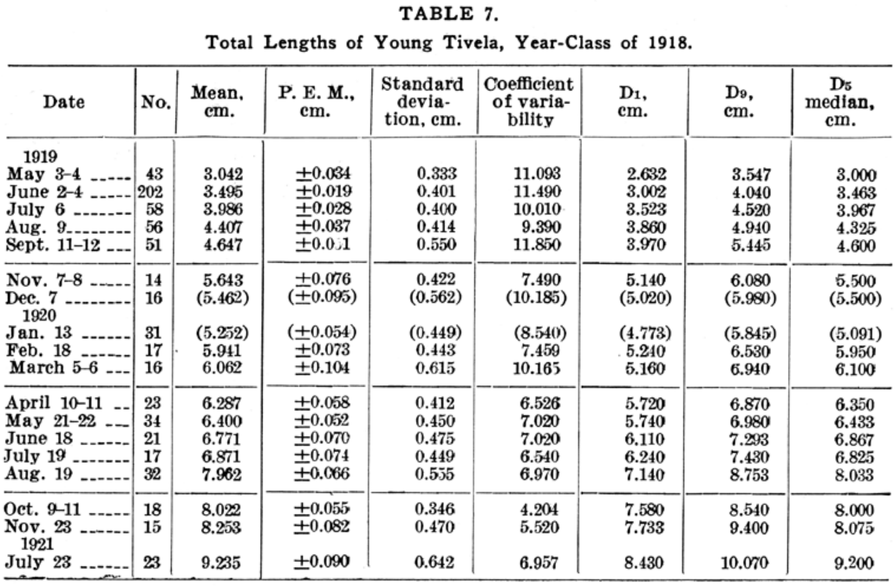


TABLE 7.

Total Lengths of Young Tivela, Year-Class of 1918.

Date	No.	Mean, cm.	P. E. M., cm.	Standard deviation, cm.	Coefficient of variability	D_1, cm.	D_9, cm.	D_5 median, cm.
1919								
May 3-4	43	3.042	±0.034	0.333	11.093	2.632	3.547	3.000
June 2-4	202	3.495	±0.019	0.401	11.490	3.002	4.040	3.463
July 6	58	3.986	±0.028	0.400	10.010	3.523	4.520	3.967
Aug. 9	56	4.407	±0.037	0.414	9.390	3.860	4.940	4.325
Sept. 11-12	51	4.647	±0.0[illegible]1	0.550	11.850	3.970	5.445	4.600
Nov. 7-8	14	5.643	±0.076	0.422	7.490	5.140	6.080	5.500
Dec. 7	16	(5.462)	(±0.095)	(0.562)	(10.185)	(5.020)	(5.980)	(5.500)
1920								
Jan. 13	31	(5.252)	(±0.054)	(0.449)	(8.540)	(4.773)	(5.845)	(5.091)
Feb. 18	17	5.941	±0.073	0.443	7.459	5.240	6.530	5.950
March 5-6	16	6.062	±0.104	0.615	10.165	5.160	6.940	6.100
April 10-11	23	6.287	±0.058	0.412	6.526	5.720	6.870	6.350
May 21-22	34	6.400	±0.052	0.450	7.020	5.740	6.980	6.433
June 18	21	6.771	±0.070	0.475	7.020	6.110	7.293	6.867
July 19	17	6.871	±0.074	0.449	6.540	6.240	7.430	6.825
Aug. 19	32	7.962	±0.066	0.555	6.970	7.140	8.753	8.033
Oct. 9-11	18	8.022	±0.055	0.346	4.204	7.580	8.540	8.000
Nov. 23	15	8.253	±0.082	0.470	5.520	7.733	9.400	8.075
1921								
July 23	23	9.235	±0.090	0.642	6.957	8.430	10.070	9.200

Table 7. Total Lengths of Young Tivela, Year-Class of 1918

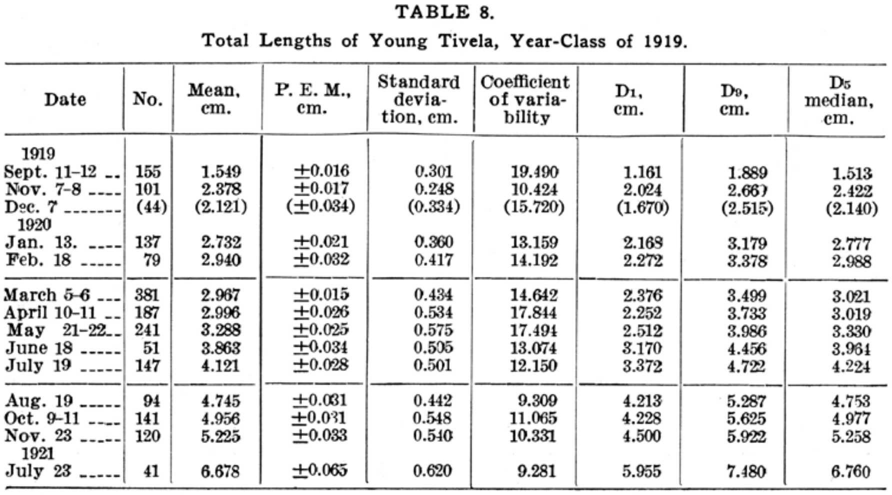


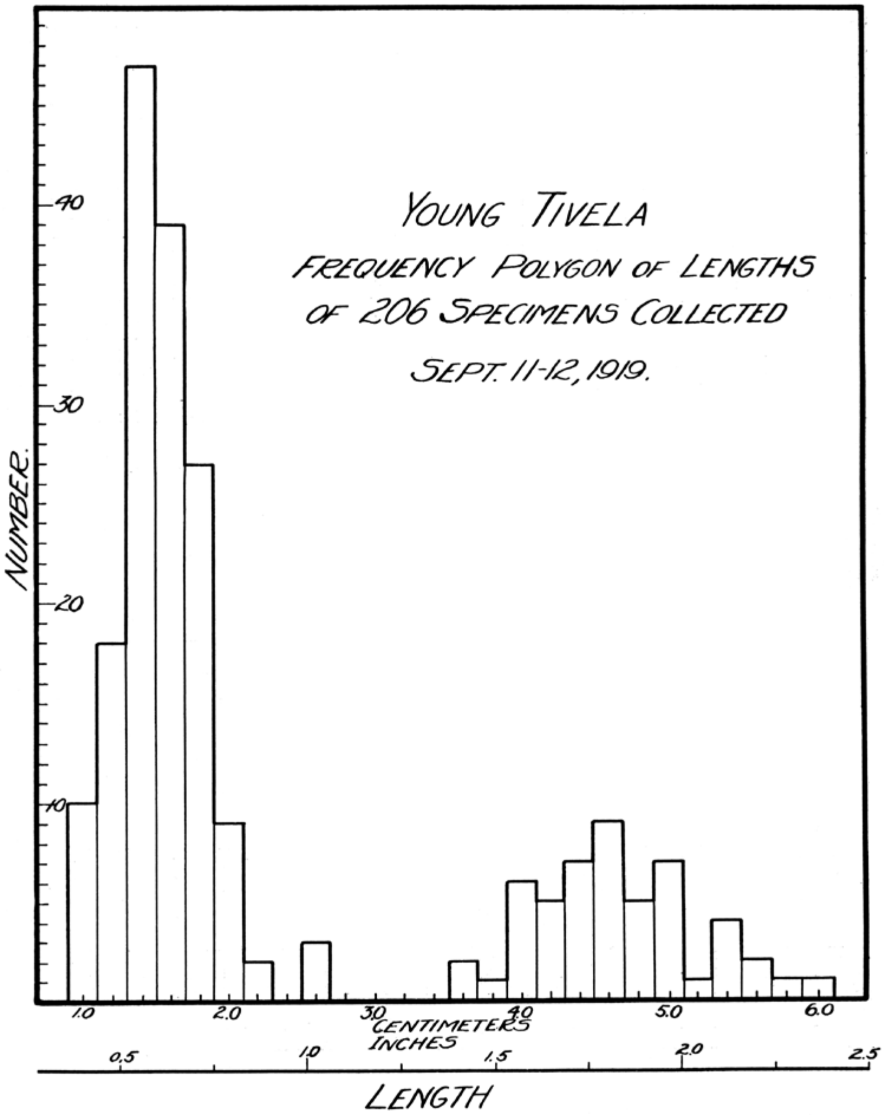
TABLE 8.

Total Lengths of Young Tivela, Year-Class of 1919.

Date	No.	Mean, cm.	P. E. M., cm.	Standard deviation, cm.	Coefficient of variability	D_1, cm.	D_9, cm.	D_5 median, cm.
1919								
Sept. 11-12	155	1.549	±0.016	0.301	19.490	1.161	1.889	1.513
Nov. 7-8	101	2.378	±0.017	0.248	10.424	2.024	2.667	2.422
Dec. 7	(44)	(2.121)	(±0.034)	(0.334)	(15.720)	(1.670)	(2.515)	(2.140)
1920								
Jan. 13.	137	2.732	±0.021	0.360	13.159	2.168	3.179	2.777
Feb. 18	79	2.940	±0.032	0.417	14.192	2.272	3.378	2.988
March 5-6	381	2.967	±0.015	0.434	14.642	2.376	3.499	3.021
April 10-11	187	2.996	±0.026	0.534	17.844	2.252	3.733	3.019
May 21-22	241	3.288	±0.025	0.575	17.494	2.512	3.986	3.330
June 18	51	3.863	±0.034	0.505	13.074	3.170	4.456	3.964
July 19	147	4.121	±0.028	0.501	12.150	3.372	4.722	4.224
Aug. 19	94	4.745	±0.031	0.442	9.309	4.213	5.287	4.753
Oct. 9-11	141	4.956	±0.031	0.548	11.065	4.228	5.625	4.977
Nov. 23	120	5.225	±0.033	0.540	10.331	4.500	5.922	5.258
1921								
July 23	41	6.678	±0.065	0.620	9.281	5.955	7.480	6.760

Table 8. Total Lengths of Young Tivela, Year-Class of 1919

The collections made on September 11–12, 1919, (see Table 6) show an entirely new group, averaging 1.55 cm. as compared with the length of 4.65 cm. in the group which we have been following. The composition of this collection is indicated by Graph 3. Obviously we were dealing with two distinct age-groups, the smaller being that hatched in 1919 and the larger that hatched in 1918, thus confirming the inference above. The further course of both groups can be followed in Graph 2, or in Table 7 and 8 on which the graph is based.



GRAPH 3. Frequency polygon showing numbers of each length of young *Tivela* collected September 11–12, 1919. The smaller group represents those hatched in 1919; the larger, the year-class of 1918.

Graph 3. Frequency polygon showing numbers of each length of young Tivela collected September 11–12, 1919. The smaller group represents those hatched in 1919; the larger, the year-class of 1918

3.14. Irregularities in growth

Let us now turn to a consideration of the features shown by the course of growth in both groups. While the general increase in value is clear, there are two types of deviation from this course that require discussion. The first comprises slight irregularities as shown in both year-groups. In the collections of young of 1918 made on November 7–9, December 7th and January 13th, a steady decrease in size is noted. Aside from the smaller number of specimens reported (see Table 7) , the collections of January 13th, which were not made by the writer, came from Pismo instead of the Oceano location discussed above. Reference to the previous discussion of the difference in size between Pismo and Oceano, page 18, will show a considerably smaller size at Pismo, and this is undoubtedly the cause of the apparent retrograde movement of the mean. The same thing will be found in the collection of clams hatched in 1919 made November 7–8, where the cause is apparently the same. For this reason these values have been bracketed in the tables and are not plotted in the graph. It will be noted in general that the graph of the clams hatched in 1919 is much more uniform in its course than that of the next larger group, due apparently to the more adequate number of specimens represented, which will be seen by reference to Tables 7 and Table 8. This greater reliability is also reflected in the small size of the probable error of the mean which is everywhere too small to be represented on the scale adopted.

3.15. Seasonal variations in growth.
In Tivela

A more important variation in the course of growth may now be considered. The means of both year-groups show a steady and uniform increase from the earliest records up to approximately November, 1919. The line in the graph connecting the average lengths has, therefore, a uniform and fairly steep slope up to this point, after which, since the increase in the means is slight, the slope is more gentle, in places nearly horizontal, until the following spring. The line representing the 1919 year-group after about April 10th, shows a distinct increase of the slope, and the same is true of that representing the 1918 year-class following approximately May 20, 1920. This steeper slope may be observed in both graphs until the succeeding autumn when at about August 20, 1920, there is a sharp decrease in rapidity of growth. Increase in length is thus shown to be more rapid in both age-groups during the summer than during the following winter. Such a phenomenon has been observed in other animals where comparable data are available. Since this effect is of primary importance in its bearing on the formation of annual rings it will be profitable to examine these data in some detail.

3.16. In plants

Seasonal growth in plants, earliest noticed and most easily studied, furnishes numerous examples of ryhthmic growth easily compared with the one at present under consideration. The curves given by D'A. W. Thompson for the growth of trees, already cited (page 17) may serve as an example, though the general phenomenon is too well known to require special emphasis.

Among invertebrates, as we have already said, the number of careful studies of growth adequate to show seasonal variation of the type we are here dealing with are few. Some unpublished data from observations by the writer on crustacea, though less satisfactory than the present series, show similar seasonal rhythms.

3.17. In insects

Insects, because of their economic importance, have received more attention than most other invertebrates, and there have been a number of instructive studies of rate of growth. These are, however, unsuitable for comparison with the present data for two reasons. The span of life is short, growth commonly being completed in a single season or at most two, and therefore the course of what may be called the life-growth, is superposed on the seasonal rhythm so that neither can easily be followed. Only when the period of growth extends over several years can the seasonal cycles be expected to show in a pure form. In the second place, such profound changes as metamorphosis cause discontinuity in growth whether total or seasonal, and this makes the interpretation of the growth curve far more difficult than in animals where growth is continuous and of the same type throughout. This point is of theoretical importance and will be considered more in detail in a future publication.

3.18. In mollusks

Results entirely free from this objection and perhaps the most satisfactory that have come to the writer's notice were obtained by Belding in his work, already cited, on the scallop and quahaug of the Massachusetts coast. We will shortly revert to these interesting data as illustrated by curves in Graph 5 (p. 33).

3.19. In fish

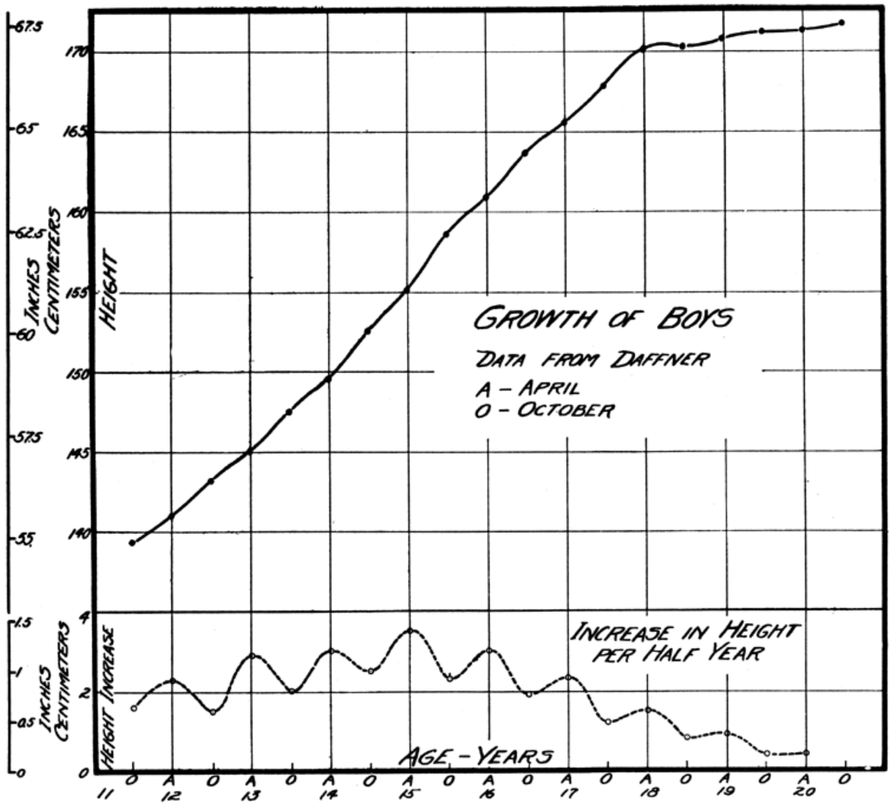
Among vertebrates, though the data are more adequate, they are still far from satisfactoryfor comparison. In fish, which of the lower vertebrates have been most studied, the method of scale reading, chiefly used, has given growth in terms of years only and not the growth within the year. Where seasonal growth has been determined it exhibits cycles of acceleration and retardation corresponding to summer and winter such as we have seen in the case of Tivela. In addition to the work of Rich (1920) already mentioned, the writer has had the privilege of examining data collected by him on the Steelhead of the Pacific Coast,[*] which shows the seasonal rhythm in an unusually clear manner. The work of Barney and Anson (1920) on the pigmy sunfish, though less extensive, shows an essentially similar seasonal variation in the rate of growth and the same may be said of the observations of Shann on Gobius minutus (1910).

3.20. In mammals

In mammals, although more growth data are available than in the groups just mentioned, seasonal variations have not usually been recognized. Apparently they are obscured by a peculiarity in the physiology of these animals that prevents as direct an action of certain external factors as occurs in the simpler groups. Since mammals maintain a constant body temperature the growing cells are almost wholly shielded from the fluctuations of external temperature which, as we shall see, are probably one of the chief causes of seasonal variation in growth. However, even man is not free from a seasonal cycle, as Daffner, Malling-Hansen (1886), Holt (1922, p. 18), Porter (1920) and various investigators have shown. Daffner's figures (1902, p. 329) are represented in Graph 4, and show clearly that boys make a distinctly greater growth in height in summer than in winter.

---

[*] Cited by his permission from unpublished manuscript; for this courtesy, as well as the clarification of view on many problems of growth which has resulted from discussion of similar work extending over a number of years and which is reflected in the present paper, my indebtedness is gladly acknowledged.



GRAPH 4. Growth of boys, showing total height at each half-year period from 11 to 20 years and increase in height during subsequent period, *i. e.*, the increase plotted above the first October represents the increase between this October (11½ years) and the following April (12 years). Data from Daffner (1902, p. 329).

Graph 4. Growth of boys, showing total height at each half-year period from 11 to 20 years and increase in height during subsequent period, i.e., the increase plotted above the first October represents the increase between this October (11½ years) and the following April (12 years). Data from Daffner (1902, p. 329)

We may then safely conclude from these examples representing a series of widely different organisms that a rhythm in the rate of growth which shows acceleration in the summer and retardation in the winter is a general and fundamental phenomenon. This seasonal rhythm has been little emphasized by workers in growth, who have dealt chiefly with those forms, the mammals, in which it is least conspicuous. It is, however, impossible to ignore the importance of a phenomenon so clearly exhibited by organisms as widely separated as trees, mollusks, crustacea, fish, and man.

3.21. Factors causing seasonal variation in growth

If such a seasonal rhythm of growth is of general occurrence what are the causes? Here we are on less firm ground. Many physical factors are known to influence growth. Any one of these might conceivably become, under special conditions, the limiting factor and so assume an apparently dominating role which it did not usually play. For example, among plants, heat and moisture are both prominent factors and each is essential in the sense that if it falls below a certain minimum growth must necessarily cease. If a plant grows in a situation where the supply of water is always adequate, as with a seaweed, the limiting factor will become temperature. In the case of a tropical or subtropical desert where growth will never fail because of lack of heat, the growing season is, on the other hand, sharply limited by the rainfall. For this reason, and because of the large number of possible factors, it is not easy to determine, by a comparison of growth with the accompanying physical conditions, which of these really affect growth and what their relative importance may be.

In the case of children the greater summer growth has been ascribed to the higher temperature, to the greater amount of light, to the more varied or adequate food, to the greater opportunity for outdoor exercise permitted by the weather and the customary arrangements of the vacation in the school year, to less illness during this part of the year, and to other factors. It is obviously difficult to evaluate so many factors, any one of which might in theory produce the observed effects, and few of which can be experimentally excluded. The problem is to a certain degree simplified in the case of a water-dwelling animal such as the fish or the clam. The temperature, for instance, follows that of the water almost absolutely and is not self-regulated as in mammals. The conditions of life are more simple than with man or the other mammals. The following factors may be mentioned, and certain of those on which we have data will then be considered. The external factors include temperature, light, hydrogen ion concentration, salinity and oxygen content of the water, currents, and food supply. Certain internal factors following directly from those mentioned above are the ability to obtain food, and the ability to digest it. As other internal factors, may be suggested the incidence of the breeding season, and the possible existence of internal rhythms.

3.22. Temperature

From what has already been said, it is clear that temperature is among the most prominent of the factors, both from its direct and from its indirect effects. It is known that practically all physiological processes are accelerated by a rise and retarded by a fall of temperature within the limits to which the animal is normally exposed. As a result of this, growth is hastened or slowed by the temperature at which it occurs.

At the same time it is indirectly influenced by the acceleration or retardation of other processes upon which it may depend. Thus the more sluggish muscular action that occurs at the lower temperatures of winter may prevent the animal from obtaining an adequate supply of food. The effect of temperature in muscular action is strikingly instanced by the case of an ant (Liometopum) observed by Sharpley (1920). Here between 10° and 40° C. the speed of the ants in the foraging columns increased in an extremely uniform manner, being approximately doubled for each increase of 10° C. In the case of the clam where muscular activity is not so prominent in food getting, the ciliary activity is slowed and consequently the amount of water passing through the mantle cavity is greatly lessened, by a fall in temperature. This would mean a distinct reduction in the amount of food available, as the food is directly proportional to the amount of water handled.

This point is of so much importance that some examples will be adduced, although it must be stated at the outset that adequate experimental data are lacking. The work of Mitchell (1912) shows that within the range of temperature studied (29.5° to 26.5° C.) the oxygen consumption is about doubled by a rise of 10° C. (Q 10=1.97). Weinland

(1919) found in Anodonta a similar effect of temperature (Q 10=2 to 3). Corresponding results have been recorded in the case of other invertebrates by various workers, as for example, Brunow (1911) for the crayfish. If the cilia, the activity of which contributes to the total metabolism, perform work in proportion to their oxygen consumption, it is obvious that a range of water temperature such as recorded by Belding (1912) from 22° to 2° C. would reduce the amount of water handled to about one-fourth with a corresponding reduction of the available food. Satisfactory experimental results on the movement of water by cilia were not available in the literature examined. Accordingly, four series of observations on the rate at which the cilia on the mantle of the sea mussel (Mytilus) move small particles were selected from class results.* From these it appears that the speed of movement increases up to an optimum at about 25° C. after which it decreases with further increase of temperature. If the velocity at 25° C. is taken as unity, that at 12.5° C. is about one-half, that at 6.25° C. about one-quarter and that at 2.5° C. about one-tenth.

Nelson has estimated from careful observations that the intake of an oyster 3 to 4 inches long amounts to 120 gallons of water in 24 hours at a temperature of 75° F. (1921 b, p. 331). Applying the above results to Nelson's estimate on the assumption that the movement of the water would be as efficient as that of the particles observed, we obtain the interesting figures given in Table 9, showing the amounts of water handled at different temperatures. From this it would appear that in winter on the eastern coast only about one-tenth as much food is available as in the warmest part of the year, while on the California coast the proportion is one-fifth. Granting that these figures are approximate only, it is clear that the direct effect of temperature upon the clam's power of obtaining food is of immense importance, even were it acting entirely alone, which as we shall see is not the case. The speed of digestion of the food, for instance, as shown by Riddle (1909) is also diminished in the cold season, but whether or not this ever becomes a limiting factor the data at hand are insufficient to determine.

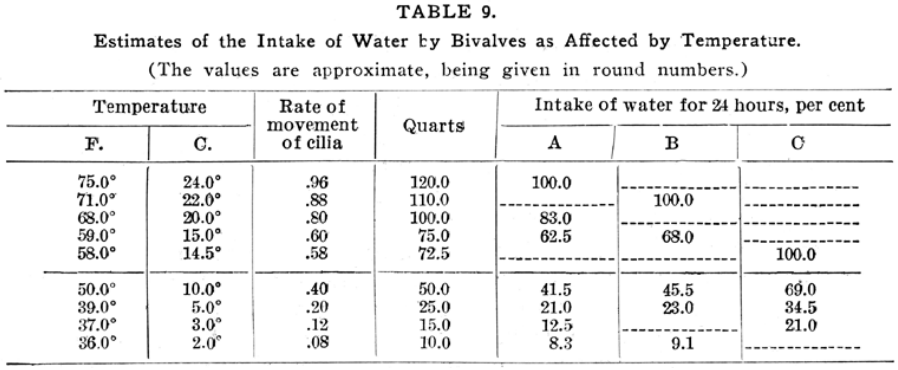


TABLE 9.

Estimates of the Intake of Water by Bivalves as Affected by Temperature.

(The values are approximate, being given in round numbers.)

Temperature		Rate of movement of cilia	Quarts	Intake of water for 24 hours, per cent		
F.	C.			A	B	C
75.0°	24.0°	.96	120.0	100.0	--------------	--------------
71.0°	22.0°	.88	110.0	--------------	100.0	--------------
68.0°	20.0°	.80	100.0	83.0	--------------	--------------
59.0°	15.0°	.60	75.0	62.5	68.0	--------------
58.0°	14.5°	.58	72.5	--------------	--------------	100.0
50.0°	10.0°	.40	50.0	41.5	45.5	69.0
39.0°	5.0°	.20	25.0	21.0	23.0	34.5
37.0°	3.0°	.12	15.0	12.5	--------------	21.0
36.0°	2.0°	.08	10.0	8.3	9.1	--------------

Table 9. Estimates of the Intake of Water by Bivalves as Affected by Temperature. (The values are approximate, being given in round numbers.)

---

[*] For the courtesy of using these observations I am indebted to my colleagues, Dr. J. R. Slonaker and Dr. J. P. Baumberger.

Indirectly, temperature may also have a pronounced effect by influencing the abundance of the microscopic animals and plants which form the food of the clam.

3.23. Light

Light also affects growth both indirectly and directly. Its indirect influence comes through its effect upon the minute plants which form so large a part of the food of the clam. Whipple has shown, for example, that within ordinary limits the growth and multiplication of diatoms is directly proportional to the intensity of the light (1896).

The direct effect of light on animal growth is less satisfactorily understood though recent work has shown how it influences at least one phase. Rickets, both in rats and man, may be prevented or cured by exposure to sunlight, or more exactly the ultraviolet rays of sunlight. Hess has demonstrated that the inorganic blood phosphate of infants may be increased by short exposures to sunlight (1921) and that it exhibits a marked seasonal variation apparently resulting from the variation in the intensity of the short wavelengths in the sunlight (1922). During winter when the sunlight is poor in ultraviolet rays the blood phosphate is low but during summer when the ultraviolet is increased over twenty fold (Clark Janet H., 1922, p. 296) the phosphate rises to a much higher level. Hess suggests that these rays are necessary for normal metabolism in infants, especially in the exchange of inorganic salts, disturbances of which cause slow or defective bone growth and hence affect height. This may serve to explain the results of Daffner and others already mentioned.

By its position in the sand and by its shell the clam is largely but not wholly screened from the sun's rays. Whether or not light affects its growth, for instance by its influence on the large exchanges of inorganic salts involved in shell formation, we have no experimental evidence to decide.

The amount of food is also influenced by currents, as conclusively shown by Belding (1912, p. 88 *et seq.*) but this is a factor varying with local conditions and without direct bearing on seasonal growth.

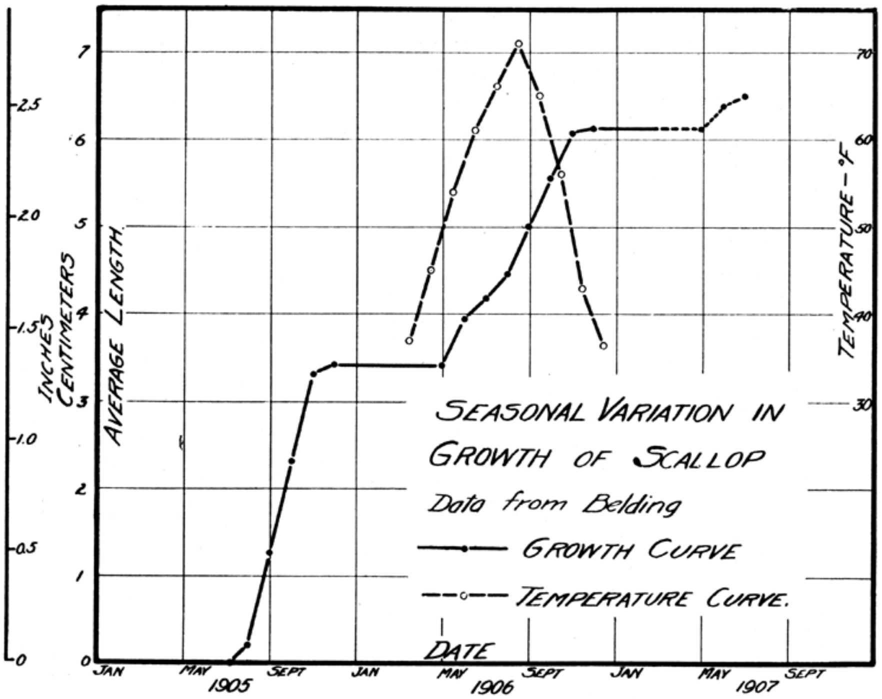
3.24. Salinity

Nelson has shown (1921 b, p. 337) that a decrease in salinity will cause closure and consequent cessation of feeding in oysters. In the case of bivalves living in bays or estuaries this would occur during the rainy season when the streams are high. This cause of slackening in growth would therefore be seasonal. Tivela, from its habitat on the open coast and away from the mouths of streams, would be comparatively free from this influence. It is true, however, that during winter storms it is forced to burrow to a greater depth and to suspend feeding for short periods at least.

3.25. Hydrogen ion concentration

Another possible factor affecting growth is the acidity or alkalinity of the sea water. While the hydrogen ion concentration of sea water is said to be very constant it varies somewhat with temperature (Clark, W. M., 1920, p. 237) and there are observations to indicate that during the cold season the water becomes slightly more acid, a change which would lead to a reduction in ciliary activity. If this is true the hydrogen ion concentration of the sea water would be an additional factor tending to retard winter growth. No data are available for the acidity of the sea water where Tivela found, nor, as far as I know, has this factor been studied in any similar case.

It will thus be seen that the majority of factors which influence growth vary in such a way as to increase the rate in the warm season and decrease it in the cold season. This would result in a high correlation between seasonal variations in temperature and variations in the rate of growth, which we have found to be the case in the Pismo clam. Where the range of temperature is greater we might expect to find the correspondence even more striking. This is well illustrated by the results of Howard (1922, Fig. 71, p. 71) or still better by Graph 5 taken from the work of Belding (1912, Fig. 89). It will be seen that from December 1 to May 1 growth in the scallop is completely suspended, the growing season being confined to a period in which the temperature rose above 45° or 49° F. If this figure is compared with Graph 2, it will be seen that, in Tivela, growth appears never to have been completely stopped (at least not in all individuals at the same time) but merely to have been greatly retarded. This difference would appear to be due mainly, though we must not hastily conclude wholly, to the greater range of temperature found on the Massachusetts coast. This, according to Belding, varies from about 71° to 37° F. or below (roughly 22° to 2° C.) while in Monterey Bay the water temperature ranged from 58.1° to 37.8° F. (about 14.5° to 3° C.).[*] Unfortunately ocean temperatures were not available for the locality where Tivela was studied and it has been necessary to use the minimum daily air



GRAPH 5. Growth of scallop from July, 1905, to July, 1907. The lengths at each month are given and the temperature during the summer of 1906. Data from Belding (1910, Fig. 91).

Graph 5. Growth of scallop from July, 1905, to July, 1907. The lengths at each month are given and the temperature during the summer of 1906. Data from Belding (1910, Fig. 91)

---

[*] These figures are from daily records smoothed by a moving average of 21 days to eliminate minor fluctuations—the extremes somewhat exceed this; for the privilege of using these data the writer is indebted to Dr. W. K. Fisher, director of the Hopkins Marine Station, where the readings were made.

temperatures taken at San Luis Obispo, the nearest Weather Bureau station. These, smoothed by a moving average of 21 days, have been plotted in Graph 2 for comparison with seasonal growth.

3.26. Internal factors

From this incomplete consideration of the influence of external conditions we must now turn to another phase, that of internal factors. Among these we must consider the possibility that such a seasonal rhythm of growth long enforced by external conditions might in some degree engender an internal rhythm which would manifest itself even in the absence of the cutsomary external stimulus. In support of such a conception might be cited Keeble's description of the behavior of a marine worm (1910, p. 62 *et seq.*) which rises to the surface of the sand when the tide is out and burrows when the tide is in. When removed to the laboratory it still follows the tidal rhythm for a period of seven or eight days and even when kept in complete darkness shows this rhythm over a period of one or two days. There are other instances of continued rhythmic response after removal of the stimulus.

The onset of the breeding season in some species by diverting the energy of the animal brings about a slackening of growth—an instance is furnished by Belding in the growth of the scallop (1910). If such a seasonal variation occurs in the Pismo clam it was not detected. The slow growth extending over a large number of seasons would, of course, tend to conceal such a variation.

In plants some very interesting observations, unfortunately few in number, are available which bear directly on this point. Coville, for instance, has shown that the blueberry of the northeastern United States, a shrub ordinarily exposed to severe winters, if transferred to a greenhouse and kept at a summer temperature stops growth and drops its leaves at essentially the same time as its fellows outside (1921). The cessation of growth in these plants was, then, independent of the falling temperature. More southern species which do not experience severe winters may continue growth during the entire year, therefore, the behavior of the blueberry is not independent of the temperature (or the external conditions) in a large sense. The behavior is adaptive in that it prevents the injury to delicate parts which would result from great cold and whether it is a rhythm impressed upon the individual plant or a selected racial trait, it is an internal rhythm in the sense we are discussing.

These experiments suggest at once the questions involved in the "physiological zero"—a temperature at which growth begins in the spring or stops in the fall. A "physiological zero" in the sense of a fixed temperature has never been found—what has been found is a series of temperatures differing for different animals and plants, and in general in accord with the optimum temperature of the climatic conditions under which the organism lives. Many plants and animals not only start but complete growth at temperatures far below the "physiological zero" of others.

A striking example of this is furnished by the animals, some of them such highly organized forms as fish, which grow and carry out all their life processes at the bottom of the Arctic Ocean at a temperature below 0° C. (salt water does not freeze above -2.5° C). An illustration more nearly related to the present discussion is found in the growth of Mya arenaria.

This species, though exposed on the Massachusetts coast to the same range of temperature as are the scallop and the quahaug does not, like them, show a complete cessation of growth in winter but like Tivela continues to grow at a much reduced rate (Belding, 1916, p. 197, 223, and Fig. 22, pl. viii). As suggested by Belding this difference is undoubtedly associated with the fact that Mya is a northern form extending from its general circumpolar distribution south along the Atlantic coast as far as Cape Hatteras, while the other two are southern species. The scallop (Pecten irradians) ranges from the Gulf of Mexico as far north as Boston (Belding, 1910, p. 12) and the quahaug (Venus mercenaria) "essentially a southern and warm-water form, is found along the Atlantic coast from the Gulf of St. Lawrence to the Gulf of Mexico" (Belding, 1912, p. 5). The two latter species, according to Belding, cease growth when the temperature falls below 49° to 45° F. (9.4° to 6.7° C.) (1910, Fig. 89; 1912, p. 88 and Fig. 43) while Mya continues to grow until a temperature of 42° to 40° F. (5.6° to 4.4° C.) is reached.

Similar differences between cultivated plants, even of the same species, are of course well known; one variety of apple or wheat will regularly mature in a certain locality where other varieties will never complete growth and the formation of fruit or seed. Though the argument from this fact is far from conclusive, one might readily imagine that an internal rhythm was widely distributed among these organisms and that the slight variations of their environment serve to throw it into action in a large degree irrespective of the intensity of these external conditions. More data bearing on this point will be cited at a later time.

Even in the effect of temperature on digestion Riddle (1909) found that an internal factor was also involved. Although the gastric digestion of frogs could be made more rapid by a rise of temperature at any time, frogs brought to a summer temperature in winter failed to show as great a rapidity as in summer.

In the end it must be admitted that at present no exact evaluation of the factors involved in seasonal growth is possible. The new facts brought to light in the present work strengthen the writer's belief, expressed on a previous occasion (Weymouth, 1918, p. 287), that temperature holds an important if not a dominant place among these. It would be unwise to maintain that it is the only factor, but its influence in such unexpected roles as that plainly shown by Thompson in his study of the run of the albacore (1917) indicates clearly that its importance has generally been under- rather than over-estimated.

3.27. Annual rings.

Previous work on annual rings

Turning from the question of a seasonal rhythm of growth, clearly shown in the present case and undoubtedly of general occurrence, and the consideration of the factors upon which it depends, let us see what evidence exists of morphological traces of this rhythm comparable to the annual bands or rings of fish scales which we have already discussed. As might be expected, marks of this character on mollusk shells have long been figured, described, and speculated upon and a small number of writers have considered more or less critically their value as an indication of age. We shall confine our attention to this latter group.

of these the earliest is apparently v. Hessling (1859) who discussed the view that these rings were annual in origin but thought that the evidence failed to prove it; all that was certain was that the smaller the mussels were the faster they grew. The first author to make an exact series of measurements was Hazay (1881) who followed the increase in length and width of some individual mussels for several years. He concluded that in the months of December, January and February no growth occurs, but that during that time of rest the soft exposed epidermis at the margin of the shell is affected by the mud so that the entire margin takes on a dark color forming a true annual ring. He estimated the ages reached by *Unio* and *Anodonta* at from 10 to 12 years.

Kellogg writing in 1910 speaks of the shell of the quahaug as follows: "From the umbo as a center, concentric lines of growth spread over the entire outer surface. Each represents what was, at one time, the edge of the shell. A cross section of a tree trunk reveals similar concentric growth lines. Each line in the section marks the cessation of growth in the fall and its resumption in the spring, so that the years of a tree's life are recorded in them. From such an analogy it might be assumed that the growth lines on a bivalve shell indicate its age, also; but the analogy is misleading. Most shells, like that of Venus, possess fine and closely crowded, as well as conspicuous, lines, all irregularly arranged. While they represent successive deposits of lime, many are formed in a summer, and no idea of age may be had from them. Differences in their distinctness and size are probably due to the irregular action of weather, tide, temperature, and the abundance or scarcity of food." (P. 14.) This distinct negative to the annual ring view coming from a person of Kellogg's wide experience with bivalves has undoubtedly had great influence.

In the same year Belding (1910), a pupil of Kellogg, reported a case in which the annual nature of the mark was so well established as to form the basis of legislative action. This was in the scallop of Massachusetts. Here the conditions are peculiar in that the animal normally survives but a single winter. To quote: "The shell of the scallop is increased by calcified secretions of the mantle, which add fine concentric rings to the growing edge. If one observes the shell closely one will find that it is made up of microscopic growth lines, due to the method of growth.

"On scallops which reach a second summer there is found a growth line, more or less pronounced, which can be likened to the year marks seen in cross-section of tree-trunks, and is given the name of the *annual growth line*. Growth lines with the oyster are helpful in determining the age, and this line marks the distinction between the adult and "seed" scallop, and has attained considerable prominence as the basis of the "seed" scallop law. * * * *The annual growth line* is formed in Massachusetts waters about May 1, when the scallops resume their growth after the cold winter months, during which all growth has ceased. Necessarily during the long period of nongrowth, from November to May, the edge of the shell has become thickened or blunted by more or less wear, and when the new growth is secreted by the edge of the mantle on the inner side of the shell a distinct ridge is formed, marking the separation of the old and new growth. * * * In some scallops it is very prominent, while in others it is difficult to discern at first glance; sometimes the shell shows a difference in color between the two parts, at other times both the old and the new shell are alike, and it is necessary to run the finger down the shell to determine the ridge. However, these cases are the exceptions, and the average growth line is especially prominent on the lower or right side of the animal, the upper valve usually being covered with numerous growths, both plant and animal, which may obscure the line.

"As the formation of the annual line is due to cessation of growth during the winter, it logically follows that any check for a less or greater time will cause slight lines, which are entirely distinct from the annual growth line and are by no means as prominent, being merely heavier concentric layers. Growth lines of this sort can be produced on young scallops at any time by interfering temporarily with their growth * * *. The growth line is not caused by the spawning season, as has been supposed * * *. Risser was the first to advocate the use of the growth line to distinguish the difference between the adult and 'seed' * * *."

It is curious that after giving this detailed and clear account of the growth line in the scallop he makes no mention of a similar mark in subsequent work on the quahaug (1912) or the soft-shell (1916) although he follows their growth through several seasons by direct observations and figures shells which obviously show annual lines.

Shortly after this Israel (1911) reported that he found no winter rest period in the mussel and that more than one ring might be formed in a single year.

In the following year Rassbach published two valuable papers (1912a and 1912b) and Lefevre and Curtis (1912) contributed a study of mussels in each case apparently without knowledge of the work of the other. The latter writers give measurement of some specimens marked and recovered but after reviewing the evidence in regard to growth lines conclude as follows. "The examination of any considerable number of shells leads to the belief that even if the annual-ring theory can be proven conclusively the rings are often not sufficiently distinct from the intervening lines to give an unquestionable record of the age."

Rassbach made a careful and detailed study, already referred to, of the structure and formation of the shell. Regarding the question of annual rings, he presents experimental evidence in the case of three mussels in which pieces were removed from the shell in order to follow its regeneration. These were recovered after a period of eleven months and all showed a distinct year ring. He considers that this supports the conclusions of Hazay and accepts without qualification the validity of these marks in the determination of age. He does not give, however, any data on the age reached by the species with which he worked.

The next important data are those of Rubbel (1913) who gives a careful series of measurements of 123 specimens of Margaritana planted and recovered after a period of about two years. He notes that the growth of the larger mussels is much less than that of the smaller specimens and that there is much variation. He states that the rings in this species are not clear and whether they are annual or not is difficult to determine. He thus cautiously leaves the question open.

In 1913 Lindsay presented before the International Congress of Zoology a short note concerning the periodicity of growth in the shell of mollusks (1914). In this she accepts the general view that "age-marks" in the shells represent an annual period and that they may be used as a basis for estimating age. No proof of this is offered nor are estimates of age in any species recorded. Ridges between the agemarks in such shells as the common cockle of Europe are considered as resulting from a lunar periodicity, presumably correlated with the tides. No proof is given beyond the observation that the ridges seldom number more than six to ten, which, allowing for a period of winter inactivity, would correspond to the number of lunar months in the year. Further treatment of the subject was promised but has not been met with in the literature.

The rings of oysters were studied by Massy (1914) in many cases of planted individuals of known age. She quotes Peterson (1908) as saying "certainly the zones of growth on the shells have something to do with growth periods (years), but it is often not easy to determine them with certainty." "I heartily agree," says Miss Massy, "with the latter statement; * * * all I can say from [the examination of] 600 samples [is that] an oyster of 18 months or two summers appears to possess at least two rings but may have five, of three summers from two to six rings and of four summers from three to seven or eight. It is obvious, therefore * * * [that] it is not of much use to apply the study of growth rings in ascertaining the age of a wild oyster."

In the same year Isely (1914) made an investigation of the rate of growth and significance of the rings in fresh water mussels by tagging experiments involving about 900 specimens. He found that the young grew more rapidly than the adult specimens and that very large individuals made hardly perceptible additions. April to September may be considered the growth months in the Mississippi valley. "Lines of arrested growth," he says, "may be called rest rings, the conspicuous ones being usually winter rest rings; very often, however, the rings may be two or more years apart, or several equally prominent rings may be formed in one year * * *. Winter rings * * * are usually sufficiently regular for use as indicators of age in estimating roughly the time required for a commercial species to reach marketable age." He makes no attempt to determine the normal course of growth either from the rings or from the data obtained by tagging.

Crozier (1914) gives a series of measurements of Dosinia discus, a clam of the southern Atlantic coast, and comments incidentally on growth rings. "It was found," he says, "that in Dosinia the dark rings are of very variable number, width and opacity, and that no correlation could be made out between shell size and band number. It is possible that the shells do not all grow at the same rate, or that the dark bands do not represent winter periods, or both."

Later Crozier (1918a) in a study of Chiton tuberculatus made use of growth lines. Although this mollusk is not a bivalve the principles involved are the same. He states that the central area of each of the segmented plates composing the shell is marked by tranverse growth lines. "On the assumption," he continues, "that these growth lines are * * * formed at the rate of one per year, it is possible to estimate the growth rate of chiton. The probable correctness of this assumption is assured, (1) by the inspection, throughout the year, of the growth of the young chitons appearing after the close of the breeding season;

(2) by direct observation that a growth-line is formed during the winter period, and (3) by the coincidence of the findings based upon the counts of growth lines with those derived from the modes in the frequency-distribution of sizes in the chiton population."

The detailed data upon these points are not presented, and hence the conclusiveness of the proof can not easily be evaluated. A general growth curve covering 12 years is presented. In a following paper (1918b) he gives further comparative growth curves for different localities but no further data on growth lines.

The most recent consideration of the question seen is that of Walton (1920b) on the cockle (Cardium edule). He mentions concentric rings thought to be annual and shows by a series of counts that these are most numerous on the largest shells. This is obviously no proof that they are annual as it would hold equally with monthly or triennial rings.*

Such a glance at the contributions of sixty years to the question of annual rings is rather confusing and seems to indicate little progress toward unanimity on the part of the workers. of these fourteen papers by thirteen different authors, one flatly denies that age can be told from the shell, two are unwilling to commit themselves, five feel that there is some sort of connection between age and the lines, but that they are of no practical use even if their annual occurrence could be established and six go on record as believing that the rings are annual, though only one of these actually makes use of the method in constructing a growth curve. In only two can the case be considered as firmly established upon adequate data. In only a few cases were the numbers of specimens examined sufficient and in these the authors came to opposing views.

In half the cases the animal considered was some species of fresh water mussel; the two best established cases, however, came from other species, the scallop and the chiton. Apparently the mussel is not a form in which the annual rings are favorable for age determination. There are several factors which may make the shell of a particular species difficult of interpretation. Other things being equal, the most rapidly growing form with the shortest life ought to be the most favorable, since the rings would be few in number and widely separated, and observations over a short period would establish whether or not they were annual. All of these conditions are exactly realized in the scallop, where at most but two rings are found, and we have seen that Belding's proof of the annual nature of the rings in this species is satisfactory and convincing. On the other hand several of the workers mention the great crowding of the lines near the margin of the shell in the mussel and it is obvious that such a condition would render difficult and uncertain both examination to determine whether the lines were formed annually and determination of age should their annual

---

* Since writing the above I have seen a paper by Mossop (1922) on the mussel (Mytilus edulis) in which the "checkmarks" in the shell have been used as a criterion of age. Proof of their annual occurrence rests on a rapid spring growth as contrasted with a slow winter growth discussed by her in a previous paper (1921). This proof appears far from rigorous, as the data are scattered and incomplete. The use of the marks is complicated by the fact that they may arise from unfavorable conditions at any time of year, and that annual checks are occasionally very faintly defined. These difficulties are elsewhere recorded for Tivela, though naturally their severity varies with the species. Data from different localities with average rates of yearly growth are given; these appear to be valuable, but are somewhat difficult of comparison because of incomplete statistical treatment.

occurrence be established. In fact, the most decisive evidence in the mussel has come from the young.

3.28. Relation of surface sculpture to annual rings

In the marine species with which the writer has worked it is clear that the form of surface sculpture of the shell is an important factor in considering growth lines and annual rings. From this point of view there are two main types of markings; in one the valves may be smooth or nearly so or there may be numerous fine concentric lines or radiating ribs of varying degrees of prominence; in the other the concentric lines are relatively few and bold. This latter group does not readily show variations in growth; the lines are not growth lines but the result of a mechanical or spatial and not a temporal rhythm of the mantle action, leading to a series of ridges of equal size and separation. This type of shell is illustrated by Dosinia in which Crozier failed to find annual rings. On the Pacific coast Amiantis is a good example. In the first group, however, careful examination will usually disclose that the faint concentric lines of the otherwise smooth shell show some sort of grouping, at certain places being crowded or accentuated or in some way distinguished. In the shells with low and numerous concentric lines the same will be observed and in those with radial sculpturing the rays will be crossed with concentric lines showing grouping.

3.29. Growth in the molluscan shell

A consideration of the growth in the molluscan shell will throw light on these lines. The shell grows by addition to its margin and inner surface from the mantle lining it, but never by addition to the outer surface. The relation of these parts at the forming margin of the shell will be more clear from a diagram. The mantle can not always be held in the position most favorable for shell secretion, the position ordinarily assumed in feeding (see A, Fig. 4), but the flap between the periostracum and the shell margin must be withdrawn or suffer injury on complete closure. The position when closed is diagrammed in B in which, however, the valves are shown slightly separated for clearness. The retraction of the margin of the mantle is accomplished by radial muscles attached to the shell at the pallial line. The growth at the margin of the valve is, therefore, of necessity discontinuous, being interrupted by each complete closing of the shell. The re-extended mantle reaches quite accurately its previous position, as the uniformity of shell shapes testifies, but there is always some slight variation of extension leading to minute differences of level and visible "lines" on the outer surface. An extreme case will illustrate this. An examination of nearly any large Pismo clam shell (and the same is true of many other species) will show one or more sharply marked lines or "breaks" where there is an interruption of the periostracum and a distinct though not necessarily deep line in the valve. These apparently occur when the shell is washed out and the edge battered against the sand, wearing off the terminal free flap of periostracum. This interrupts the continuity of the periostracum and interferes with the accurate adjustment of the edge of the mantle in the immediately following growth and as a result a permanent scar marks what was the edge of the shell at the time of the accident. In the shell shown in Figure 5 the injury to the mantle was local and unusually severe so that growth at this point

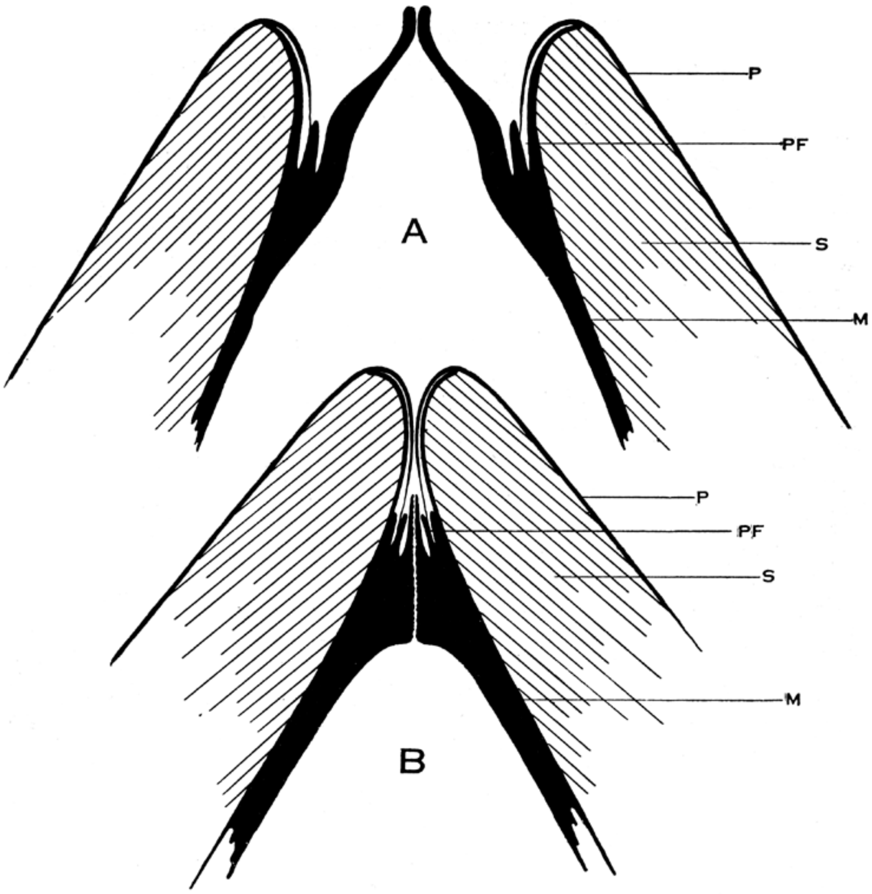


FIG. 4. Diagram showing relation of mantle to shell margin. A, slightly opened as in normal feeding. B, closed. S, shell. P, periostracum. M, mantle. PF, pallial fold.

FIG. 4. Diagram showing relation of mantle to shell margin. A, slightly opened as in normal feeding. B, closed. S, shell. P, periostracum. M, mantle. PF, pallial fold

had not become normal even approximately a year after the accident. The shell margin was not worn as the continuity of the periostracum proves, but the "line" resulting from the inability of the mantle to resume the former position is well shown. Though most pronounced near the point of injury, the line may be traced around what was then the entire margin of the shell.

In the Pismo shell some variation in the crowding of the fine growth lines may be noted but two other features are more conspicuous. One is the elevation or depression of certain groups of growth lines and the other is a difference of color. As already noted (page 8) a purplish pigment is deposited in certain parts of the shell. In most shells certain growth lines are much more deeply colored than others, giving rise to distinct and often conspicuous rings (see Fig. 6) which usually coincide with the elevations or depressions just mentioned. As might be inferred from what has just been said of the formation of the shell, these surface differences should be accompanied by deeper structural differences and such proves to be the case. The bivalve shell is ordinarily stated to be composed of three layers which, beginning with the outside, are (1) the periostracum, (2) the outer *vertical* or *prismatic*

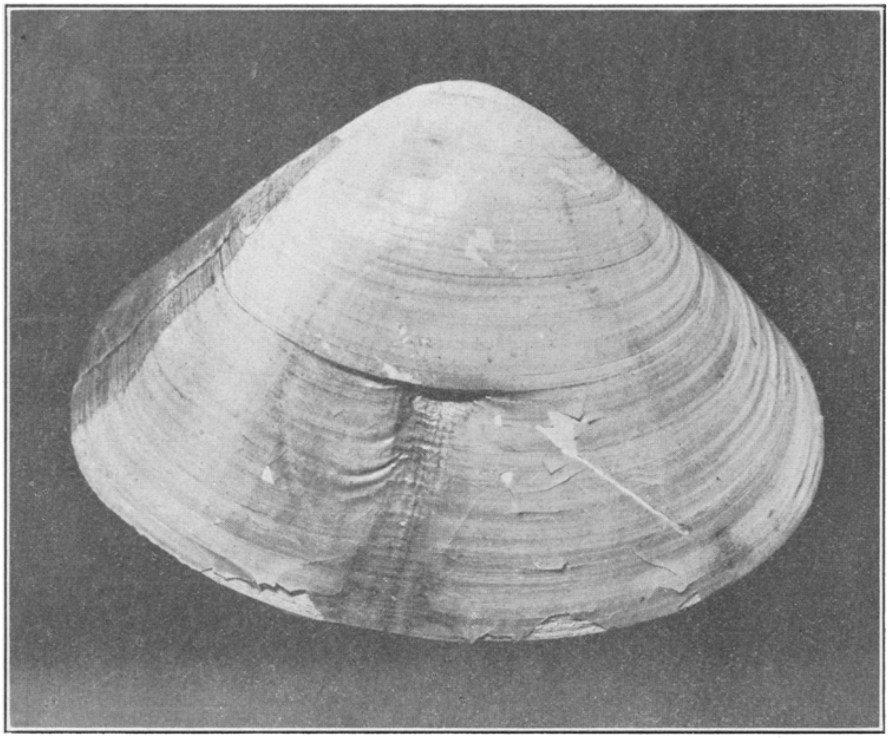


FIG. 5. Exterior of *Tivela* shell showing scar or break caused by injury.

FIG. 5. Exterior of Tivela shell showing scar or break caused by injury

layer, and (3) the *nacreous* or *mother-of-pearl* layer which lines the shell. It is commonly held that, of the shell proper, the prismatic layer is formed by the edge of the mantle while the nacreous layer is secreted by the whole inner surface. It is obvious that the entire mantle takes part in the formation of the shell, but the margin is by far the most active; if this were not so the resulting shell would be as thick as wide. Although in all common bivalves the mantle is most active at its margin yet the relative activity of its various parts, which differs widely with different species, gives rise to clearly contrasted types of shells. Those forms in which the margin of the mantle is very active and its inner surface very inactive produce shells which are essentially of the same thickness throughout, as in the mussel (Mytilus), while those forms in which there is greater activity over the entire inner surface develop massive shells; of this group the Pismo clam is a conspicuous example.

3.30. Layers in shell of Tivela

In Tivela a fourth region can be distinguished in the section of the shell and at the same time the finer structure of the shell shows very clearly the fundamental continuity of all the layers. By reference to Fig. 7 these layers may be identified. Below the periostracum is a *vertical layer* arising from the extreme edge of the mantle, where the growth is the most rapid. Immediately following this is what may be called the *oblique layer* arising from the less active part of the mantle edge as far back as the point of attachment of the orbicular muscle at the pallial line. Inspection of these layers shows them to be continuous and together homologous

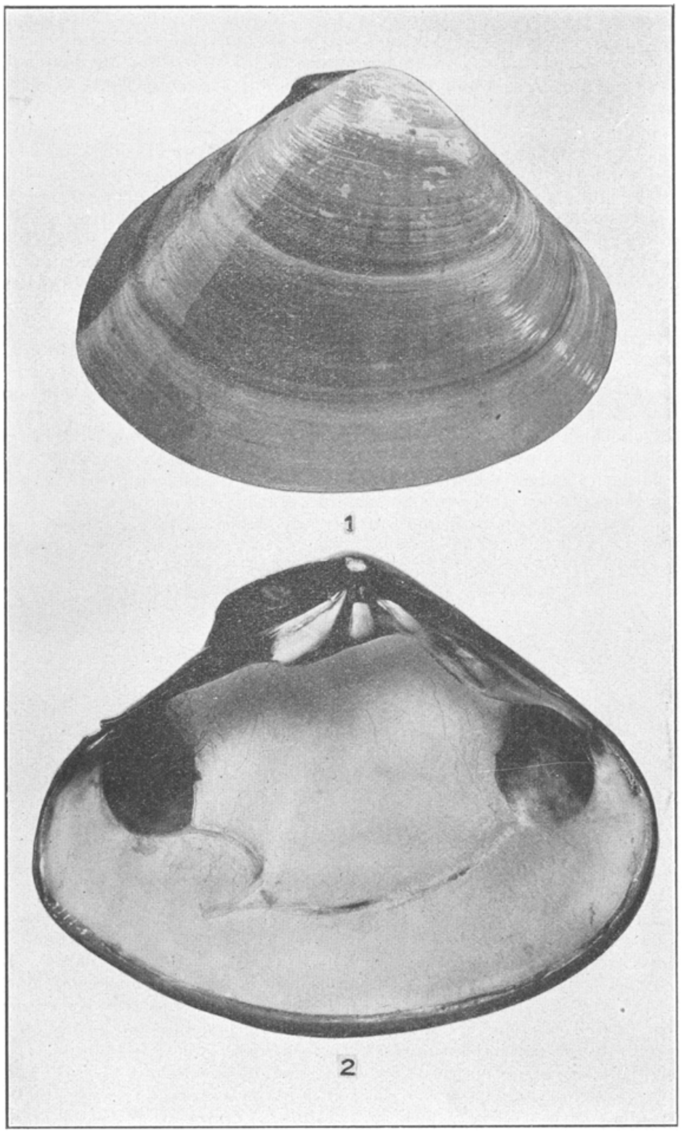


Fig. 6. *Tivela* shell in fourth summer. Note annual rings on exterior.

FIG. 6. Tivela shell in fourth summer. Note annual rings on exterior

to the *vertical* or *prismatic* layer mentioned above. The fourth or *nacreous* layer lies next and will be seen to owe its origin to that part of the mantle within the pallial line. It is stated that the prismatic layer in the fresh water mussels and possibly in the majority of shells consists of calcite, while the nacreous layer consists of aragonite (for example Rassbach, 1912b, p. 364). Material from both the vertical and nacreous layers was tested in the case of the Pismo clam, but although there exist differences in hardness (the vertical layer grading 4 or 5 in the customary hardness scale of the mineralogist while the nacreous layer is about 6) both layers gave with cobalt nitrate a lilac color indicating aragonite and not calcite.

3.31. Microscopic structure of shell

The continuity of these three layers as seen in the polished section of the shell by the naked eye or a low power lens is interrupted by lines which cross their boundaries in a course parallel to the inner surface of the shell (see Fig. 7) terminating on the exterior at the points already alluded to as marked by pigment. In the ground section, these lines are more translucent than the surrounding shell, resembling closely the nacreous layer and in marked contrast with the greater part of the vertical layer which is quite opaque. In their vertical course through the latter, if the shell is not too thick, they permit the passage of light and when the entire valve is held before a lamp these translucent regions show as bright rings following the course of the groups of growth lines marked by the purplish pigment already described.

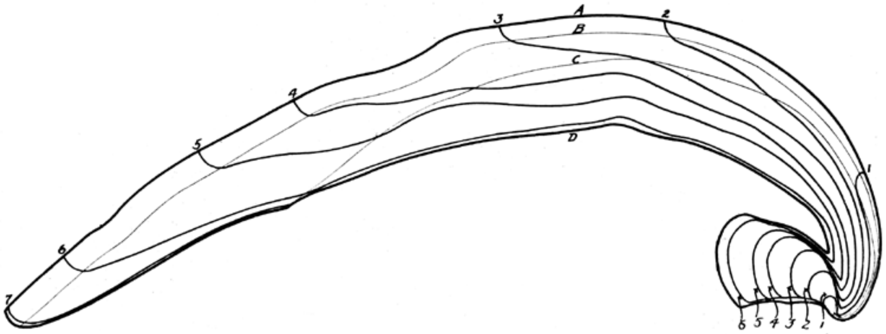


FIG. 7. Diagram of section of *Tivela* shell showing structure. A (outer line), periostracum. A-B, vertical layer. B-C, oblique layer. C-D, nacreous layer. 1-1, 2-2, 7-7, translucent lines ending on exterior in annual rings; these correspond to the inner surface of the shell during the first, second . . . . seventh winter of the clam's life.

FIG. 7. Diagram of section of Tivela shell showing structure. A (outer line), periostracum. A-B, vertical layer. B-C, oblique layer. C-D, nacreous layer. 1-1, 2-2, 7-7, translucent lines ending on exterior in annual rings; these correspond to the inner surface of the shell during the first, second .... seventh winter of the claim's life

A closer examination with the microscope of thin mounted sections shows that the entire shell is composed of extremely thin lamellae, alternately translucent and relatively opaque, lying parallel to the surface. The lines just mentioned as giving rise to translucent rings result from a group of crowded translucent lamellae between which the opaque lamellae are much reduced. The lamellae may be followed from the outer surface through the vertical layer and oblique layer without any interruption. At the line of separation between the oblique and nacreous layers the continuity is not so apparent, but the groups of translucent lines can readily be followed. As the inner margin of the section is approached it will be seen that these lines parallel quite accurately the inner surface of the valve and are obviously the expression of some type of rhythm in the deposition of the shell. Without further analysis of this interesting point it will be sufficient for our present purpose to show that these conspicuous groups of translucent lines mark what was once the inner surface of the shell in the same way that the "growth lines" show on the surface what was once the margin. It will also be apparent that the pigmented rings visible on the surface are not superficial but are the expression of a structural feature passing through the entire shell. The minute structure and details of formation of the shell were considered to be outside the scope of the present work: one or two points of interest may, however, be mentioned incidentally. An examination of the available literature fails to show work dealing with any form closely allied to Tivela or having a shell of the same massive type. The forms most commonly figured are fresh water mussels (*Anadonta*, etc.); this is true of the detailed work of Rassbach (1912a, 1912b), Rubbel (1911),

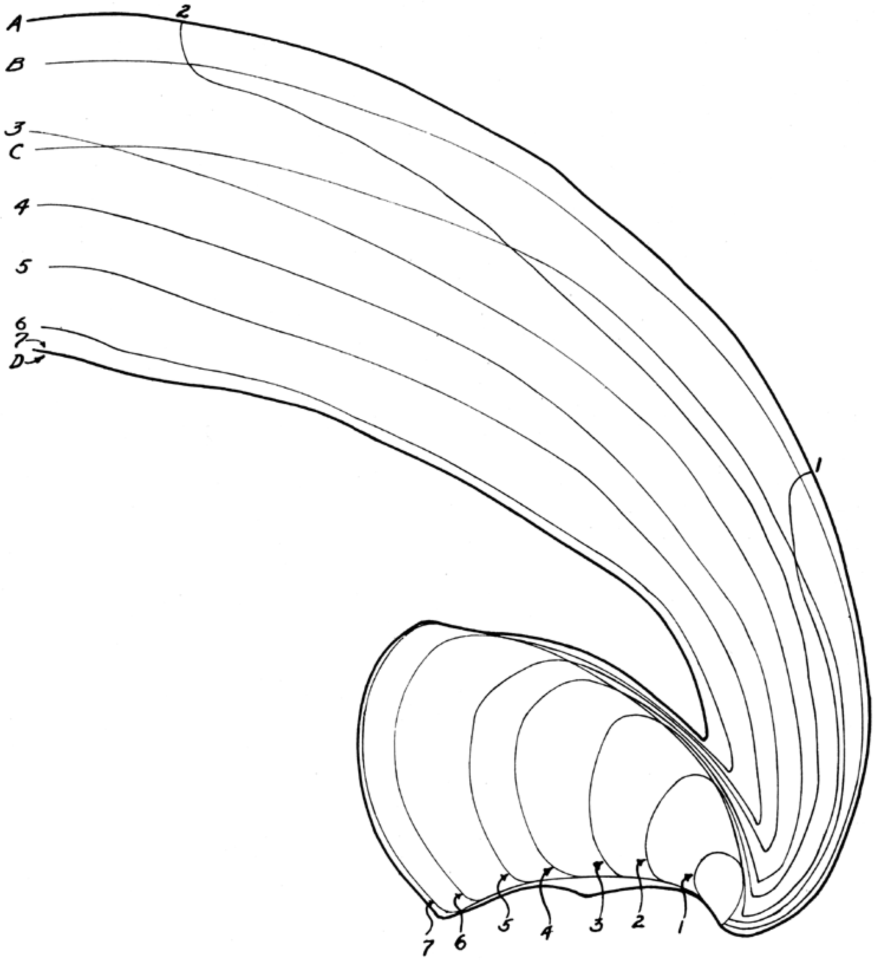


FIG. 8. Detail of umbo and hinge tooth enlarged from preceding figure; lettering same.

FIG. 8. Detail of umbo and hinge tooth enlarged from preceding figure; lettering same

Biedermann (1902), and Pfund (1917). The structure of the shell of Tivela differs widely from those figured; for instance, no "prisms" have been observed either in the entire shell, in polished surfaces, or in microscopic sections, although a special effort was made to find them; perhaps associated with this, the "prismatic" layer or the vertical and oblique layers with which it is homologous are far less sharply differentiated from the nacreous layer.

The fact that in *Mytilus* the prisms show clearly through a hand lens in the old portions of the shell, although near the growing edge they can not be made out, raises the possibility that the prisms may develop as the result of secondary changes occurring in the exposed shell after its formation. Whether this prove true or not, it is clear from the younger portion of the *Mytilus* shell that the "prisms" are tranversed nearly at right angles by the fine lamellae mentioned above which pass over from the nacreous layer, and the same condition is also figured and described by Rassbach (1912, p. 400, Fig. 24), and Rubbel (1911, see figure on p. 297). This serves clearly to show that these lamellae passing through all the layers and corresponding to former inner surfaces of the shell are indications of the activity of the entire mantle in shell formation and that the "layers" do not differ as fundamentally as the conventional descriptions would indicate.

3.32. The lamellae

These lamellae have recently been studied by Pfund (1917) in relation to the production of colors by mother-of-pearl. He finds that in the nacreous layer of fresh water mussels they are extremely fine and regular, not suffering in comparison with the diffraction gratings produced by the most delicate machinery. They number from 9000 to 20,000 to the inch, and by a more delicate optical method each lamella was found to measure from .0004 to .0006 mm. in thickness. As a physicist, he raises a query as to their mode of formation, pointing out that they are far too numerous to represent seasons. This is obviously the case. In Tivela though less fine and regular they are still very thin, measuring from .0025 mm. to over .01 mm. and a rough determination of the number between the successive translucent groups, corresponding to the pigmented rings on the exterior, gives from 150 to 300. These lamellae apparently correspond to the fine growth lines on the surface of the shell. If the rings, as I propose to show, are annual, the lamellae must represent either a short time rhythm of about the magnitude of individual days or tides, or some physico-chemical periodicity, as suggested by Pfund, related to the crystalline structure of the calcium carbonate of which they are formed and recalling such appearances as Liesegang's rings.

The lamellae are, in general, comparable to the circuli of fish scales of which a considerable number, though less than in the case of the lamellae are found between the crowded zones known to correspond to the seasons. The exact mode of formation and significance of the circuli are not known.

The nature and origin of the lamallae are not however topics vital to the present inquiry, which is concerned with the periodicity of the transparent zones or rings formed by a modification of groups of these lamellae. The evidence presented is from observation and independent of any explanation of their origin.

3.33. Data as to annual nature of rings

The pigmented rings on the surface of the shell were noticed by the writer in his first examination of the Pismo clam and from the regularity of their arrangement were inferred to be annual in origin. Subsequent examination of literature showed the wide differences in opinion in regard to such markings, but already two lines of work had been planned to test the assumption of their annual occurrence. One was the observation of shells during the year with particular attention to the relation of such rings to the margin at different seasons; and the other was the marking of clams and the examination of the relation of these known marks to the margin upon their recovery.

Although over 470 clams were marked and released, and a reward offered for their return, none were recovered. Whether this was due to defective "planting" or an unwillingness of the diggers to return clams below legal size, which were chiefly selected for this experiment is uncertain. Fortunately, the first method, particularly in the case of the young, has furnished conclusive evidence in itself for the annual occurrence of the rings; this evidence we will now consider.

3.34. Measurement of rings

The method of collecting and the results obtained on growth in total length have already been presented. In all of the specimens measured the occurrence of rings and their size was carefully determined. This was greatly facilitated by the discovery of the translucent character of these marks, the reason for which has just been explained. Use was made of a strong electric light shielded except for an aperture somewhat smaller than the shell to be examined. Each shell was placed over this aperture and its translucent portions noted, very much as aggs are "candled." The appearance of a shell under these conditions is shown in Fig. 9. The "flare" of light about the shell was due to an imperfect fitting of shell and screen. It will be noticed that in general the older and thinner portion near the umbo is more translucent and the ring is very clearly defined. To the eye the markings are even more apparent as the transmitted light is of a reddish cast which does not as readily affect the photographic plate. In Fig. 10 is illustrated a larger shell (that shown in Fig. 6) with three rings which may easily be identified,

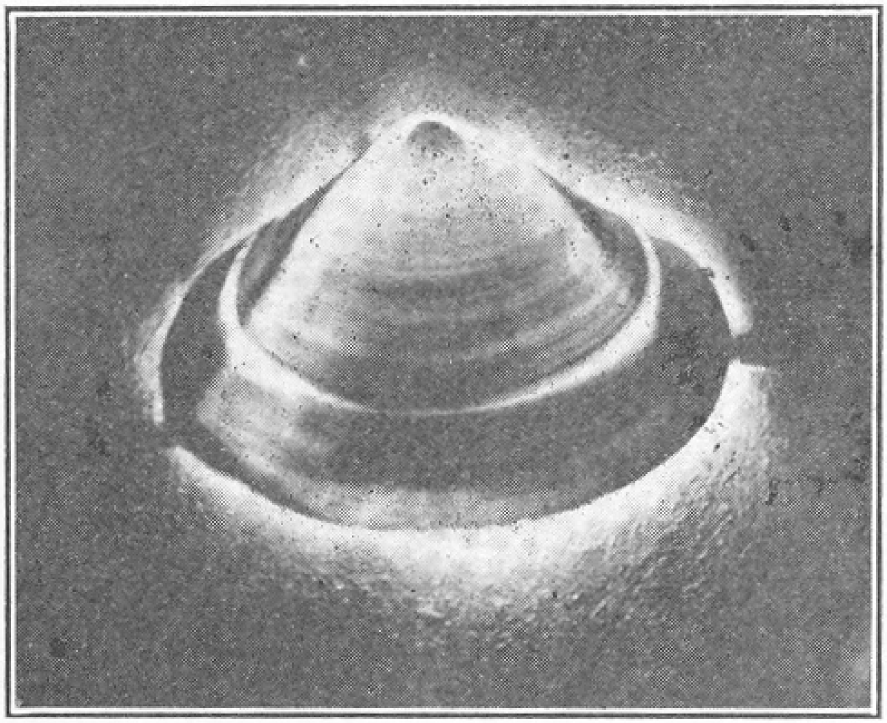


FIG. 9. Photograph of *Tivela* shell, natural size, as seen when examined before an electric light, to demonstrate the translucent nature of the annual rings. Small clam in second summer.

FIG. 9. Photograph of Tivela shell, natural size, as seen when examined before an electric light, to demonstrate the translucent nature of the annual rings. Small clam in second summer

though in the thicker shells this method is not as successful as in the young.

The greatest diameters of these translucent rings, checked, of course, by surface appearance and differences in color, corresponding to the total lengths of the shells at the time when the rings were formed, were measured. These measurements were recorded, usually by a second person, and at a considerably later date tabulated and averaged so that there could be no influence of "expectation" in the measurement. In a small percentage of cases two, three, or even more, closely placed translucent lines are found instead of one, and in such it may be difficult to decide which to measure, but at most this can give rise to only a small error in total length.

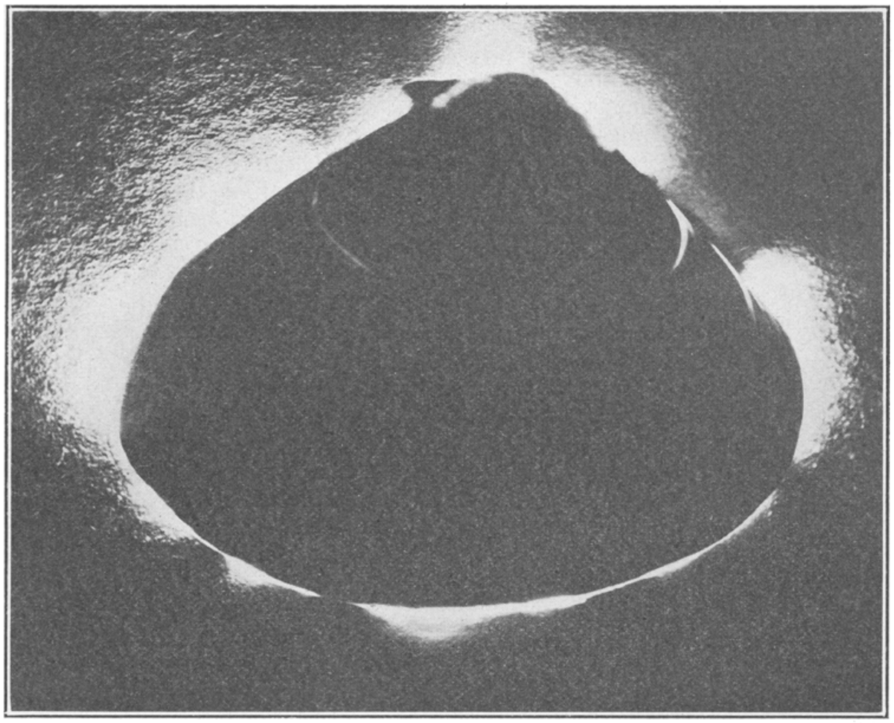


Fig. 10. The shell shown in Fig. 6, as seen when examined before a light. Compare for position of the three annual rings.

FIG. 10. The shell shown in Fig. 6, as seen when examined before a light. Compare for position of the three annual rings

3.35. Proof of annual nature of rings

The clams of the earliest collections (May 3–4, 1919) had, as stated, an average total length of 3.042 cm. The rings of this collection representing the total lengths of the class of 1918 at the time of ring formation, averaged 2.275 cm. If the supposition that the formation of the ring occurred at approximately the same time in all individuals is correct, then any subsequent collection should show rings of this same size, subject only to such variation as we have noted in the total lengths of the young. Such, indeed, proved to be the case; during over two years 660 specimens from 18 collections gave a mean ring-length of 2.54 cm., while the means of the individual collections lay between 2.2 cm. and 2.75 cm. (See Table 10, Table 11, Table 12, Table 13 and Table 14.)

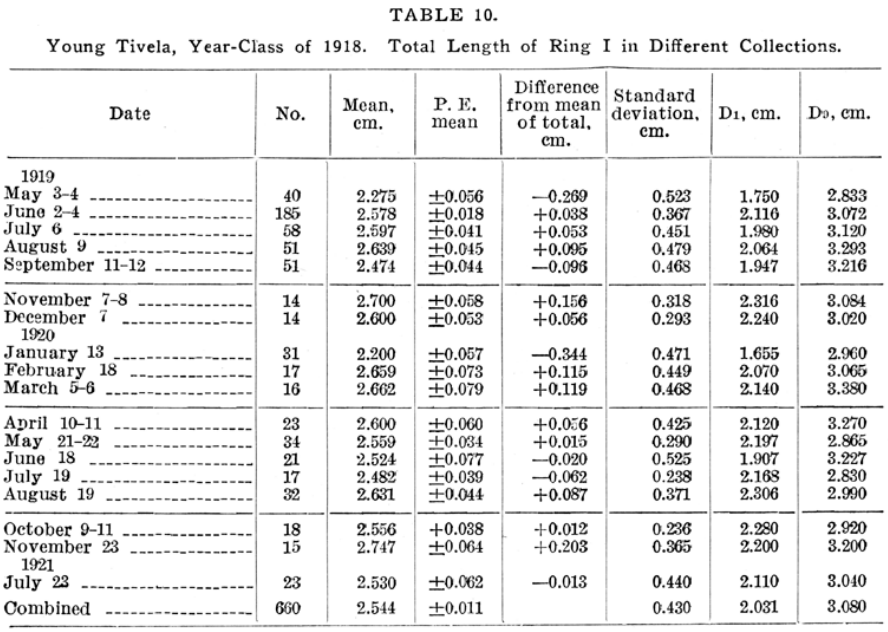


TABLE 10.

Young Tivela, Year-Class of 1918. Total Length of Ring I in Different Collections.

Date	No.	Mean, cm.	P. E. mean	Difference from mean of total, cm.	Standard deviation, cm.	D_1, cm.	D_9, cm.
1919							
May 3-4	40	2.275	±0.056	—0.269	0.523	1.750	2.833
June 2-4	185	2.578	±0.018	+0.038	0.367	2.116	3.072
July 6	58	2.597	±0.041	+0.053	0.451	1.980	3.120
August 9	51	2.639	±0.045	+0.095	0.479	2.064	3.293
September 11-12	51	2.474	±0.044	—0.096	0.468	1.947	3.216
November 7-8	14	2.700	±0.058	+0.156	0.318	2.316	3.084
December 7	14	2.600	±0.053	+0.056	0.293	2.240	3.020
1920							
January 13	31	2.200	±0.057	—0.344	0.471	1.655	2.960
February 18	17	2.659	±0.073	+0.115	0.449	2.070	3.065
March 5-6	16	2.662	±0.079	+0.119	0.468	2.140	3.380
April 10-11	23	2.600	±0.060	+0.056	0.425	2.120	3.270
May 21-22	34	2.559	±0.034	+0.015	0.290	2.197	2.865
June 18	21	2.524	±0.077	—0.020	0.525	1.907	3.227
July 19	17	2.482	±0.039	—0.062	0.238	2.168	2.830
August 19	32	2.631	±0.044	+0.087	0.371	2.306	2.990
October 9-11	18	2.556	+0.038	+0.012	0.236	2.280	2.920
November 23	15	2.747	±0.064	+0.203	0.365	2.200	3.200
1921							
July 23	23	2.530	±0.062	—0.013	0.440	2.110	3.040
Combined	660	2.544	±0.011		0.430	2.031	3.080

Table 10. Young Tivela, Year-Class of 1918. Total Length of Ring I in Different Collections

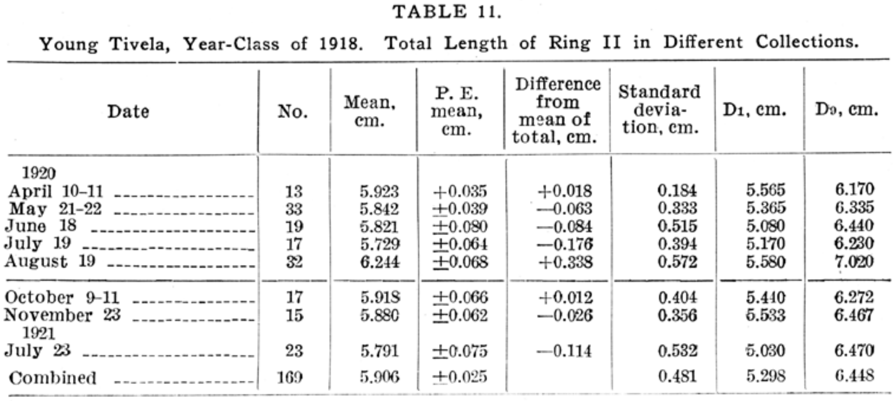


TABLE 11.

Young Tivela, Year-Class of 1918. Total Length of Ring II in Different Collections.

Date	No.	Mean, cm.	P. E. mean, cm.	Difference from mean of total, cm.	Standard deviation, cm.	D_1, cm.	D_9, cm.
1920							
April 10-11	13	5.923	+0.035	+0.018	0.184	5.565	6.170
May 21-22	33	5.842	±0.039	—0.063	0.333	5.365	6.335
June 18	19	5.821	±0.080	—0.084	0.515	5.080	6.440
July 19	17	5.729	±0.064	—0.176	0.394	5.170	6.230
August 19	32	6.244	±0.068	+0.338	0.572	5.580	7.020
October 9-11	17	5.918	±0.066	+0.012	0.404	5.440	6.272
November 23	15	5.880	±0.062	—0.026	0.356	5.533	6.467
1921							
July 23	23	5.791	±0.075	—0.114	0.532	5.030	6.470
Combined	169	5.906	±0.025		0.481	5.298	6.448

Table 11. Young Tivela, Year-Class of 1918. Total Length of Ring II in Different Collections

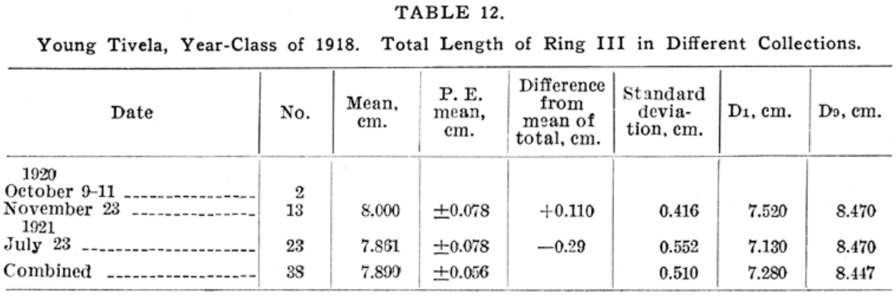


TABLE 12.

Young Tivela, Year-Class of 1918. Total Length of Ring III in Different Collections.

Date	No.	Mean, cm.	P. E. mean, cm.	Difference from mean of total, cm.	Standard deviation, cm.	D_1, cm.	D_9, cm.
1920							
October 9-11	2						
November 23	13	8.000	±0.078	+0.110	0.416	7.520	8.470
1921							
July 23	23	7.861	±0.078	—0.29	0.552	7.130	8.470
Combined	38	7.899	±0.056		0.510	7.280	8.447

Table 12. Young Tivela, Year-Class of 1918. Total Length of Ring III in Different Collections

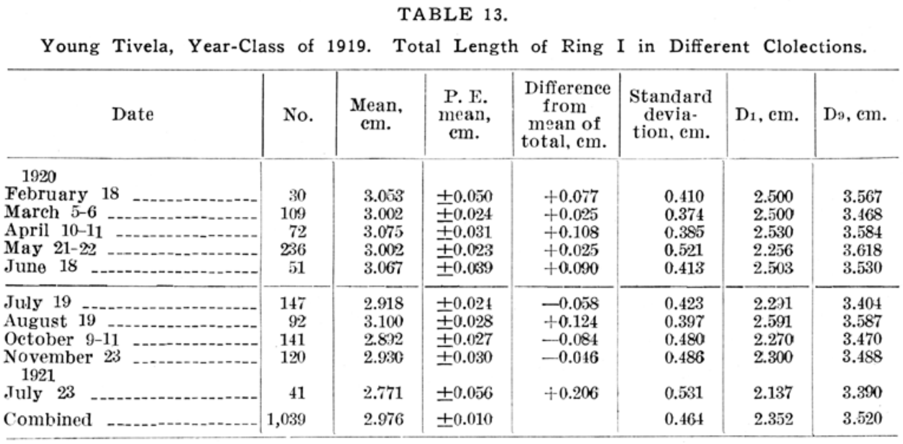


TABLE 13.

Young Tivela, Year-Class of 1919. Total Length of Ring I in Different Clolections.

Date	No.	Mean, cm.	P. E. mean, cm.	Difference from mean of total, cm.	Standard deviation, cm.	D_1, cm.	D_9, cm.
1920							
February 18	30	3.053	±0.050	+0.077	0.410	2.500	3.567
March 5-6	109	3.002	±0.024	+0.025	0.374	2.500	3.468
April 10-11	72	3.075	±0.031	+0.108	0.385	2.530	3.584
May 21-22	236	3.002	±0.023	+0.025	0.521	2.256	3.618
June 18	51	3.067	±0.039	+0.090	0.413	2.503	3.530
July 19	147	2.918	±0.024	—0.058	0.423	2.291	3.404
August 19	92	3.100	±0.028	+0.124	0.397	2.591	3.587
October 9-11	141	2.892	±0.027	—0.084	0.480	2.270	3.470
November 23	120	2.930	±0.030	—0.046	0.486	2.300	3.488
1921							
July 23	41	2.771	±0.056	+0.206	0.531	2.137	3.390
Combined	1,039	2.976	±0.010		0.464	2.352	3.520

Table 13. Young Tivela, Year-Class of 1919. Total Length of Ring I in Different Cloections

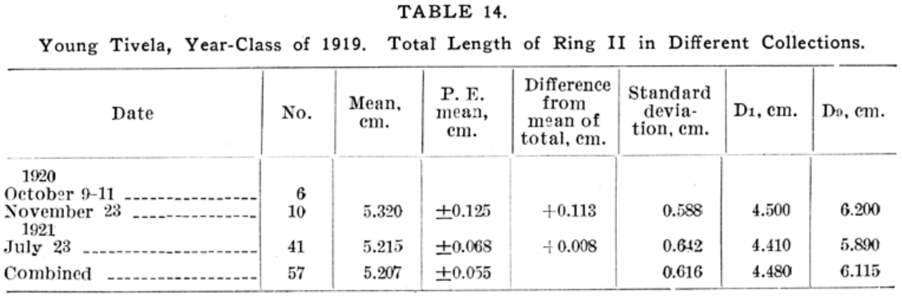


TABLE 14.

Young Tivela, Year-Class of 1919. Total Length of Ring II in Different Collections.

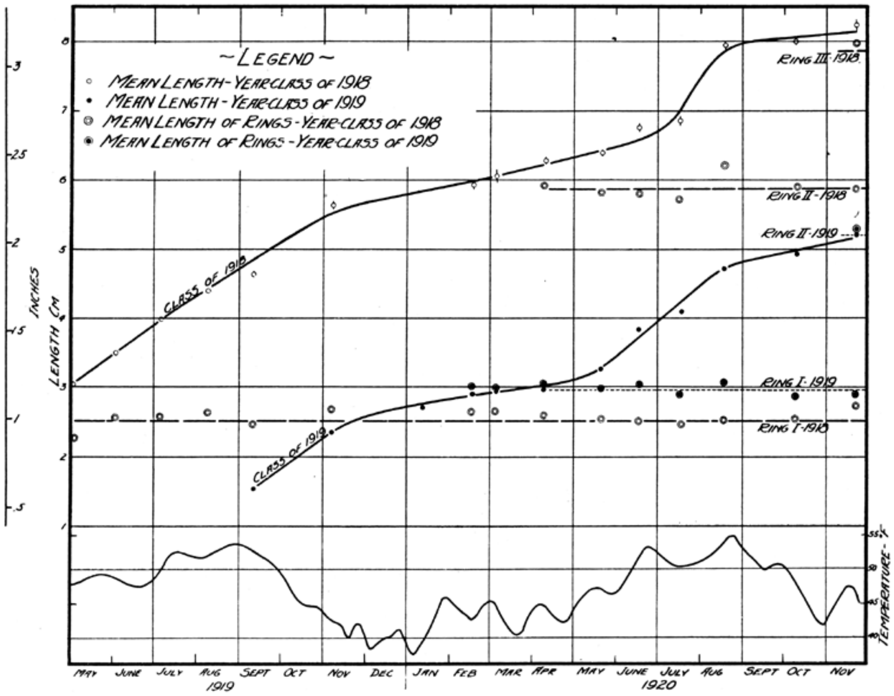
Date	No.	Mean, cm.	P. E. mean, cm.	Difference from mean of total, cm.	Standard deviation, cm.	D_1, cm.	D_9, cm.
1920							
October 9-11	6						
November 23	10	5.320	±0.125	+0.113	0.588	4.500	6.200
1921							
July 23	41	5.215	±0.068	+0.008	0.642	4.410	5.890
Combined	57	5.207	±0.055		0.616	4.480	6.115

Table 14. Young Tivela, Year-Class of 1919. Total Length of Ring II in Different Collections

Since these variations do not exceed the variations found in the total lengths of clams under similar conditions it may safely be concluded that in the year-class of 1918 all the rings were formed at essentially the same time.

In the fall of 1919 the young of the 1919 year-class showed no rings. These first appeared in the collections of February, 1920, and subsequent to that date all clams showed rings the mean total length of which was 2.98 cm. As may be seen from Table 13, the agreement between the ten collections comprising 1039 specimens is equally as good as that in the case of the 1918 year-class. At approximately the same time as the first ring appeared in the class of 1919 a second ring appeared in the class of 1918 with a total length of 5.92 cm. All specimens of the year-class of 1918 collected subsequently showed a ring of approximately this total length in addition to the one we have previously mentioned. In November, 1920, the appearance of the second ring in the year-class of 1919 and a third ring in the year-class of 1918 was noted. Before taking up the consideration of the exact time of occurrence of these rings and the agreement in their size in the different year-classes, it will be well to point out the fundamental significance of the facts established regarding their occurrence. The young of the 1919 year-class previous to the first winter showed no evidence of any ring. The young of the 1918 year-class subsequent to the winter of 1918–19 and of the 1919 year-class subsequent to the winter of 1919–20, both showed a single ring and no second ring was observed until the passing of the second winter following their hatching.

The material examined, consisting of nearly two thousand young specimens collected over a period of more than two years, is more ample than that of any previous study of the rings of the molluscan shell. The observation thus soundly based, that a ring is formed each winter and but one each winter, is sufficient to prove beyond doubt the annual nature of these rings. During the same period the position of the ring in relation to the shell margin was noted in all adults and many measurements were taken. In the spring the ring lay at or near the margin; during summer and autumn the space between the ring and the margin steadily increased until the appearance of a new ring at the extreme margin in late autumn or winter. The general relationship of the ring to the shell-margin thus confirms the above conclusion. The placing on a firm observational basis of the annual nature of the rings in Tivela, I consider the most important fact established by the present investigation. It furnishes an accurate method of age determination which may easily be extended to most marine bivalves and which is destined, I believe, to be as useful in this field as the method of scale readings has proved with fish.



GRAPH 6. Graph showing the total length and the length of the different rings of young *Tivela* on various dates from May, 1919, to November, 1920. (The mean total lengths, dates, and temperatures are reproduced from Graph 2.) The lines through the mean ring lengths represent the mean of all determinations for each type of ring.

Graph 6. Graph showing the total length and the length of the different rings of young Tivela on various dates from May, 1919, to November, 1920. (The mean total lengths, dates, and temperatures are reproduced from Graph 2.) The lines through the mean ring lengths represent the mean of all determinations for each type of ring

3.36. Immediate cause of occurrence

Having set forth the proofs of the annual nature of these rings, and before taking up the application of this fact to the question of normal growth, certain points regarding the details of their occurrence would naturally suggest themselves. Is the size of the ring dependent upon some external factor, as, for instance, the sudden onset of cold weather or the occurrence of storms which interfere with feeding, or do the rings occur when the clam has reached a certain size, or are both external conditions and size, factors in their incidence? Certain data bearing on these questions are at present under consideration and it is hoped that a further analysis of this point may be attempted in a succeeding publication.

It will be noticed that Ring I is not the same size in the year-class of 1919 as in that of 1918. The same is true of Ring II, and neither of these is the same size as Rings I and II which will be presented in the next section as the average for normal growth. It is thus clear that not only is there individual variation in the size of the ring but this size varies, often widely, between seasons. This fact is illustrated by Table 15. page 55, showing the size of Ring I for material (discussed in the next section) where it is possible to tell the year in which the growth took place. These variations probably result from differences in the length and the character of the season intervening between hatching and the onset of the slower growth of the first winter.

Another point bearing on this question may be here presented. It might be expected that if the rings resulted from external factors they would be more distinct in northern waters with lower temperatures than in tropical waters. This is true, for instance, of certain species of trees which under the uniform conditions of the tropics are said not to show annual rings. With this in mind a number of species of the Veneridae and related forms were inspected.[*] From a cursory examination which did not include more than a few specimens of each species it was not apparent that rings varied in distinctness between colder and warmer waters, although the localities included the West Indies, certain islands of the Tahiti group, and other situations where no great range of temperature might be expected. A similar comparison within the species here treated (Tivela stultorum) has been possible in only one case where a collection of specimens from Turtle Bay (San Bartholome), Lower California, was examined. Here the rings were exactly of the same distinctness as in similar material from Oceano. This might be taken to support the idea previously suggested that an internal rhythm tending to express itself in alternating rapid and slow growth is always present and that a slight external change may serve to determine the times of expression of this internal tendency. This is perhaps further suggested by the known fact that irregularities in speed of growth showing a less clear rhythm are observed for instance in the growth of the mammalian foetus where the external conditions are very uniform, especially as regards temperature. (Meyer, 1914, p. 501.)

---

[*] For the courtesy of examining these specimens the writer wishes to acknowledge his indebtedness to Mrs. T. S. Oldroyd, of Stanford University.

3.37. Applicability and reliability of ring method of age determination

Before applying the conception here developed of the annual nature of the rings to an extensive determination of age, it will be necessary to consider, first, its applicability to the adult and, second, the possibility of its use in other species. The accuracy of such a method is of course a matter of prime importance, and one has a right to inquire whether the identification of the rings is so easy as to be beyond dispute or so difficult as to be uncertain and largely affected by personal bias. It is necessary to determine the position and number of rings by inspection, as no purely mechanical method can be devised for their identification. Whenever possible both surface appearance and the results of translumination have been used as mutual checks. There remain cases where an exact answer to the question of age is impossible. During the examination of great numbers of young (the writer has measured nearly 2000 and observed many others) uncertainty regarding rings has arisen in hardly more than one per cent. These doubts were chiefly as to the exact point which should be measured in a diffuse and ill-defined or double ring—the number of rings was seldom uncertain. The difficult cases fall among the adults and are of two kinds.

In all clams that have reached an age of ten or twelve years the rings near the margin become extremely crowded and the exact number difficult of determination. For instance, in a particular case, after repeated careful countings the worker may be in doubt as to whether there are 12 or 13 rings, or in another specimen, whether the count should be recorded as 17, 18, or 19. The error thus introduced is slight and by no means fundamental. At these ages the growth is slow and the normal variation in size considerable, so that an error of a year will not perceptibly affect the average and the errors are sometimes in excess and sometimes in defect.

A second type of difficulty is more troublesome. Occasionally shells are found in which the rings are extremely faint and ill-defined or in which the growth between successive rings is extremely unequal or in which there are secondary rings apparently not annual. Two or three rings in close succession separating one or two periods of growth obviously less than the average may come from two distinct causes; they may be genuine year rings defining one or two seasons of poor growth, or one of the rings may not be a year ring but one due to injury or other particular cause for slackening of growth. It has been shown that such rings are formed at the time of an injury or even a marked change, as transference to an aquarium, and that they may become as prominent as year rings. In some cases they may be identified by evidence of injury to the shell at this time or by the character of the mark, which, since it is due to a short cessation of growth is usually narrower and may not be translucent. Undoubted year marks, however, are not always of equal clearness. For instance, in the commercial catch examined November 9, 1919, it was possible to identify in many cases the ring corresponding to the winter of 1916–17 (at that time the fourth from the margin) and it was noted that in the majority of instances it was far less distinct than those corresponding to other years. This led to inquiry and it was learned from the clammers that this winter had been the mildest and most free from surf of the preceding nine years. According to the same reports the winter of 1913–14 was marked by the heaviest surf. This ring proved more than usually prominent in a somewhat smaller proportion of the cases. A faint year ring like that of 1916–17, if observed in a single specimen, might be taken for a secondary ring, but in the present instance, of course, merely served to show the accuracy of the ring method. On another occasion a characteristic year mark was encountered in a small collection made at the mouth of Anaheim Slough near Long Beach on May 16, 1919. Here the mark of the previous winter (1918–19) in the great majority of clams of all ages consisted of a heavy ring followed at a distance of about 5 mm. by a much fainter one.

These instances will serve to illustrate the difficulties as well as the unexpected aids encountered in age determination. In a considerable number of cases a check on the practical working of the method was furnished by the independent determination of age by the writer and various associates. In all such tests the agreement was very assuring, and it is the writer's belief that any competent observer, after a short period of instruction, could read accurately eighty or ninety per cent of the shells of this species. Some few shells remain illegible and such were excluded from the final records; in some where doubt existed between two values differing by only one year, as 7 or 8, the records were used, the age being considered midway between the two values. of 409 measurements of total size, 60—or 14.7 per cent—were of this character.

As regards other species, I feel confident that among the Pacific coast marine forms with which I am familiar, all exhibit year rings and that in the majority of cases these are distinctive enough to furnish a reliable index of age. of the remainder, most could be deciphered by careful study, though it is obvious that some would be difficult. The method is undoubtedly of wide application and of great value as a tool in the investigation of life histories.

3.38. The normal course of growth as determined from the annual rings

Having established for the species under consideration the reliability of the annual rings as an indication of age, we are in a position to attack the problem outlined at the beginning of the present section—the determination of the normal course of growth (see p. 15). To do this we must know the age and the size, whether length or weight, of many individuals. An examination of adult clams will now furnish this information; the age of an individual can be found by counting the annual rings, its length or weight may be directly measured. It is furthermore possible to get data not only on the total length but also on the length at each winter of the clam's life by measuring the separate rings. From these data the norm for growth in the species may be established. Before undertaking the determination of this norm the method of collecting the necessary data and its special fitness for this purpose will be considered.

3.39. Method of collecting data

During trips made to Oceano for the collection of young clams taken for the market by local diggers were examined. These clams were dug from the entire Pismo-Oceano beach at all seasons of the year from May, 1919, to November, 1920, and were examined without conscious selection for size except in one case where a special effort was made to get data on the largest sizes. They may, therefore, be considered a fair sample of the adult population of this beach. In all, records for

411 adult specimens were used. In all of these the total length was measured as described (see p. 19), in most cases the height, and in many the thickness and weight. In the majority the total lengths of the first five to seven rings were recorded, and in a less number the size of all rings or of certain rings representing selected ages were measured. After excluding doubtful cases, 1598 lengths of rings and 382 total lengths were available from the 411 specimens mentioned.

3.40. Data represent average climatic conditions

As the clams furnishing these measurements ranged from four to twenty-six years of age, the mean lengths present a much more accurate picture of the growth of a species than in the case of a short-lived animal where the chance succession of two or three years either markedly favorable or unfavorable to growth might profoundly affect the observed sizes. The data really represent an average of climatic conditions from 1894 to 1920. The importance of this point is not always appreciated, and growth based on specimens in captivity or on observations of animals from their native habitat during a single season are regarded as representative. How widely the growths may vary from season to season in a single locality may be seen from the following data where the growth in length for the first year has been calculated for those cases in which enough specimens of a particular year could be identified to make the means significant. The mean for all adults (241 specimens) includes the figures given for the years 1915–16 to 1911–12 and other scattered records for known years as well as many in which the date of the first year's growth is unknown. The records for 1919–20 and 1918–19 were not included in the total as the numbers of the young examined were so large as to be wholly disproportionate to the other years and data for their growth in the third, fourth, and subsequent years of course are not yet available. It will be seen that initial growths ranging from 2.05 to 2.90 cm. are represented, this variation of 14.7 per cent depending presumably on the time between the spawning date and that of ring formation and the temperature, food, and other conditions during this period.

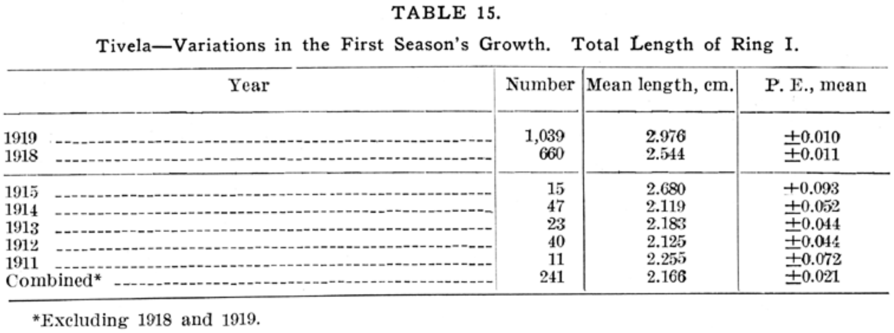


TABLE 15.

Tivela—Variations in the First Season's Growth. Total Length of Ring I.

Year	Number	Mean length, cm.	P. E., mean
1919	1,039	2.976	±0.010
1918	660	2.544	±0.011
1915	15	2.680	+0.093
1914	47	2.119	±0.052
1913	23	2.183	±0.044
1912	40	2.125	±0.044
1911	11	2.255	±0.072
Combined*	241	2.166	±0.021

*Excluding 1918 and 1919.

Table 15. Tivela—Variations in the First Season's Growth. Total Length of Ring I

The extensive data on the young (year-classes of 1918 and of 1919) apparently represent particularly favorable seasons and, if these were taken for the first three years' growth, would give figures far too high. This error is avoided by the use of data from the adult where over twenty years are thrown together. For an animal with a life span of three or four years this could only be avoided by collecting data on a number of successive years.

3.41. Data uninfluenced by seasonal growth

Another advantage which these data possess is that the course of the entire life-growth, as based upon them, is practically uninfluenced by seasonal growth. The growth during each year would, to be sure, if a complete record were available, show the accleration and retardation noted in the young, but such rhythms repeated ten to twenty-six times, according to the age of the clam, would give rise merely to minor irregularities in the general course of life-growth. As a matter of fact, the points in the life curve furnished by this method represent the sizes at but one season for each year, that of winter when rings are formed, and hence present comparable stages of each seasonal cycle. When we deal with a score of such comparable points the general course of the life-growth is very accurately defined.

In short-lived forms, on the other hand, but a few comparable points from seasonal cycles are available for the determination of the course of the life-growth. This is conspicuously true of insects in which the life-history is often comprised in a single year; in this case, if the animals live under natural conditions, there is no basis for distinguishing between seasonal growth and life-growth. This advantage of data from a long-lived form such as the Pismo clam is of marked theoretical importance, as I believe that serious confusion has arisen from basing general conclusions regarding the life-growth in organisms, on forms in which seasonal and total growth are inextricably confused.

3.42. Relation of total lengths to ring lengths

The measurements of rings represent the length of the clams at the completion of the season's growth, but the total lengths always include a portion of an additional season's growth, and so are not directly comparable. Since the dates of capture are varied, the measurements were combined by adding one-half year beyond that indicated by the last ring in the cases where the total lengths were measured, a method which would give reliable results where the numbers were large and the dates evenly distributed through the year.

3.43. Length at each age

These data are presented in three tables, one (Table 16) of the lengths of the rings, one (Table 17) of the total lengths, and one (Table 18) formed by their combination. On this latter is based the graph of length on age (Graph 7) As in the case of the young, this graph gives not only the means but the first and ninth deciles between which are included 80 per cent of the cases, and the mean minus three times the standard deviation and the mean plus three times the standard deviation giving the probable extreme lengths at the given age. Freehand curves have been drawn through the values other than the mean to make the general trend more apparent. The line passing through the means represents the values derived from a formula which has been fitted to all of the data represented by the means. This is of the general form $y = a - bc^{X}$, in which y is the length in centimeters and x the age in years. In the present case the constants have the following values: $\text{length (cm.)} = 15.602 - 17.24 \text{ X } .798^{\text{age (years)}}$.

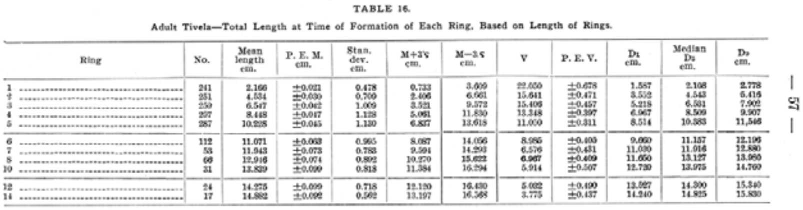


TABLE 16.

Adult Tivela—Total Length at Time of Formation of Each Ring, Based on Length of Rings.

Ring	No.	Mean length cm.	P. E. M. cm.	Stan. dev. cm.	M+3ς cm.	M−3ς cm.	V	P. E. V.	D_1 cm.	Median D_2 cm.	D_3 cm.
1	241	2.166	±0.021	0.478	0.733	3.609	22.050	±0.678	1.587	2.108	2.778
2	251	4.534	±0.030	0.700	2.406	6.661	15.641	±0.471	3.552	4.543	6.416
3	250	6.547	±0.042	1.009	3.521	9.572	15.406	±0.457	5.218	6.531	7.902
4	297	8.448	±0.047	1.128	5.061	11.830	13.348	±0.397	6.967	8.509	9.907
5	287	10.228	±0.045	1.130	6.837	13.618	11.050	±0.311	8.514	10.383	11,546
6	112	11.071	±0.063	0.995	8.087	14.056	8.985	±0.405	9.660	11.157	12.196
7	53	11.943	±0.073	0.783	9.594	14.293	6.576	±0.431	11.030	11.916	12.880
8	66	12.946	±0.074	0.892	10.270	15.622	6.967	±0.409	11.650	13.127	13.960
10	31	13.829	±0.099	0.818	11.384	16.294	5.914	±0.507	12.720	13.975	14.760
12	24	14.275	±0.099	0.718	12.120	16.430	5.032	±0.490	13.527	14.300	15.340
14	17	14.882	±0.092	0.562	13.197	16.568	3.775	±0.437	14.240	14.825	15.830

Table 16. Adult Tivela—Total Length at Time of Formation of Each Ring, Based on Length of Rings

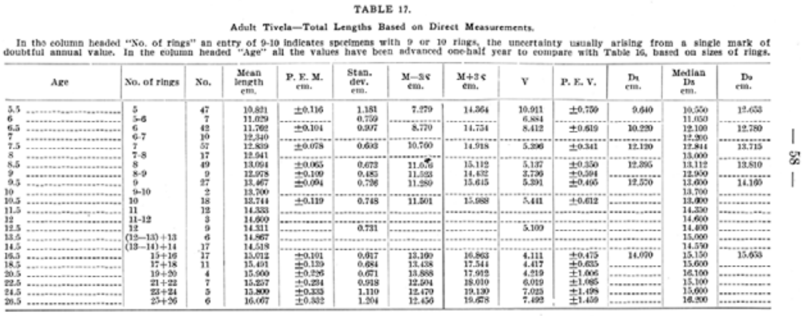


TABLE 17.

Adult Tivela—Total Lengths Based on Direct Measurements.

In the column headed "No. of rings" an entry of 9-10 indicates specimens with 9 or 10 rings, the uncertainty usually arising from a single mark of doubtful annual value. In the column headed "Age" all the values have been advanced one-half year to compare with Table 16, based on sizes of rings.

Age	No. of rings	No.	Mean length cm.	P. E. M. cm.	Stan. dev. cm.	$M-3\sigma$ cm.	$M+3\sigma$ cm.	V	P. E. V.	D_1 cm.	Median D_5 cm.	D_9 cm.
5.5	5	47	10.831	±0.116	1.181	7.279	14.364	10.911	±0.759	9.640	10.550	12.653
6	5-6	7	11.029		0.759			6.884			11.050	
6.5	6	42	11.762	±0.104	0.997	8.770	14.754	8.412	±0.619	10.220	12.100	12.780
7	6-7	10	12.340								12.200	
7.5	7	57	12.839	±0.078	0.693	10.760	14.918	5.396	±0.341	12.120	12.844	13.715
8	7-8	17	12.941								13.000	
8.5	8	49	13.094	±0.065	0.673	11.076	15.112	5.137	±0.350	12.895	13.112	13.810
9	8-9	9	12.978	±0.109	0.485	11.523	14.433	3.736	±0.594		12.950	
9.5	9	27	13.467	±0.094	0.726	11.289	15.645	5.391	±0.495	12.570	13.600	14.160
10	9-10	2	13.700								13.700	
10.5	10	18	13.744	±0.119	0.748	11.501	15.988	5.441	±0.612		13.600	
11.5	11	12	14.333								14.350	
12	11-12	3	14.600								14.600	
12.5	12	9	14.311		0.731			5.109			14.400	
13.5	(12—13)+13	6	14.867								15.000	
14.5	(13—14)+14	17	14.518								14.550	
16.5	15+16	17	15.012	±0.101	0.617	13.160	16.863	4.111	±0.475	14.070	15.150	15.653
18.5	17+18	11	15.491	±0.139	0.684	13.438	17.544	4.417	±0.635		15.600	
20.5	19+20	4	15.900	±0.226	0.671	13.888	17.912	4.219	±1.006		16.100	
22.5	21+22	7	15.257	±0.234	0.918	12.504	18.010	6.019	±1.085		15.100	
24.5	23+24	5	15.800	±0.335	1.110	12.470	19.130	7.025	±1.498		15.600	
26.5	25+26	6	16.067	±0.332	1.204	12.456	19.678	7.492	±1.459		16.200	

— 58 —

Table 17.
Adult Tivela—Total Lengths Based on Direct Measurements

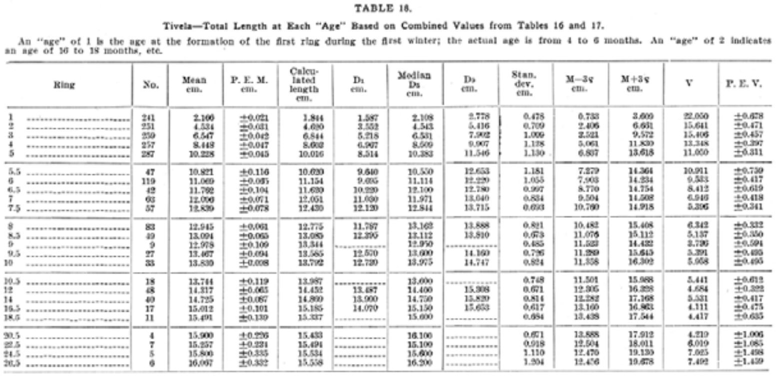


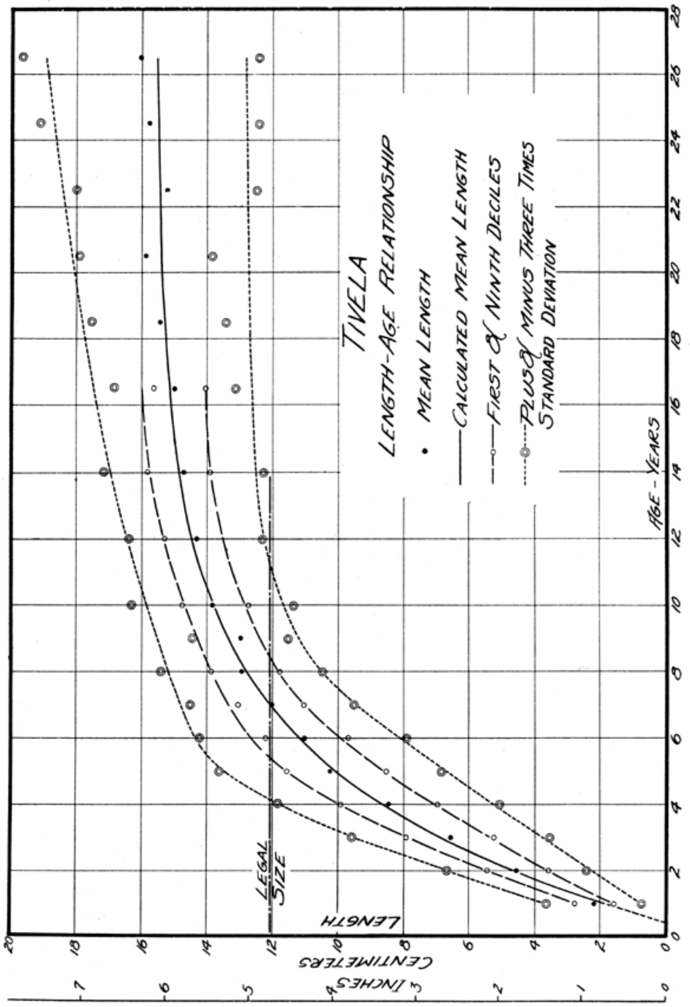
TABLE 18.

Tivela—Total Length at Each "Age" Based on Combined Values from Tables 16 and 17.

An "age" of 1 is the age at the formation of the first ring during the first winter; the actual age is from 4 to 6 months. An "age" of 2 indicates an age of 16 to 18 months, etc.

Ring	No.	Mean cm.	P. E. M. cm.	Calculated length cm.	D_1 cm.	Median D_2 cm.	D_3 cm.	Stan. dev. cm.	M−3σ cm.	M+3σ cm.	V	P. E. V.
1	241	2.166	±0.021	1.844	1.587	2.108	2.778	0.478	0.733	3.600	22.050	±0.678
2	251	4.534	±0.031	4.620	3.552	4.543	5.416	0.709	2.406	6.661	15.641	±0.471
3	259	6.547	±0.042	6.844	5.218	6.531	7.902	1.009	3.521	9.572	15.406	±0.457
4	257	8.448	±0.047	8.602	6.907	8.509	9.907	1.128	5.061	11.830	13.348	±0.397
5	287	10.228	±0.045	10.016	8.514	10.383	11.546	1.130	6.837	13.618	11.050	±0.311
5.5	47	10.821	±0.116	10.620	9.640	10.550	12.653	1.181	7.279	14.364	10.911	±0.759
6	119	11.069	±0.065	11.154	9.695	11.114	12.220	1.055	7.903	14.234	9.533	±0.417
6.5	42	11.762	±0.104	11.620	10.220	12.100	12.780	0.997	8.770	14.754	8.412	±0.619
7	63	12.006	±0.071	12.051	11.030	11.971	13.040	0.834	9.504	14.508	6.946	±0.418
7.5	57	12.839	±0.078	12.430	12.120	12.844	13.715	0.693	10.760	14.918	5.396	±0.341
8	83	12.945	±0.061	12.775	11.787	13.163	13.888	0.821	10.482	15.408	6.342	±0.332
8.5	49	13.094	±0.065	13.085	12.395	13.112	13.810	0.673	11.076	15.112	5.137	±0.350
9	9	12.978	±0.109	13.344	....	12.950	....	0.485	11.523	14.432	3.736	±0.594
9.5	27	13.467	±0.094	13.585	12.570	13.600	14.160	0.726	11.289	15.645	5.391	±0.495
10	33	13.830	±0.098	13.792	12.720	13.975	14.747	0.824	11.358	16.302	5.958	±0.495
10.5	18	13.744	±0.119	13.987	....	13.600	....	0.748	11.501	15.988	5.441	±0.612
12	48	14.317	±0.065	14.452	13.487	14.400	15.308	0.671	12.305	16.328	4.684	±0.322
14	40	14.725	±0.087	14.869	13.900	14.750	15.820	0.814	12.282	17.168	5.531	±0.417
16.5	17	15.012	±0.101	15.185	14.070	15.150	15.653	0.617	13.160	16.863	4.111	±0.475
18.5	11	15.491	±0.139	15.337	....	15.600	....	0.684	13.438	17.544	4.417	±0.635
20.5	4	15.900	±0.226	15.433	....	16.100	....	0.671	13.888	17.912	4.220	±1.006
22.5	7	15.257	±0.231	15.494	....	15.100	....	0.918	12.504	18.011	6.019	±1.085
24.5	5	15.800	±0.335	15.534	....	15.600	....	1.110	12.470	19.130	7.025	±1.498
26.5	6	16.067	±0.332	15.558	....	16.200	....	1.204	12.456	19.678	7.492	±1.459

Table 18.
Tivela—Total Length at Each "Age" Based on Combined Values from Tables 16 and 17



GRAPH 7. Graph of life growth of *Tivela*, showing the total length for specimens of all ages up to 26 years. The solid points show the mean length of each age; the solid line represents a curve fitted to these observations. Additional means from ½ to 10½ were used in determining the line, but were omitted from the graph to avoid confusion. The open circles represent the first and ninth decils, as in Graph 2, and include between them 80 per cent of the specimens; the double circles mark the extreme variations of size (based on three times the standard deviation above and below the mean). Thus while the average clam of seven years has just reached legal size (4¾ inches or about 12 cm.), some may be as small as 9.5 cm. and some as large as 14.5 cm. Or by following the horizontal line marked "legal size" it will be seen that this may be reached as early as 4 or as late as 11 years, although the average is 7 years and 80 per cent fall between 7½ and 8½ years.

Graph 7. Graph of life growth of Tivela, showing the total length for specimens of all ages up to 26 years. The solid points show the mean length of each age; the solid line represents a curve fitted to these observations. Additional means from ½ to 10 ½ were used in determining the line, but were omitted from the graph to avoid confusion. The open circles represent the first and ninth decils, as in Graph 2, and include between them 80 per cent of the specimens; the double circles mark the extreme variations of size (based on three times the standard deviation above and below the mean). Thus while the average clam of seven years has just reached legal size (4 ¾ inches or about 12 cm.), some may be as small as 9.5 cm. and some as large as 14.5 cm. Or by following the horizontal line marked "legal size" it will be seen that this may be reached as early as 4 or as late as 11 years, although the average is 7 years and 80 per cent fall between 7 ½ and 8 ½ years

For the present this may be looked upon merely as an impersonal method of obtaining a smoothed curve each point of which is in some degree dependent upon all the available data. It is hoped that the method of derivation and the possible significance of this formula may be considered at a future time. These lines must not be interpreted as representing the actual growth which, as has just been pointed out, shows a seasonal rythm, the course of growth consisting, as shown by the data on the first two years' growth in the young (Graph 2) or Belding's figures on the quahaug (Graph 9. fine line), of a series of cycles rising step-like by rapid summer growths alternating with slow winter growths. Through comparable parts of these winter plateaus corresponding to the time of ring formation, the generalized curve passes. Neither do the abscissae, though labeled for convenience "age," represent years of age, but rather the first, second, etc., winters of the clam's life. The actual age at the first winter varies with the date of the breeding season, but may be assumed as four to seven months. Since the age at the first winter may vary by more than a month, we would expect the size of Ring I to be more variable than that of subsequent rings, as the proportional differences in age would never again be so great.

Taking the curve to represent the trend of the growth in length, it will be seen that growth is most rapid at the earliest period which our data represent and that its velocity constantly and uniformly decreases up to the greatest age of which we have records.

3.44. Comparison with growth in other localities

It would be interesting if this well-defined course of growth could be compared with similar data from other localities. Although collections and measurements have been made at other points, these data are not extensive enough to justify detailed comparison. One small collection from Turtle Bay (San Bartholome) in Lower California already alluded to is, however, worth recording. The measurements are given in Table 19, and the course of growth determined from them and plotted as in Graph 7 is represented in Graph 8 along with the corresponding portion of the growth curve of clams from Oceano. None of the specimens were over four years old and consequently the further course of growth can not be determined. It will be noticed that starting at practically the same size for Ring I the southern specimens steadily outstripped the northern as far as the records go. No larger specimens were included in the shipment but whether this was because they could not be found or because small ones were purposely selected could not be learned.

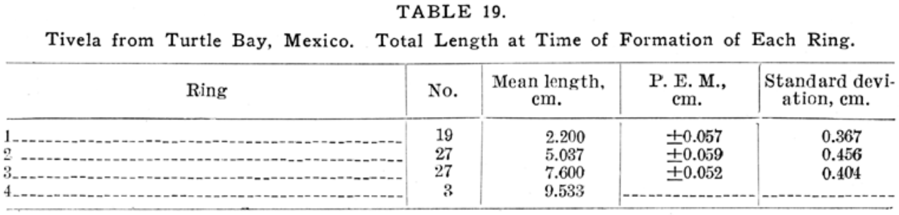
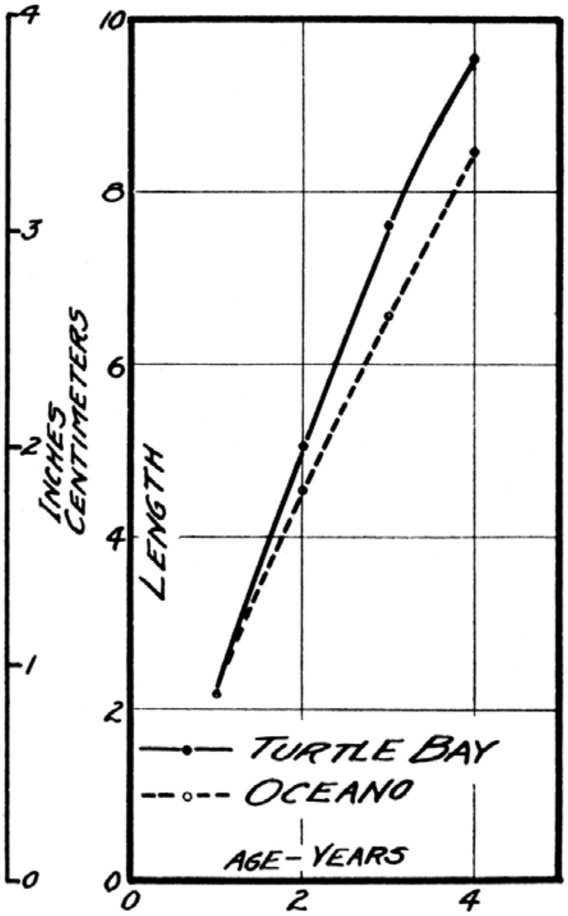


TABLE 19.

Tivela from Turtle Bay, Mexico. Total Length at Time of Formation of Each Ring.

Ring	No.	Mean length, cm.	P. E. M., cm.	Standard deviation, cm.
1	19	2.200	±0.057	0.367
2	27	5.037	±0.059	0.456
3	27	7.600	±0.052	0.404
4	3	9.533		

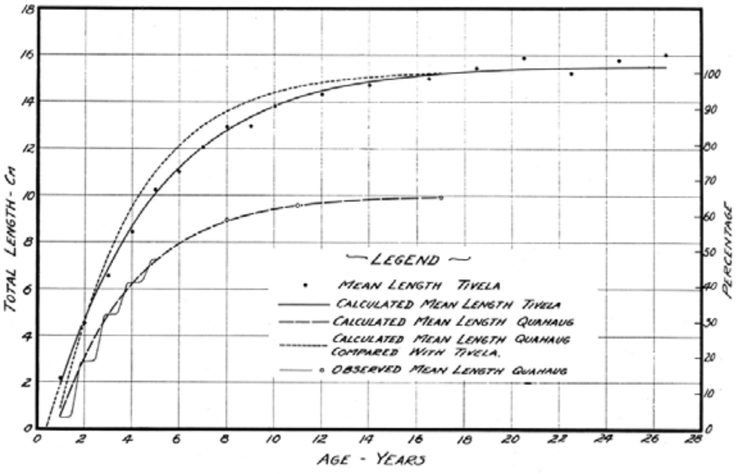
Table 19.
Tivela from Turtle Bay, Mexico. Total Length at Time of Formation of Each Ring



Graph 8. Showing the total length of Tivela from Turtle Bay, Mexico, in comparison with those from Pismo-Oceano at ages up to 4 years

3.45. Comparison with growth in other animals

The general form of the curve representing the growth in length (it should be noted that this is very different from growth in weight) in the Pismo clam is similar in type to that found in many of the animals for which we have comparable data. Comparison with a related species, the quahaug of the Atlantic Coast, with serve to illustrate this similarity. In Graph 9 the growth of Tivela is repeated (solid points and solid line) and on the same scale are shown corresponding data for the quahaug as determined by Belding from direct observation (circles and fine line). The two curves obviously are of the same type; this is confirmed by the fact that the same type of formula by which the curve was fitted to the data in the Pismo clam may be applied (with a change of constants only) to that for the quahaug. The fit thus obtained is shown by the long dashes and it is clearly as good as might be expected in dealing with scanty data. These two curves present other features of interest when compared in a different manner. If the length at 17 years is taken as 100 per cent for each species, the proportionate size or rate of growth at any age may be compared. The dotted line represents the curve of the quahaug on this basis; both it and the curve of the Pismo clam should be referred to the percentage scale on the right for this purpose. The various percentages of the length at 17 years are reached earlier by the quahaug; for example, 80 per cent is reached at about six years by the quahaug but at seven by the Pismo clam. It is clear, however, that the continuation of the curve for the quahaug would cross that for Tivela. Or, to express the relationship



GRAPH 9. Comparison of growth in the Pismo clam and the quahaug. (Data for quahaug from Belding, 1912, p. 87 and Fig. 44.)

Graph 9. Comparison of growth in the Pismo clam and the quahaug. (Data for quahaug from Belding, 1912, p. 87 and Fig. 44.)

in other terms, the rate of proportional growth of the quahaug is greater than that of Tivela up to approximately seven years, after which it becomes less. It would be interesting, if the data were available, to see in how many cases where related forms reach different definitive sizes the smaller showed at first a more rapid and later a less rapid proportional growth.

We have presented the data on the total lengths at the various ages; it is proposed also to present similar figures for the weights at the various ages; but before this can be done it is necessary to show the relation existing between the various linear dimensions, and between them and weight.

3.46. Height and thickness at each length

In 640 specimens the three dimensions of length, height (width), and thickness (see page 19) were available; these are shown in Table 20 and in Graph 10, the two latter measurements are shown plotted against length. It is evident that both height and thickness increase in direct proportion to length so that a constant shape is preserved. The solid lines show the average ratios between length and height and between length and thickness at the different lengths, and it is plain that such a simple tangent relationship represents quite accurately the ratios at all sizes. The numerical values are: [height = 0.746 x length; thickness = 0.442 x length] .

Essentially the same condition was found by Crozier in his study of the clam Dosinia (1914). Here though a different set of measurements were compared, all were found to increase practically in direct proportion to the increase in length. It is clear that after the larval stages are past and the lamellibranch shell formed, its general shape does not materially alter with age. This entire question is discussed at some length by D'A. W. Thompson (1917, p. 561). This statement requires a slight qualification in the case of very old specimens. In many species there is an actual regression in the activities of the mantle in extreme cases, so that the new shell added to the interior fails to reach the extent of previous additions and the length and height measured to the actual margin may decrease while the thickness is increasing slightly. Such cases are very exceptional, but there is a tendency among old Pismo clams for the growth in length to persist in a somewhat larger degree at the siphonate end than at the anterior end, while the reverse is true of the thickening at the margin. This gain of thickness over length is not apparent until an age of ten to fifteen years, and does not show at all in the data presented above.

A number of investigators have considered the shape of fish; mention may be made of the work of Crozier and Hecht on the weakfish (1914), and a later extension of the same methods to a number of species by Hecht (1916) who also reviews earlier studies. In all cases a variety of dimensions (body length, depth and thickness, head length, tail length) were found to maintain a constant ratio to each other at all total sizes, so that among fish it is apparent that the form is not altered with growth, at least after the conclusion of the larval period.

In mammals and birds, on the other hand, the shape changes materially between birth or hatching and the adult stage. The significance of this difference is not clear; it would be desirable to have data from a wide variety of unrelated animals for comparison on this point.

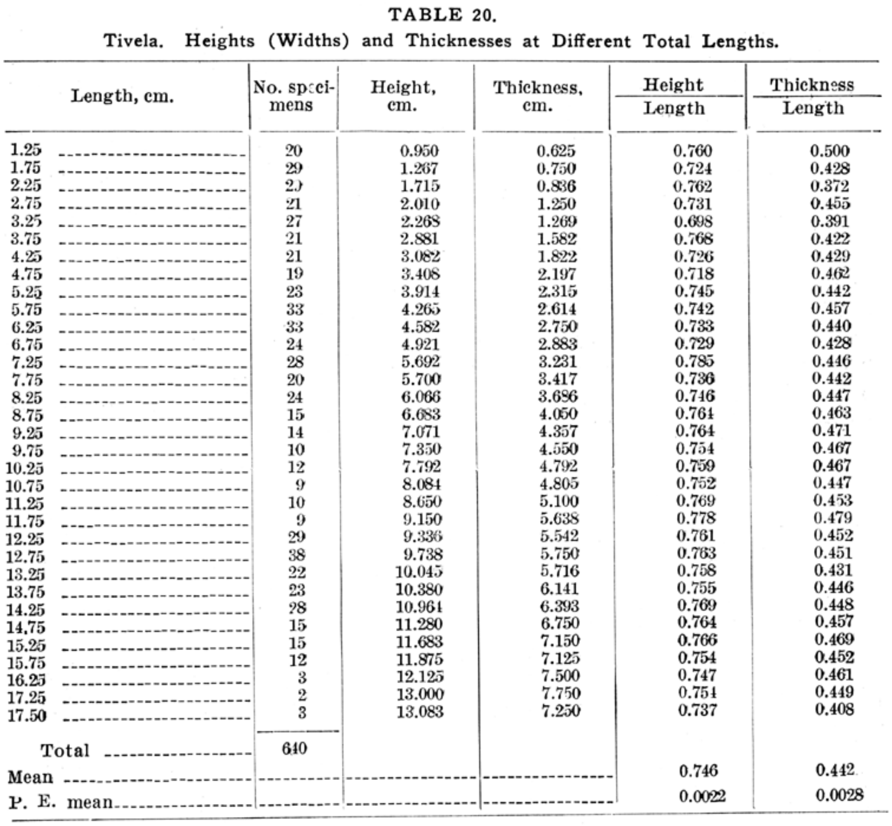
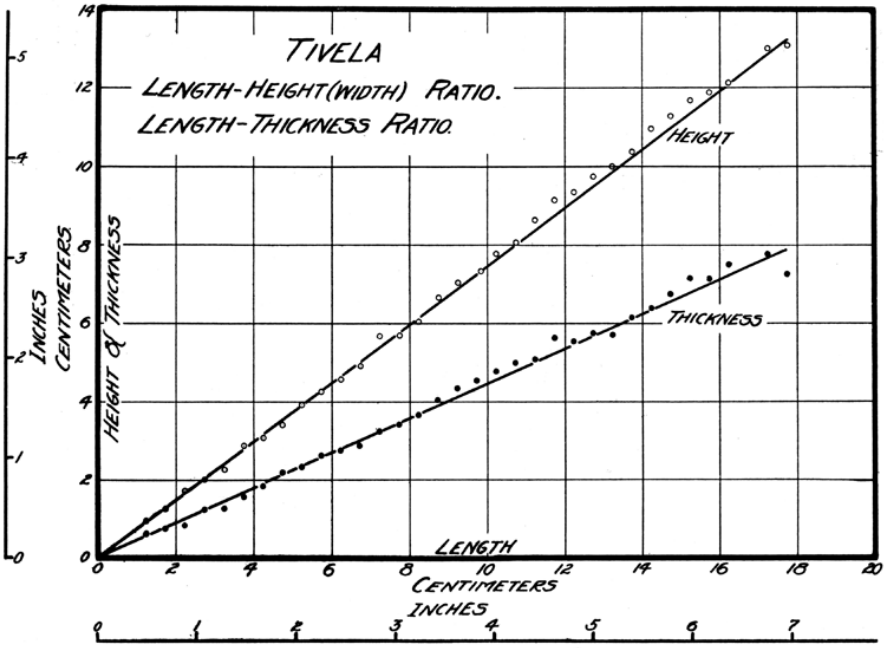


TABLE 20.

Tivela. Heights (Widths) and Thicknesses at Different Total Lengths.

Length, cm.	No. specimens	Height, cm.	Thickness, cm.	Height / Length	Thickness / Length
1.25	20	0.950	0.625	0.760	0.500
1.75	29	1.267	0.750	0.724	0.428
2.25	20	1.715	0.836	0.762	0.372
2.75	21	2.010	1.250	0.731	0.455
3.25	27	2.268	1.269	0.698	0.391
3.75	21	2.881	1.582	0.768	0.422
4.25	21	3.082	1.822	0.726	0.429
4.75	19	3.408	2.197	0.718	0.462
5.25	23	3.914	2.315	0.745	0.442
5.75	33	4.265	2.614	0.742	0.457
6.25	33	4.582	2.750	0.733	0.440
6.75	24	4.921	2.883	0.729	0.428
7.25	28	5.692	3.231	0.785	0.446
7.75	20	5.700	3.417	0.736	0.442
8.25	24	6.066	3.686	0.746	0.447
8.75	15	6.683	4.050	0.764	0.463
9.25	14	7.071	4.357	0.764	0.471
9.75	10	7.350	4.550	0.754	0.467
10.25	12	7.792	4.792	0.759	0.467
10.75	9	8.084	4.805	0.752	0.447
11.25	10	8.650	5.100	0.769	0.453
11.75	9	9.150	5.638	0.778	0.479
12.25	29	9.336	5.542	0.761	0.452
12.75	38	9.738	5.750	0.763	0.451
13.25	22	10.045	5.716	0.758	0.431
13.75	23	10.380	6.141	0.755	0.446
14.25	28	10.964	6.393	0.769	0.448
14,75	15	11.280	6.750	0.764	0.457
15.25	15	11.683	7.150	0.766	0.469
15.75	12	11.875	7.125	0.754	0.452
16.25	3	12.125	7.500	0.747	0.461
17.25	2	13.000	7.750	0.754	0.449
17.50	3	13.083	7.250	0.737	0.408
Total	640				
Mean				0.746	0.442
P. E. mean				0.0022	0.0028

Table 20.
Tivela. Heights (Widths) and Thicknesses at Different Total Lengths



GRAPH 10. Showing the height and thickness of *Tivela* for each length.

Graph 10. Showing the height and thickness of Tivela for each length

3.47. Weight-length relationship

From the preceding facts it might be expected that the weight would vary directly as the cube of the length (or height or thickness) as has been found to be the case in many animals, for instance in the edible crab (Weymouth, 1918, p. Q85), or in the various species of fish discussed above. Such a relation does in general hold, but far from exactly. If at the various lengths the ratio [weight / length^3] is determined it will be found that this is not constant but increases with increase in length, indicating that the weight increases at some faster rate, that is, as some higher power than the cube. An exact determination of this relationship, to be treated more in detail elsewhere, shows that the length must be raised to the 3.157 power to give a constant, or to express as a formula: weight (is grams) = .168 X length (in cm.)$^{3.157}$

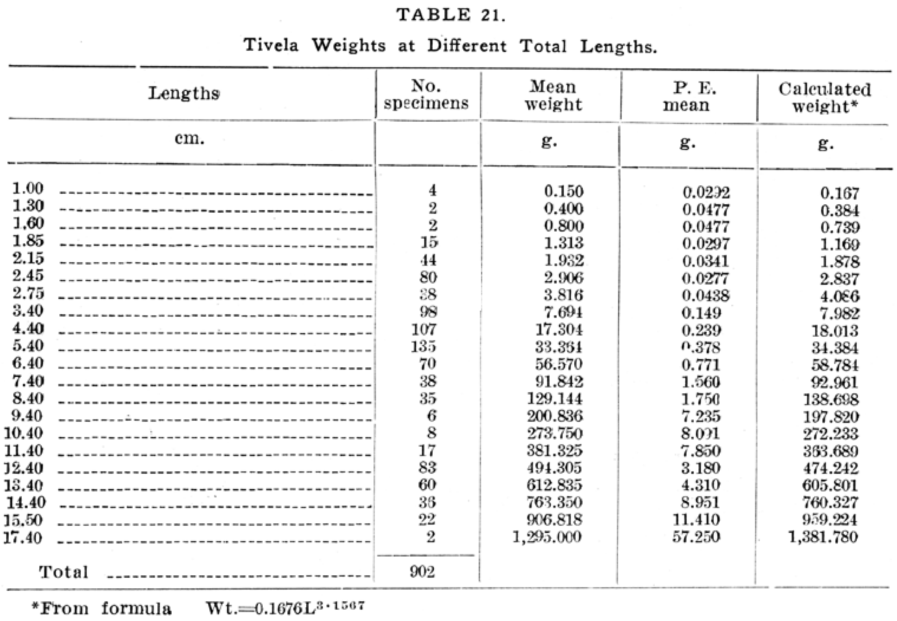


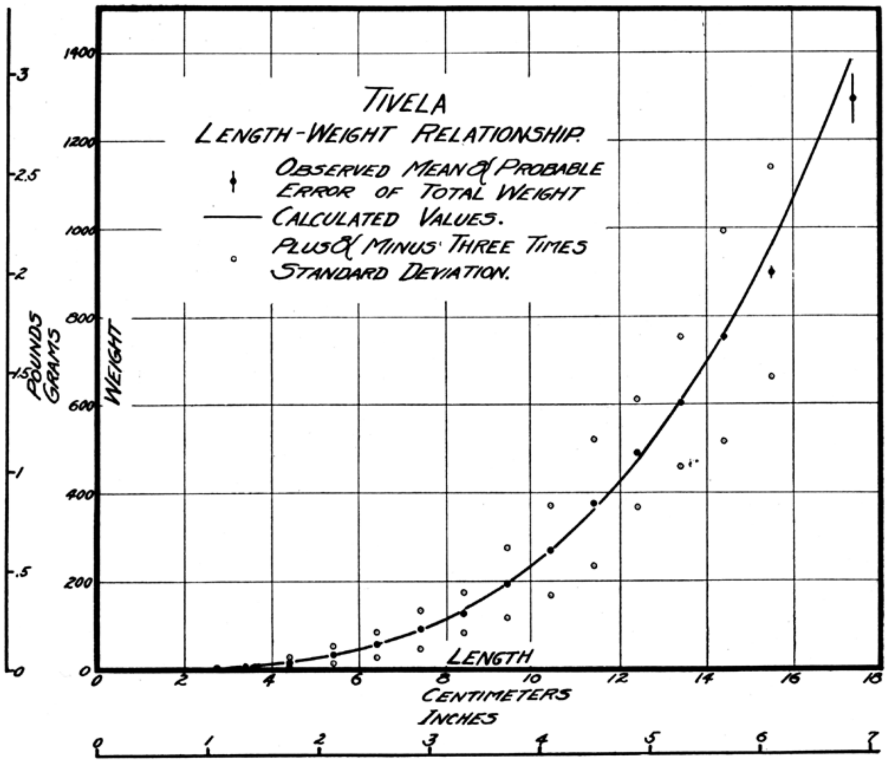
TABLE 21.

Tivela Weights at Different Total Lengths.

Lengths	No. specimens	Mean weight	P. E. mean	Calculated weight*
cm.		g.	g.	g.
1.00	4	0.150	0.0292	0.167
1.30	2	0.400	0.0477	0.384
1.60	2	0.800	0.0477	0.739
1.85	15	1.313	0.0297	1.169
2.15	44	1.932	0.0341	1.878
2.45	80	2.906	0.0277	2.837
2.75	38	3.816	0.0438	4.086
3.40	98	7.694	0.149	7.982
4.40	107	17.304	0.239	18.013
5.40	135	33.354	0.378	34.384
6.40	70	56.570	0.771	58.784
7.40	38	91.842	1.560	92.961
8.40	35	129.144	1.750	138.698
9.40	6	200.836	7.235	197.820
10.40	8	273.750	8.091	272.233
11.40	17	381.325	7.850	363.689
12.40	83	494.305	3.180	474.242
13.40	60	612.835	4.310	605.801
14.40	36	763.350	8.951	760.327
15.50	22	906.818	11.410	959.224
17.40	2	1,295.000	57.250	1,381.780
Total	902			

*From formula Wt.=$0.1676L^{3 \cdot 1567}$

Table 21.
Tivela Weights at Different Total Lengths



GRAPH 11. Showing the total weight of *Tivela* for each length. The solid points represent the mean weights; the solid line the curve fitted to these observations; the open circles the extremes of weight for each length as determined by three times the standard deviation above and below the mean.

Graph 11. Showing the total weight of Tivela for each length. The solid points represent the mean weights; the solid line the curve fitted to these observations; the open circles the extremes of weight for each length as determined by three times the standard deviation above and below the mean

3.48. Weight at each length

In Table 21 are presented the mean weights of clams of each length based upon 902 specimens and these same data are shown in Graph 11. The points in the graph represent the mean weights and the range of weight determined (as in Graph 7) by adding three times the standard deviation to the mean for the heaviest and subtracting a like amount for the lightest. The line represents the relationship expressed by the formula above and it will be seen that its agreement with the mean weights is very good except in the largest sizes where the number of specimens is so small that it is difficult to tell whether the lack of agreement is accidental or systematic. The mean weights of the shell are similarly represented in Table 22 and Graph 12. It will be seen that roughly 75 per cent of the total weight is furnished by the shell so that this becomes the dominant factor in all questions of weight. The shell is very dense, having a mean specific gravity of 2.41 (13 small specimens, determined fresh).

From the above relationships it is evident that some dimension, probably of the shell, since this practically determines the weight, increases much more rapidly than do length, height, or thickness. The thickness of the individual valves is the only other dimension involved, but no extensive series of measurements of this have been attempted as it proved a difficult one to obtain with accuracy, and was not, of

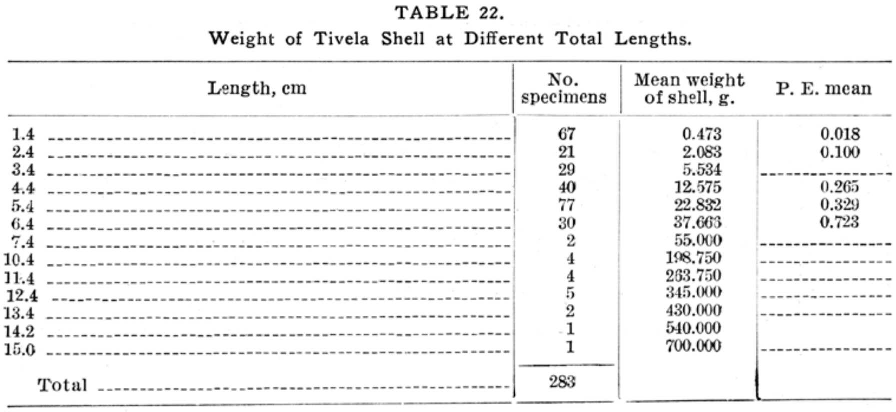
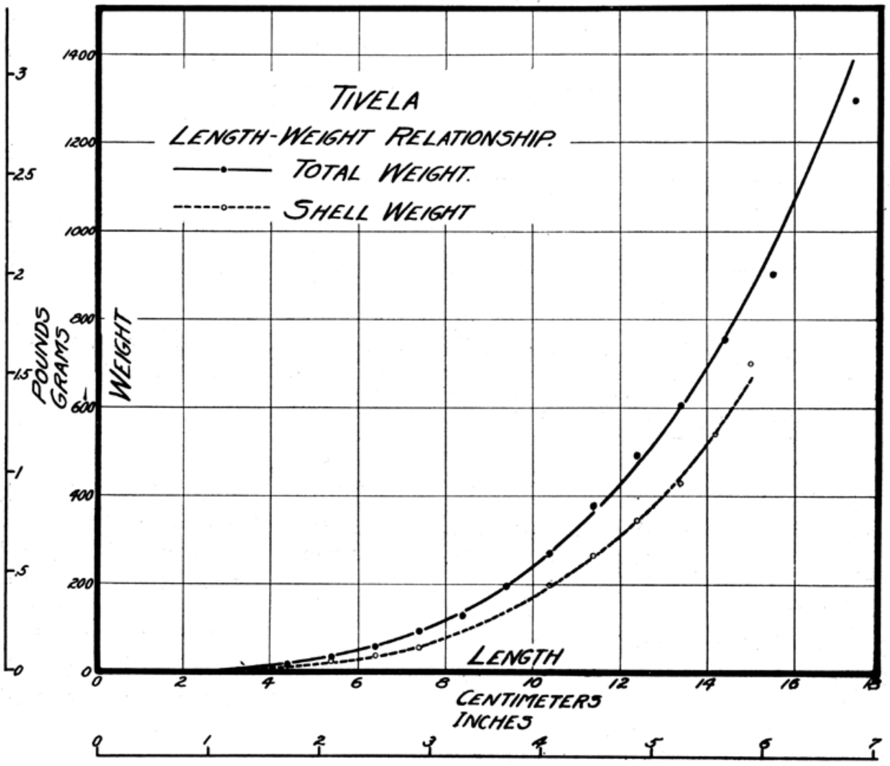


TABLE 22.

Weight of Tivela Shell at Different Total Lengths.

Length, cm	No. specimens	Mean weight of shell, g.	P. E. mean
1.4	67	0.473	0.018
2.4	21	2.083	0.100
3.4	29	5.534	-----
4.4	40	12.575	0.265
5.4	77	22.832	0.329
6.4	30	37.663	0.723
7.4	2	55.000	-----
10.4	4	198.750	-----
11.4	4	263.750	-----
12.4	5	345.000	-----
13.4	2	430.000	-----
14.2	1	540.000	
15.0	1	700.000	-----
Total	283		

Table 22.
Weight of Tivela Shell at Different Total Lengths



GRAPH 12. Showing the weight of the shell of *Tivela* for each length. (The mean total weight is repeated from Graph 10.)

Graph 12. Showing the weight of the shell of Tivela for each length. (The mean total weight is repeated from Graph 10.)

course, available in the live adults measured in the commercial catch. An examination of a few specimens indicates that the thickness of the individual values increases markedly in the larger shells. As may be seen from Fig. 11, in which outlines of sections of a large and a small shell are reduced to the same size for comparison, all parts except those near the margin are thicker in the larger shell, and this is particularly true of the hinge teeth and the region about the umbo. In this difference of shell thickness undoubtedly lies the explanation of the deviation of the length-weight ratio from the simple cubic relationship commonly found.

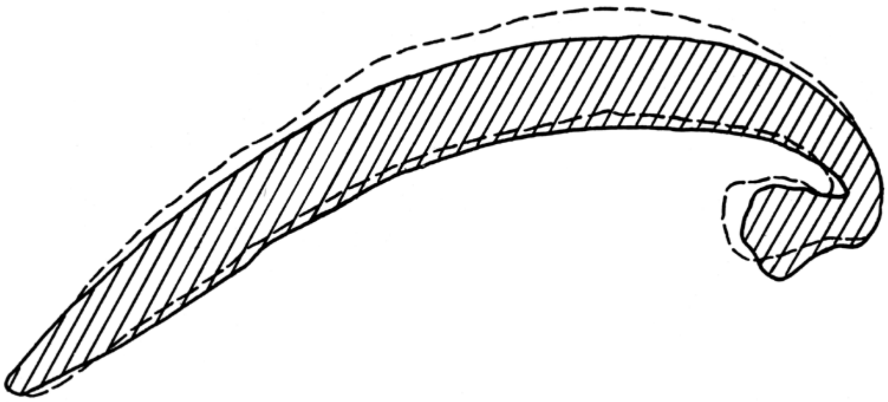


FIG. 11. Sections of old and young *Tivela* shells reduced to same size for comparison. Shaded outline, section of young *Tivela* in second summer, measuring 4.39 cm. (along line of section). Dotted outline, section of *Tivela* with seven rings measuring 9.39 cm.

FIG. 11. Sections of old and young Tivela shells reduced to same size for comparison. Shaded outline, section of young Tivela in second summer, measuring 4.39 cm. (along line of section). Dotted outline, section of Tivela with seven rings measuring 9.39 cm

3.49. Weight at each age

The course of growth in weight is presented in Table 23 and Graph 13, in which the weight at each age is shown. It should be compared with Graph 7, in which the age scale is the same. The weights have been derived from the lengths plotted in Graph 7 by the use of the formula given above; the points representing the weights have been calculated from the actual mean lengths and the solid line represents the conversion of the smoothed line of Graph 7 into weights.

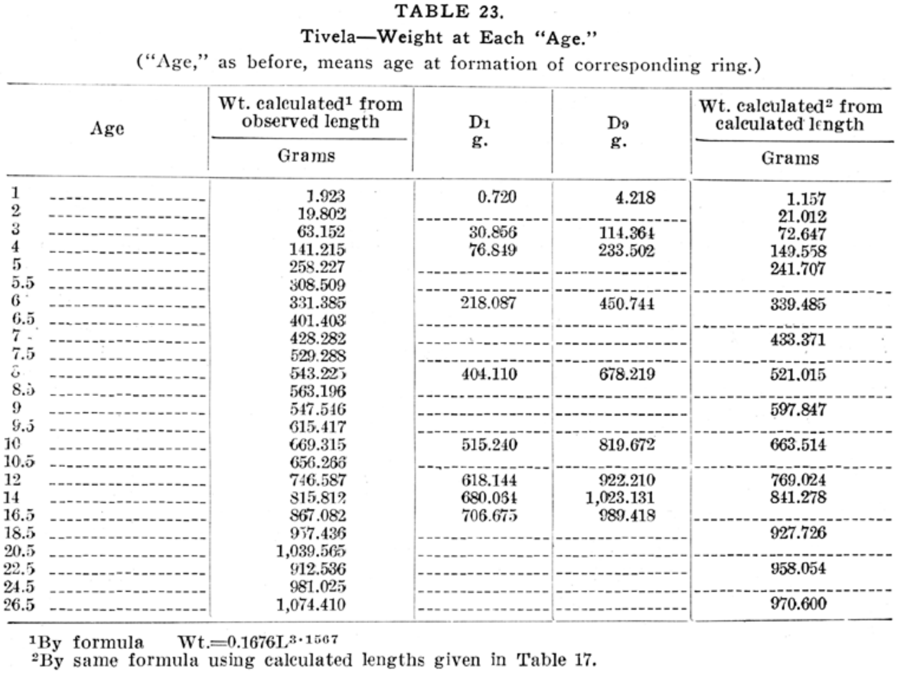


TABLE 23.

Tivela—Weight at Each "Age."

("Age," as before, means age at formation of corresponding ring.)

Age	Wt. calculated[1] from observed length	D_1 g.	D_9 g.	Wt. calculated[2] from calculated length
	Grams			Grams
1	1.923	0.720	4.218	1.157
2	19.802	-----	-----	21.012
3	63.152	30.856	114.364	72.647
4	141.215	76.849	233.502	149.558
5	258.227	-----	-----	241.707
5.5	308.509	-----	-----	-----
6	331.385	218.087	450.744	339.485
6.5	401.403	-----	-----	-----
7	428.282	-----	-----	433.371
7.5	529.288	-----	-----	-----
8	543.225	404.110	678.219	521.015
8.5	563.196	-----	-----	-----
9	547.546	-----	-----	597.847
9.5	615.417	-----	-----	-----
10	669.315	515.240	819.672	663.514
10.5	656.266	-----	-----	-----
12	746.587	618.144	922.210	769.024
14	815.812	680.064	1,023.131	841.278
16.5	867.082	706.675	989.418	-----
18.5	957.436	-----	-----	927.726
20.5	1,039.565	-----	-----	-----
22.5	912.536	-----	-----	958.054
24.5	981.025	-----	-----	-----
26.5	1,074.410	-----	-----	970.600

[1] By formula Wt.$=0.1676L^{3.1567}$

[2] By same formula using calculated lengths given in Table 17.

Table 23.
Tivela—Weight at Each "Age."
("Age," as before, means age at formation of corresponding ring.)

Graph 13. Showing the weight of Tivela for each age up to 26 years. Compare with Graph 7, showing length in the same manner

It will be noted that in this mode of representation, the growth (here in terms of weight instead of length) proceeds less rapidly at first than later, reaching its maximum at about six years, whereas when length is the criterion it is most rapid at the first point at which it can be determined, one year. The curve also continues to rise as far as 26 years rather more steeply than was the case with length. The relation to legal size is also interesting. Stated in terms of length, the clam of legal size (4 ¾ in.) is considerably over half the size of the greatest length recorded for any age, while in terms of weight it is distinctly less than half the weight of a 16-year old clam. This is but another way of emphasizing the greater food value of the larger individuals and the desirability of reserving the stock to be taken until it has reached a period where the yearly addition to bulk has begun to fall off materially. The heaviest clam observed weighed 3 lbs. 2 ½ oz. (1.415 kg.), measured 17.75 cm. (almost 7 in.) in total length and was 18 years of age.* Clams of over four pounds are reported by the fishermen; two were stated to have weighed 4 lbs. 3 oz. (1.89 kg.) and 4 lbs. 1 ½ oz. (1.858 kg.)

4. BREEDING HABITS

A knowledge of the breeding habits of the adult and of the mortality of the larvae and young is obviously of prime importance in any economic species; in a slow-growing form like the Pismo clam, living in a habitat particularly exposed to unusually destructive influences, this is doubly true. No data concerning the breeding habits in this species have been reported beyond some preliminary notices by Heath (1913, 1916). The same may be said concerning most other west coast species of bivalves. Stafford has recorded the dates of the spawning of the oyster in British Columbia for the years 1912 to 1916 inclusive (1917, p. S103), and these with one exception fall in May. That these dates can not be carried over to another species is shown by the observations of Edmondson on Oregon forms (1920, 1922) in which dates for various species were found to range from February to September. None of these forms are, however, closely related to Tivela, so that little can be inferred from these results.

4.1. Source of data on breeding habits

With the intention of determining the breeding season and clearing up related questione, a considerable number of adults were examined over a period of two years. Unfortunately the data are not as conclusive as might be wished, due to several causes. In the first place the adults available for study came chiefly from the catches of commercial diggers, as previously stated, and since these were restricted by small bag limits and many of their shipments were promised to regular customers, it was sometimes difficult to obtain sufficient numbers for examination. Where canning or other similar operations are in progress, material for examination may be obtained without loss to the canners, but where the clams are shipped alive to the markets, as is exclusively the case with the Pismo clam, this is not true. Satisfactory examination requires a compound microscope and laboratory conditions, and most of the records are from specimens collected and shipped by Mr. J. A. Beckett of Oceano, to whose hearty cooperation, as elsewhere acknowledged, the writer is greatly indebted.

4.2. Both eggs and sperm produced in same gonad

A number of observations were made before it was found that the Pismo clam was hermaphroditic, producing eggs and sperm from the same gonad. This condition is stated to be unusual among the bivalves, although it has long been known among some species of oysters and certain other forms, as the scallop. Edmondson states that of the Oregon species examined by him, the cockle (Cardium corbis) is along hermaphroditic (1920, p. 197). Several forms of hermaphrodism are found

---

* The writer wishes to acknowledge the courtesy of Mr. G. A. Johnson of Oceano, in sending him this specimen.

among the mollusks, in some the production of sperm occurring at one age or season of the year and the production of eggs at another, in some there are separate ovaries and spermaries, while in others there is a mixed gonad. Edmondson figures such a mixed gonad in Cardium, adjacent follicles producing eggs and sperm. No careful histological examination has been made, but from study of fresh specimens it appears that the gonad is also mixed in the case of Tivela, material from all parts of the visceral mass showing both eggs and sperm. The coexistence of mature eggs and active sperm, though observed, is by no means the rule. When large numbers of mature eggs are present, active sperm are seldom or never encountered. When active sperm are abundant a few mature eggs are usually seen but these are apparently remnants of a preceding crop of eggs which were not extruded at the previous spawning. That eggs and sperm are produced in succession is indicated by the fact that the eggs encountered with large numbers of motile sperm usually show retrogressive changes such as the formation of large oil droplets which are often associated with resorption of eggs in other species.

4.3. Size and number of eggs

The eggs are small, measuring on the average when mature .07 mm. (about 1/350 of an inch) though a few have been encountered as large as .1 mm. In consequence, the numbers are enormous, even exceeding those recorded for the oyster. A few calculations of the number were made in the following manner. The visceral mass was cut open and the eggs (which in the cases selected ran fairly freely) were scraped into a small graduate and the volume measured. This method would of course include ovarian tissue and immature eggs and sperm, and thus give too large a volume. Microscopic examination indicates that this error would not be great. On the other hand, it was impossible to remove all of the eggs, so that these sources of error tend to offset each other. From the known diameter of the eggs as measured by an eyepiece micrometer the volume was caluculated, and the total volume of the eggs divided by that of a single egg gave the total number of eggs. The most serious error comes from disregarding the space between the eggs which because of their shape will not "pack" without some loss. Theoretically this loss amounts to between 25 and 26 per cent; rough determinations of the amount of water taken up by fine dry shot give a percentage of approximately 30. In the following table the calculated results have been reduced from the maximum figure by 30 per cent to allow for this source of error and the totals are presented in round numbers. Even thus reduced it will be seen that the three specimens average 75,000,000

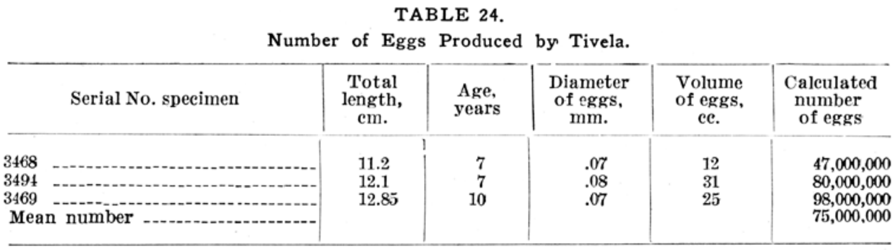


TABLE 24.

Number of Eggs Produced by Tivela.

Serial No. specimen	Total length, cm.	Age, years	Diameter of eggs, mm.	Volume of eggs, cc.	Calculated number of eggs
3468	11.2	7	.07	12	47,000,000
3494	12.1	7	.08	31	80,000,000
3469	12.85	10	.07	25	98,000,000
Mean number					75,000,000

Table 24. Number of Eggs Produced by Tivela

eggs apiece, a figure approaching the present population of the United States. It will also be noted that the smallest specimen had by far the smallest number of eggs, a fact serving to emphasize the importance of the larger and older individuals as breeders. For purposes of comparison Table 25 has been prepared, including similar data on three other bivalves in which the eggs have been studied. It is interesting to note that the Pismo clam exceeds in fecundity the oyster, the quahaug, and the scallop. It is probable that this fact is associated with the greater hazard to which the eggs and larvae are exposed, as it alone of the four species is found exclusively on beaches directly exposed to the ocean. In egg size it is seen to be intermediate between the scallop and the quahaug, though it must be remembered that this is subject to much variation and individuals are found in which the average egg size is considerably above or below these figures.

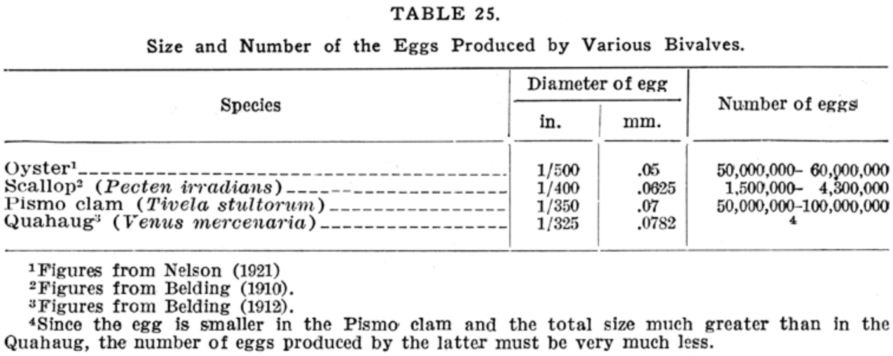


TABLE 25.

Size and Number of the Eggs Produced by Various Bivalves.

Species	Diameter of egg		Number of eggs
	in.	mm.	
Oyster[1]	1/500	.05	50,000,000– 60,000,000
Scallop[2] (*Pecten irradians*)	1/400	.0625	1,500,000– 4,300,000
Pismo clam (*Tivela stultorum*)	1/350	.07	50,000,000–100,000,000
Quahaug[3] (*Venus mercenaria*)	1/325	.0782	[4]

[1] Figures from Nelson (1921)

[2] Figures from Belding (1910).

[3] Figures from Belding (1912).

[4] Since the egg is smaller in the Pismo clam and the total size much greater than in the Quahaug, the number of eggs produced by the latter must be very much less.

Table 25. Size and Number of the Eggs Produced by Various Bivalves

4.4. Spawning season

Let us turn now to the data bearing on the spawning season. These are presented in the following table (26) in which are shown for each date the number of specimens examined, the number having eggs that could be measured, and the sizes of eggs as determined by an eyepiece micrometer under the microscope. The number of small eggs is inadequately represented; some immature eggs were generally present but only those of such size as to indicate possible maturity during the current or next following season were measured. During August, 1921, when about half of the specimens examined had spawned their eggs, the average size of the eggs in the others, which from appearance were judged to be ripe, was slightly over .07 mm. which we have therefore assumed as the size at maturity. It will be seen that with one exception all the diameters recorded for the large eggs do not differ significantly from this although the records cover all the year except December, January and February. From this we must infer an extended spawning season, or at least that in one locality many specimens are in readiness to spawn over a period of approximately six months. It has been shown repeatedly in the oyster that the onset of spawning is due to a rise in the water temperature (for example, Nelson, 1921a, p. 9) and the same was found true by Belding in the case of scallop (1910, p. 21, 22) and the quahaug (1912, p. 15, 16). It may well be that in the present case sex products are matured some time before the actual spawning season which might vary from year to year with the temperature conditions.

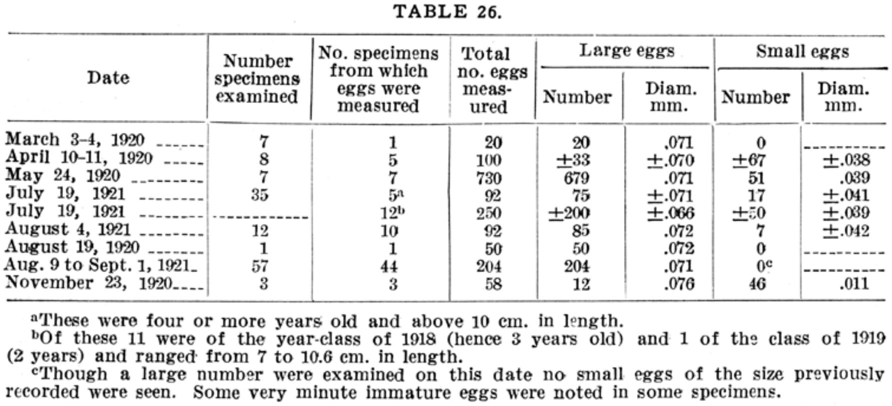


TABLE 26.

Date	Number specimens examined	No. specimens from which eggs were measured	Total no. eggs meas-ured	Large eggs		Small eggs	
				Number	Diam. mm.	Number	Diam. mm.
March 3-4, 1920	7	1	20	20	.071	0	----------
April 10-11, 1920	8	5	100	±33	±.070	±67	±.038
May 24, 1920	7	7	730	679	.071	51	.039
July 19, 1921	35	5[a]	92	75	±.071	17	±.041
July 19, 1921	----------	12[b]	250	±200	±.066	±50	±.039
August 4, 1921	12	10	92	85	.072	7	±.042
August 19, 1920	1	1	50	50	.072	0	----------
Aug. 9 to Sept. 1, 1921	57	44	204	204	.071	0[c]	----------
November 23, 1920	3	3	58	12	.076	46	.011

[a] These were four or more years old and above 10 cm. in length.

[b] Of these 11 were of the year-class of 1918 (hence 3 years old) and 1 of the class of 1919 (2 years) and ranged from 7 to 10.6 cm. in length.

[c] Though a large number were examined on this date no small eggs of the size previously recorded were seen. Some very minute immature eggs were noted in some specimens.

Table 26

An alternative interpretation would be that of two spawning seasons during the year, as claimed by Edmondson in the case of Paphia staminea (1920, p. 195). Since his record of spring spawning is from one part of the Oregon coast and that of late summer from a different part, they would appear to require confirmation. In the present case the writer, for reasons soon to be given, does not think two seasons probable.

In the material of March, April and May, though from their size and appearance the eggs were thought mature, no individuals were encountered that appeared to be "spent," that is, to have extruded the eggs. The collection of July 19 contained two or three "spent" individuals, that of August 4 about one-third "spent" specimens, while by the latter part of August one-half had clearly spawned and the few examined in November had all spawned. This would indicate that in 1921 spawning occurred during approximately two months, from the middle of July to the middle of September. Belding found (1912, p. 15) that the spawning season of the quahaug on the Massachusetts coast was of a similar length, extending from the middle of June to the middle of August, while Mactra solidissima, a form inhabiting, like Tivela, open beaches, spawned in June and July (1909).

It will also be noted from the table that the small eggs measuring about .04 mm. in the earlier collections disappear from the extensive material of late August and September to be replaced in those of November by much smaller, immature eggs measuring .01 mm. One would infer that the larger of the immature eggs had matured and been extruded and that the very small ones of November were destined to ripen in the following year.

We may, therefore, conclude that Tivela is an hermaphroditic mollusk producing eggs and sperm, probably successively, in immense numbers and extruding them during the late summer. We will now turn to a consideration of the larvae and young, from which we may get more light on the spawning season.

5. LARVAE

5.1. Larval life

Our knowledge of the larval life is a blank. Neither artificial fertilization, which waited the identification of the spawning season, or towing for the free-swimming larvae, difficult because of the exposed situations in which they must be sought, have been carried out. Judging from all the related forms the eggs and sperm are extruded and the fertilized eggs and the larvae into which they speedily develop are found at the surface of the water with other minute organisms collectively known as plankton. All free-swimming larvae are subject to a great mortality as the plankton serves as a source of food to a great variety of rapacious animals. In the case of the Pismo clam, in addition to this risk the loss from natural causes must be unusually great as the eggs and larvae may be swept out to sea or up and down the coast to localities unfitted to become the home of this exclusively sand-dwelling species. These losses must exceed those of species spawning in bays or estuaries less exposed to surf or currents and in which the bottom where the larvae first settle is less disturbed. This fact is, I believe, reflected in the enormous egg production and in the great variation encountered in the numbers of the young resulting from the spawnings of different years; a subject that will be discussed in detail later.

The length of the free-swimming period is not known. In the related quahaug of Massachusetts, Belding (1912, p. 23) puts the free-swimming period at from one to two weeks, depending upon the temperature of the water. The free-swimming period of the larvae of Mactra, a clam found on the Atlantic coast in a habitat comparable to Tivela, is stated by Belding to be about five days (1909). At the end of this time the larvae settle in the sand and soon assume the habits and appearance of the adult.

6. YOUNG

6.1. Habits of young

The subsequent growth of the young has been discussed; it remains to consider the habits and their significance. During the season of 1919 the young occurred in immense numbers and afforded an unusual opportunity for observation. When first reported they already averaged 1.55 cm. in total length though some individuals were as small as 1 cm. The larvae at the time of "setting" were therefore not met with, and during the two following seasons the young were so scarce that though an effort was made to obtain this stage it was not successful. Judging from their subsequent growth in 1919 the young must have settled in the sand during July, which agrees with the previous estimate of the breeding season.

6.2. Importance of byssus in young

As is well known some bivalves, for example the mussels, are supported on rocks exposed to the heaviest surf, by an attachement of fine threads called the byssus. Though present in most attached forms, as the mussels, and in some free forms, as the scallops, the adults of practically all burrowing species lack this structure. As has been shown for the soft clam (Mya) and the quahaug (*Venus*), the young of Tivela is for a time provided with a byssus. The method of formation and significance of this organ are discussed by Belding (1912, p. 27 *et seq.*) and much that he says applies with equal force to the present case.

The independent discovery of the byssus in the young of Tivela, Paphia, and Macoma, [*] here recorded, convinces the writer that its occurrence as a juvenile organ is much more common than usually supposed and that its importance for this stage of life is very great. Certainly it is of prime importance in the case of the Pismo clam. This will be apparent from a consideration of the habits of the young. Since the adult is found only on exposed sandy beaches, it is clear that the young that by chance settle in any different locality fail to survive and establish themselves. The successful young artist must, therefore, be adapted to life in loose sand. In the calmest of weather the surface sand of this typical habitat is in motion, and if the surf is even moderately active this motion extends downward to a depth of several inches and becomes violent, as one realizes when an attempt is made to set a stake for a temporary landmark in observing a particular locality, or even to stand quietly in one spot in the wash of the waves. With the exception of the larvae which might be left stranded by the crest of a high wave on a receding tide, all are exposed to this wave action during the greater part of the time. As the highest levels reached by the tide are without young, the larvae either do not settle here, or, if they do settle, fail to survive the long exposures between tides. The successful young must, therefore, maintain themselves in the constantly moving sand of a wave-beaten coast without the comparative quiet and shelter furnished by seaweed or gravel to most bay inhabiting forms. It is very difficult to see how these minute young clams, even though unusually active, could survive without the anchor of a byssus to maintain them in this unstable ground.

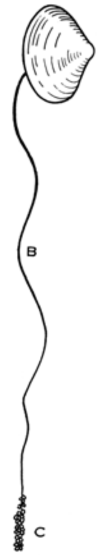


FIG. 12. Diagram of young Tivela with byssus. A, surface of sand. B, byssus with attached sand grains at C. Natural size

On September 11 to 13, 1919, the majority of the young were apparently furnished with byssi though in careless and hasty digging these were easily broken and passed unnoticed. If the young clams are carefully supported and the sand washed away it is possible to secure a complete byssus. The byssus thus obtained is seen to consist of a single unbranched fine amber-colored thread passing directly down into the sand and encrusted for about 5 mm. at the tip with sand grains either attached directly to it or to very short branches (Fig. 12). This anchor of sand grains will not permit it to be pulled through the surrounding packed sand and if force is exerted the byssus breaks; to obtain this portion requires very careful manipulation. The following measurements of length were made on the beach; clam 10 mm. long, byssus 55 mm. long; clam 12 mm., byssus 53 mm.; clam 16 mm., byssus 84 mm.; clam 17 mm., byssus 92 mm.; another byssus 45 mm.

---

[*] Young Paphia staminea of 4 to 5 mm. in length were observed to form byssus threads which were attached to the containing vessel or to other shells (May 19, 1919). Similar observations were made on young Macoma nasuta.

long was obtained from a clam of unrecorded length. It will be seen that the byssus averages a little over five times the length of the clam, and as the clam is usually buried about its own length this provides an anchor at a depth of from 7 to 11 cm. (3 to 4 in.) below the surface of the sand. The measurements represent the normal length; the thread is elastic and may easily be stretched to twice these lengths. Its strength is considerable, considering its minute size; if the animal is held up by the byssus it will support this weight readily and only breaks on a pull roughly double as great.

The efficacy of the byssus as an anchor was tested by digging carefully alongside individual clams until the waves undermined them. In these cases, although thrown back and forth by the waves, the byssus held each clam securely while it was again digging in.

As the clams increase in size the byssus disappears and on November 8 it was found that only the smallest clams, approximately 2 cm. in length were so provided. Apparently after this size the greater weight and power of burrowing must suffice to maintain them on the beach.

It will thus be seen that although the adult Tivela, like practically all true burrowing bivalves, is without a byssus, this structure constitutes an important juvenile organ by aid of which the unusual conditions of the normal habitat of this clam are successfully met.

6.3. Method of burrowing

The young clams burrow actively by means of the relatively enormous foot thrust between the slightly opened valves. Three specimens which were timed buried themselves in 20 seconds, and a fourth in 40 seconds, when placed on wet sand. The extent and appearance of the foot, which is very thin and ends in a knife-like point, is indicated in the accompanying sketch drawn to scale from life (Fig. 13). The young show the orientation already mentioned, always burrowing with the hinge toward the open sea.

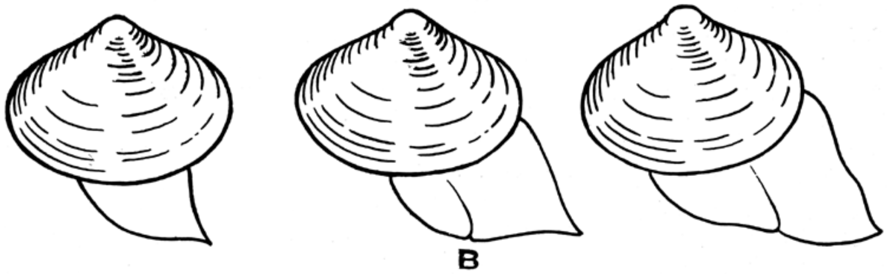


FIG. 13. Diagram of foot of young *Tivela* in three successive stages of extension during process of burrowing. B, byssal groove.

FIG. 13. Diagram of foot of young Tivela in three successive stages of extension during process of burrowing. B, byssal groove

6.4. Method of cross-sectioning and value of data obtained

The distribution of the young on the beach is very sharply defined and characteristic, a condition probably connected, as we shall see, with the transition from the larval to the post-larval habits of life. The data on this point may be briefly presented. As previously stated, the size of the small clams was found to vary across the beach so that a "cross-section" was required to give a fair sample of the population. This was obtained as follows. In the region selected for study (as stated, a point just north of the old wharf at Oceano) a trench was dug with a clam fork of known width from near

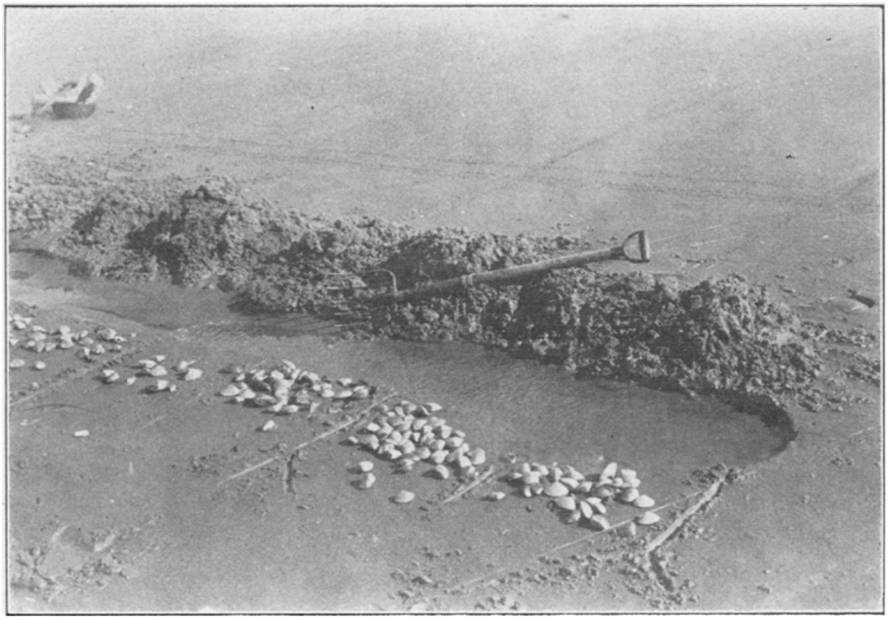


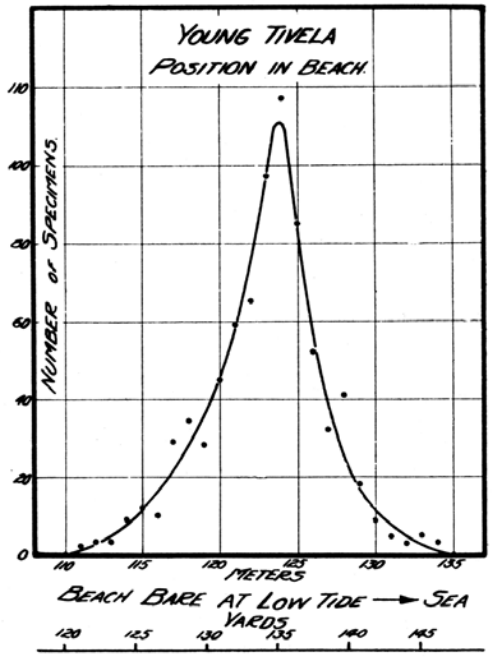
Fig. 14.

FIG. 14

the last high tide mark to a point as low as could be reached, which with an extreme low tide on the very gently sloping beach characteristic of this stretch of coast was often as much as 90 meters (98 yards) from the starting point. Each meter of the trench was marked off, all the sand thrown out and sorted and the young clams laid alongside the trench for counting. The appearance of a section of such trench is shown in Fig. 14. From the data thus obtained it is possible to show the relative abundance of the young of each year-class present at different levels on the beach, to study differences in size at these levels, to make a census of the actual numbers per mile of beach, and to attack a variety of important problems. We will consider first the relative abundance at different levels, and the differences in size, after which the data on the physical characteristics of this zone and their possible influence on the young will be taken up. Later the important question of the relative abundance of the young, of different year-classes, the enemies and the mortality of the young, will be treated in this order. The writer wishes to emphasize the unusual opportunity here presented for the study of a species under natural conditions. Since these clams are relatively stationary it is possible to estimate at any time from such a cross-section or series of cross-sections the actual number of animals present with an accuracy only exceeded in the case of domestic or confined animals, where the conditions are largely artificial, or with plants. For this reason a somewhat extended treatment of the results will be attempted, and it is hoped that certain phases of this study may in the future be followed out more in detail.

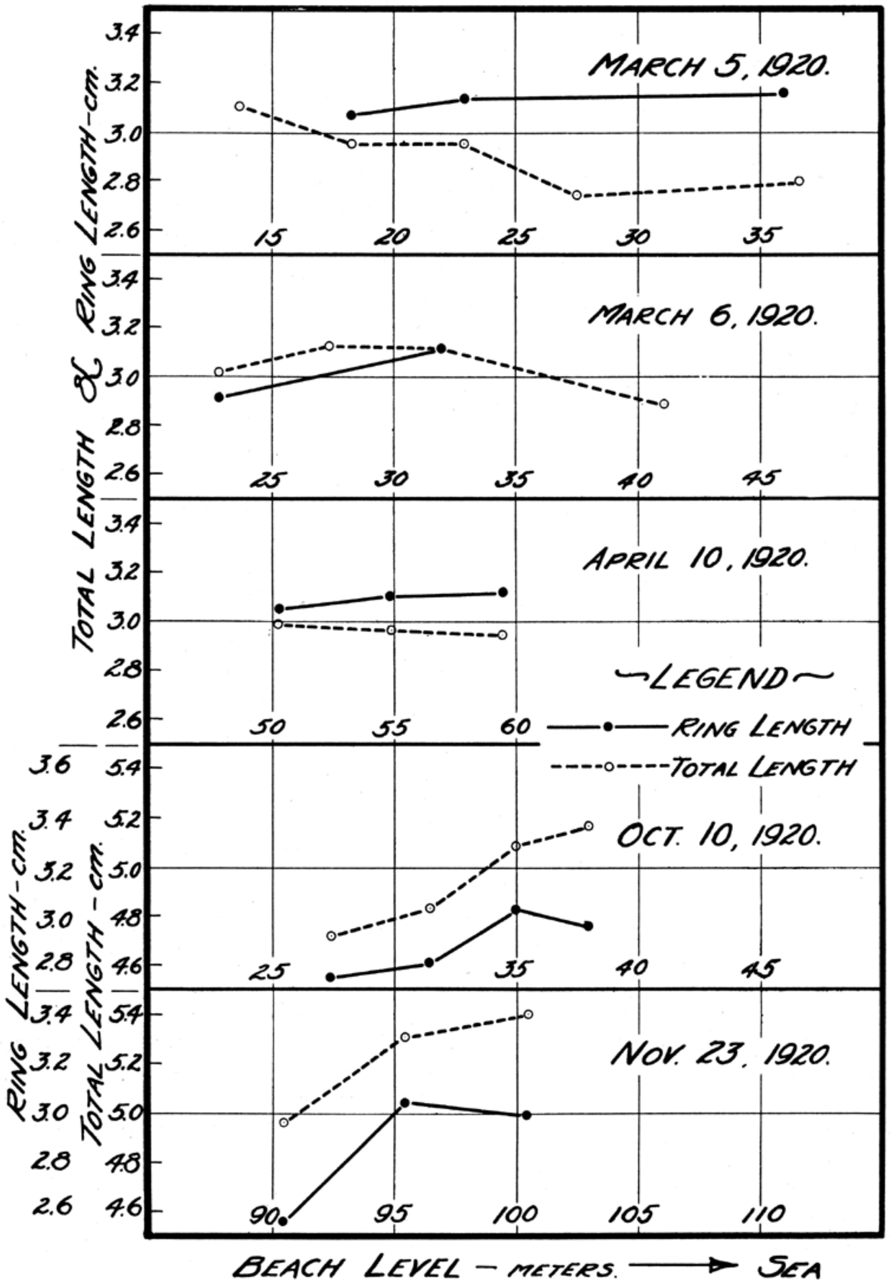
6.5. Distribution of young on beach

During a period of two years cross-sectioning was carried out on seven occasions. The general results obtained will be presented shortly (Table 29) , but first it is desirable to consider the distribution on the beach. In Graph 14 is shown the numbers of young clams obtained in each meter of such a trench one-quarter of a meter wide (a little less than 10 inches) in a typical case, that of November 23, 1920. The form of the other frequency curves is essentially similar. A word of explanation must be given concerning the levels on the beach which are not readily comparable on the different dates. No fixed datum is possible on these beaches where no landmark short of a well-driven pile can lay claim to permanency. In some cross-sections measurements were made from a small sand dune about 100 meters above high tide. This does not, however, obviate changes due to erosion or filling which on this gently shelving beach may alter the relation of high and low tide to such a dune. In most cases the datum was the level reached by the previous high tide. Though this varies with the particular tide, the surf, and other factors, it and the low water level, nevertheless, define an important biological region—the intertidal zone—and it is probably to the physical conditions characterizing this, that the distribution of the clam is related. The "peak" of the frequency curve just referred to falls near the center of the intertidal zone and the concentration about this point is very marked. This concentration is well shown by the figures of October 10. Here a trench 90 meters long was dug from the last high tide line as far into the water as it was possible to work. The first clam was encountered at 22 meters from high tide, the last at 84, so that 100 per cent were included in 62 meters. Cutting off 1 per cent from each end we find that the remaining 98 per cent are included between 24 and 46 meters, or in a space of 22 meters. Similarly, 90 per cent are found in 13 meters, 80 per cent in 10 meters, and 50 per cent in only 5 meters. In still deeper water no accurate census can be made.



Graph 14. Showing the numbers of young Tivela obtained at different levels on the beach

Occasional specimens are encountered but they amount to probably less than 1 per cent and are negligible. The striking fact is that the young of the Pismo clam is confined to the intertidal zone, and that 90 per cent are concentrated in a strip 13 meters wide (a little over 14 yards) at a level never deeply covered and exposed at nearly every tide. This situation is of the utmost significance in considering the question of mortality.



GRAPH 15. Showing the total lengths and ring-lengths of young *Tivela* at different levels on the beach on different dates.

Graph 15. Showing the total lengths and ring-lengths of young Tivela at different levels on the beach on different dates

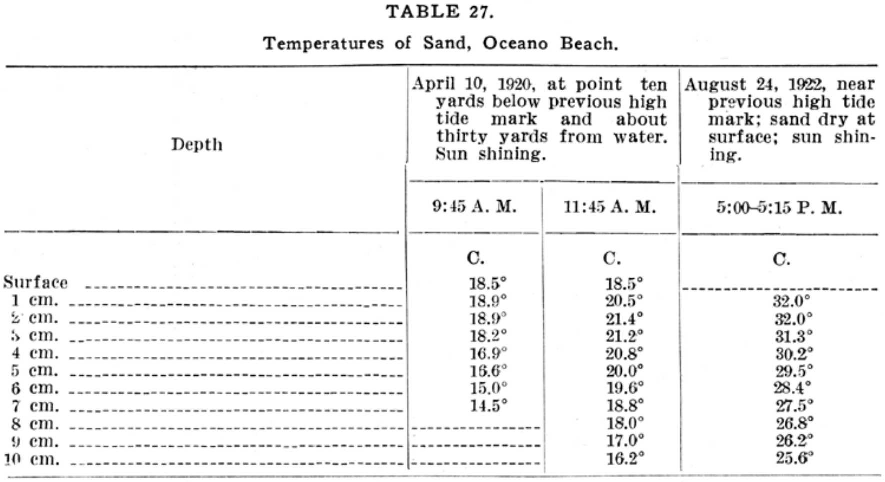
6.6. Physical conditions of habitat

Within this zone the sizes at different levels have been found to vary as previously shown in Table 4, p. 19. On the five occasions when this point was studied clams of the same age were sometimes found to be larger at the lower levels and sometimes at the higher levels. This appears from the data to be systematic rather than accidental. Let us consider the physical characteristics of this zone as contrasted with deeper water, to see whether they furnish the key to the limitations of distribution and the differences of size. The intertidal zone, as here encountered presents many interesting features, and merits more exact study than it has yet received. On the Pismo-Oceano beach it is populated by immense numbers of animals which, neglecting minute forms, consist almost wholly of Pismo and razor clams, two burrowing anomurans related to the crabs (Emerita and Blepharipoda) and some annelid worms (chiefly Glycera). All these forms are highly specialized and show peculiar though widely differing adaptations to the special conditions under which they live. These adaptations have been pointed out in some detail in the case of Emerita (Weymouth and Richardson, 1912). Certain features of the physical conditions which these animals encounter have been recorded by W. F. Thompson (1919) in connection with the breeding habits of the grunion, a small fish which lays its eggs in this zone on the beaches of southern California. The results which he obtained and the present observations indicate that a more detailed study of the physical characteristics of this zone in relation to its specialized fauna would be very profitable.

The highest levels are, of course, bare for too long a period for the clam to obtain the necessary water—this probably sets the upper limit. This zone, as a whole, differs from that at which the adults are now dug in commercial numbers (from two to four or five feet deep at low tide) by a greater variation in temperature and by an intermittent supply of water which probably carries more oxygen and more food.

TABLE 27.

Temperatures of Sand, Oceano Beach.



Depth	April 10, 1920, at point ten yards below previous high tide mark and about thirty yards from water. Sun shining.		August 24, 1922, near previous high tide mark; sand dry at surface; sun shining.
	9:45 A. M.	11:45 A. M.	5:00–5:15 P. M.
	C.	C.	C.
Surface	18.5°	18.5°	—
1 cm.	18.9°	20.5°	32.0°
2 cm.	18.9°	21.4°	32.0°
3 cm.	18.2°	21.2°	31.3°
4 cm.	16.9°	20.8°	30.2°
5 cm.	16.6°	20.0°	29.5°
6 cm.	15.0°	19.6°	28.4°
7 cm.	14.5°	18.8°	27.5°
8 cm.	—	18.0°	26.8°
9 cm.	—	17.0°	26.2°
10 cm.	—	16.2°	25.6°

Table 27.
Temperatures of Sand, Oceano Beach

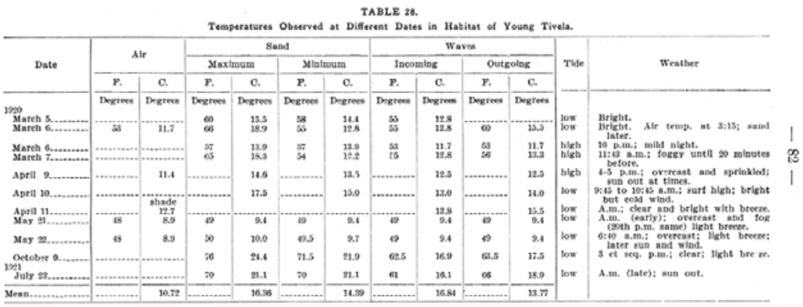


TABLE 28.

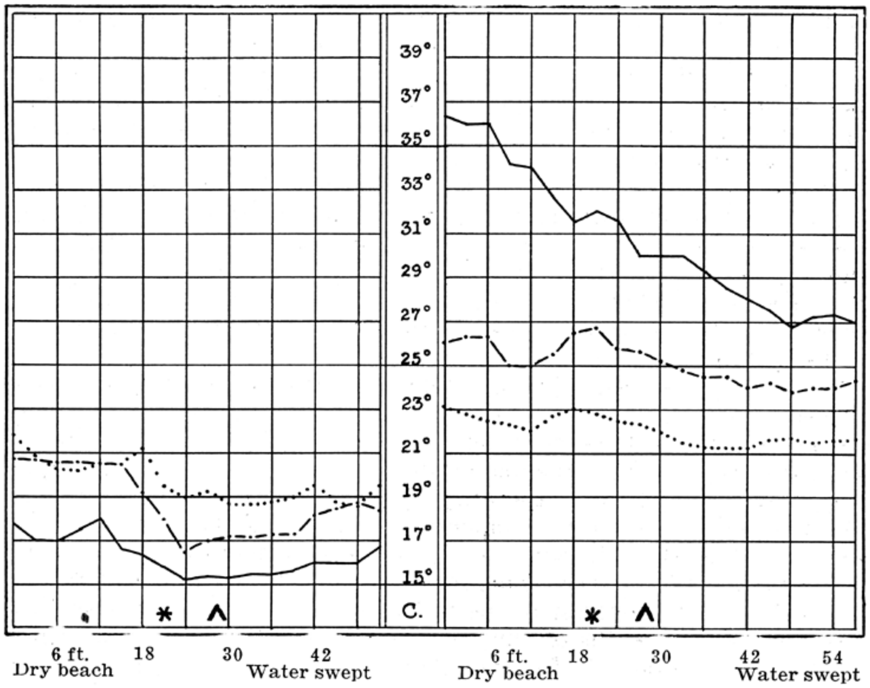
Temperatures Observed at Different Dates in Habitat of Young Tivela.

Date	Air		Sand				Waves				Tide	Weather
			Maximum		Minimum		Incoming		Outgoing			
	F.	C.	F.	C.	F.	C.	F.	C.	F.	C.		
	Degrees	Degrees	Degrees	Degrees	Degrees	Degrees	Degrees	Degrees	Degrees	Degrees		
1920												
March 5			60	15.5	58	14.4	55	12.8			low	Bright.
March 6	53	11.7	66	18.9	55	12.8	55	12.8	60	15.5	low	Bright. Air temp. at 3:15; sand later.
March 6			57	13.9	57	13.9	53	11.7	53	11.7	high	10 p.m.; mild night.
March 7			65	18.3	54	12.2	55	12.8	56	13.3	high	11:43 a.m.; foggy until 20 minutes before.
April 9		11.4		14.6		13.5		12.5		12.5	high	4-5 p.m.; overcast and sprinkled; sun out at times.
April 10				17.5		15.0		13.0		14.0	low	9:45 to 10:45 a.m.; surf high; bright but cold wind.
April 11		shade 12.7						13.8		15.5	low	A.m.; clear and bright with breeze.
May 21	48	8.9	49	9.4	49	9.4	49	9.4	49	9.4	low	A.m. (early); overcast and fog (20th p.m. same) light breeze.
May 22	48	8.9	50	10.0	49.5	9.7	49	9.4	49	9.4	low	6:40 a.m.; overcast; light breeze; later sun and wind.
October 9			76	24.4	71.5	21.9	62.5	16.9	63.5	17.5	low	3 et seq. p.m.; clear; light breeze.
1921												
July 23			70	21.1	70	21.1	61	16.1	66	18.9	low	A.m. (late); sun out.
Mean		10.72		16.36		14.39		16.84		13.77		

Table 28.
Temperatures Observed at Different Dates in Habitat of Young Tivela

6.7. Temperature

When the sun shines the sand becomes warm to the touch at the surface and this heating extends to a depth of several centimeters, as every one who has frequented the beach knows; below this, again, the sand feels cool. This is illustrated by a series of temperatures of the sand at different depths taken on April 10, 1920 (Table 27) . At 9:45 on a sunny morning the sand at a depth of 2 cm. had a temperature of 18.9° C. and at 4 cm. (about the depth at which the young clams are found) of 16.9° C. Two hours later the temperatures at these two depths had risen to 21.4° and 20.8° respectively. At greater depths the heating was approximately the same, 3°. At the surface the bulb of the thermometer was partially exposed to the air which was cooler than the sand and the recorded temperatures are too low, as was found by careful checking on a subsequent occasion. The still higher temperatures of a sunny afternoon at a somewhat higher level of the intertidal zone are illustrated by the figures of August 24, 1922. From Table 28 it will be seen that during the day the sand is warmer than the sea; the average difference of the observations is 3.6° C. and in one case the sand was 7.5° C. warmer.



GRAPH 16. Showing temperatures of beach across high tide line. Left hand of figure: 11 p.m. May 14, 1919. Air temperature 15.2° C. Water, 17.9° C. Two hours after high tide of 5.6 feet. Right hand of figure: 4:30 p.m. May 14, 1919. Air temperature 18.5° C. Water 24.0° C. Seven hours after high tide of 3.6 feet, seventeen hours after tide of 5.6 feet.

At surface: ———————
At three inches down: —.—.—.—
At six inches down: . . . .
Line of dry surface sand: *
Line of loose sand: Λ

Graph 16

The sand entirely covered by water has, of course, the temperature of the sea which shows little daily or seasonal variation when compared with the land. The sand at intermediate levels on a bright day shows intermediate temperatures, being heated by the sun and cooled by the waves. The waves are, in turn, warmed by the warmer sand. Such a series of sand temperatures at different levels on the beach are shown in Graph 16[*] . The surface temperatures in the afternoon of a warm day are represented by the solid line in the right hand half of the figure. The portion of the beach occupied by Tivela would be the outer third of the graph where the temperatures are the lowest.

The effect of the sand on the water is greater than might be expected. If the temperature of the ocean water, as far out as can be reached by wading, is compared with that of an incoming wave at a level sometimes covered and sometimes bare, the two will be found essentially the same. If, now, the temperature of the last part of the same wave is taken as it drains off the beach it will prove distinctly higher, showing a material warming during its contact with the warm sand. This effect could only occur on a wide beach where the wave is spread out in a thin layer and brought into contact with a large surface of warm sand. The amount of this heating is shown by Table 28 where the temperature of the outflowing wave exceeds that of the incoming wave by as much as 2.8° C. in some cases. Those occasions where no difference is shown are equally instructive, as they occur on overcast or foggy days or at night when there has been no opportunity for the sun to heat the sand.

Wesenberg-Lund (1912) has observed a similar higher temperature in the littoral region of the Baltic Sea, where, in the sun, he records a water temperature of 7° at a distance of less than a meter from the edge of the ice at a time when the air temperature was 0.5° C. He considers this high littoral temperature a general phenomenon of considerable biological importance, particularly in the hatching of eggs in the spring.

It will thus be seen that on bright days the young clam enjoys a temperature slightly but distinctly higher than that encountered by the average adult, a difference which as we have seen would favor more rapid growth. On the other hand, during cloudy weather or at night when there is wind the evaporation from the surface of the wet sand would materially lower its temperature. This may be noticed in the early morning when the sand feels warmer at a depth of a few centimeters than at the surface. This condition is well shown in the left half of Graph 16. In contrast to the temperatures in the day the surface is cooler than at depths of three or six inches, or than the sea water. No figures are available for the incoming and outgoing waves under these conditions, nor is it easy to say during what portion of the time this condition would prevail.

Though no exact evaluation of this factor is possible, it is clear that the young clam in the intertidal zone encounters a greater daily and seasonal variation of temperature than it would at a lower level and that this varies with the part of the zone in which the clam is found. In general it is probable that its growth here is more rapid than it would be at a lower level.

---

[*] Reproduced by permission from W. F. Thompson, (1919.)

6.8. Food and oxygen

The other factor of water supply must be considered. The small organisms which form the food of the clam, though found to a considerable depth in the sea are more numerous at the surface, and it is probable that the water thrown upon the beach is the richest that would be encountered. It is also plain that from the action of the surf the incoming wave contains as much oxygen as it will take up. In both these ways the situation would be favorable, but there is this to offset the advantage, that during part of the time the water does not reach the clams and therefore they are unable to feed. The most favorable position in the intertidal zone would seem to be at the lower levels as far as food is concerned. Accurate data on the question of food would be difficult to get, but again on the whole it seems probable that the natural habitat would be more favorable than the beach at a lower level.

From Table 4 or Graph 15 it is seen that the larger clams are found at the higher levels in the spring but at the lower in the fall. The explanation may be hazarded that in the early part of the year the higher temperature of the higher levels more than compensates for the shorter feeding time, but that later when the temperature of all locations is much higher the longer feeding periods of the lower levels give the clams an advantage that is reflected in a more rapid growth.

6.9. Reasons for position on the beach

We may conclude that the young occupy a zone different from, and in general more advantageous than, that in which the adult is now usually found. Why are they found here? Primarily, because this is the level at which the free-swimming larvae first reach the sand. They can not move far up the beach and survive, but the possibility of movement outward to deeper water seems unhindered. Though the Pismo clam is an active burrower, and some forms, as the razor clam, have been seen to move along at the surface, it is doubtful if in the present case there is much if any horizontal movement from their own activities. It is more probable that they are often washed out and again dig in, which would lead to a slow distribution downward from the level at which they settled. The adults are found predominantly at a lower level, but as we have seen, this is, in great part, the result of selective fishing. The bulk of the individuals may, under normal conditions, have remained in the intertidal zone while a small portion may have been scattered into deeper water by slow migration or by chance washing out. The young of the second and third years seem to occupy a position somewhat farther out than those of the first year, but whether this is due to selective mortality, or to migration, either active or passive, can not be established. The concentration of the class of 1919 seems to have become less marked with each season since spawning, which would also indicate a slow scattering downward.

6.10. Abundance of different year-classes

Turning from the physical conditions of the habitat of the young, let us consider the actual and relative abundance of the different year-classes. As already pointed out in discussing the growth of the young, the first two year-classes were easily recognized in collections. As soon as the young spawned in the summer of 1919 appeared, it was clear that they were far more numerous than those of the previous year (the class of 1918). On the other hand the young of the next two years proved scarce and difficult to obtain. In Table 29 are presented the results of the various cross-sections, showing the actual and relative numbers of each year-class present at the time of digging. The steady dominance of the class of 1919, comprising from 90 to 99 per cent, is the striking feature of these data. The class of 1918 comes next in importance, with from less than 1 to 9 per cent, while 1920, 1921, and 1922 are represented in most cases by a fraction of one per cent. The year-class of 1917, like these last three, must have been a failure, as very few specimens have ever been encountered.

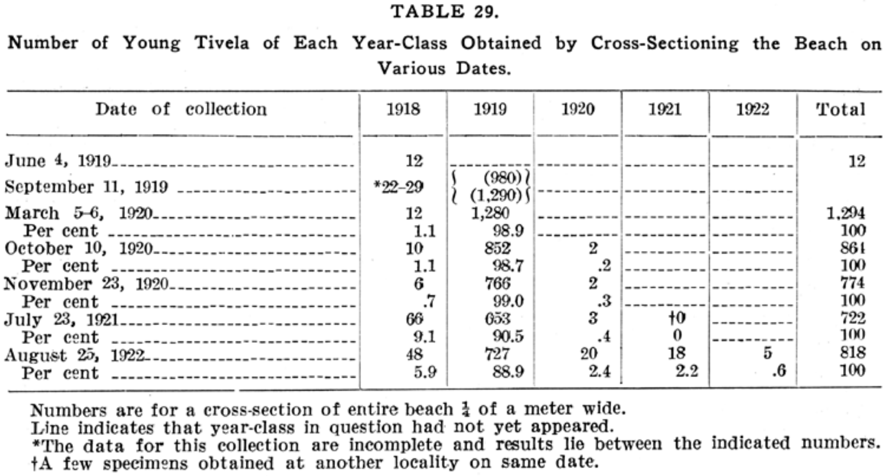


TABLE 29.

Number of Young Tivela of Each Year-Class Obtained by Cross-Sectioning the Beach on Various Dates.

Date of collection	1918	1919	1920	1921	1922	Total
June 4, 1919	12	—	—	—	—	12
September 11, 1919	*22-29	(980) (1,290)	—	—	—	
March 5-6, 1920	12	1,280	—	—	—	1,294
Per cent	1.1	98.9	—	—	—	100
October 10, 1920	10	852	2	—	—	864
Per cent	1.1	98.7	.2	—	—	100
November 23, 1920	6	766	2	—	—	774
Per cent	.7	99.0	.3	—	—	100
July 23, 1921	66	653	3	†0	—	722
Per cent	9.1	90.5	.4	0	—	100
August 25, 1922	48	727	20	18	5	818
Per cent	5.9	88.9	2.4	2.2	.6	100

Numbers are for a cross-section of entire beach ¼ of a meter wide.
Line indicates that year-class in question had not yet appeared.
*The data for this collection are incomplete and results lie between the indicated numbers.
†A few specimens obtained at another locality on same date.

Table 29. Number of Young Tivela of Each Year-Class Obtained by Cross-Sectioning the Beach on Various Dates

6.11. Total numbers of young

From these figures the writer has previously estimated the total numbers of young on the beach (Weymouth, 1921). These estimates may be here repeated with the addition of some later data. The productive area of the Pismo-Oceano beach is about eight miles in length; of this the northern end appears each year to receive the thickest "set" of young. The point at which the counts were made is not at the northern end but near the middle where the conditions may fairly be considered average. A conservative estimate of the population of the entire beach might be arrived at by considering that we are dealing with six miles of beach similar to that cross-sectioned. Since the trench was 25 cm., or a trifle less than 10 inches wide, each mile of the beach would contain from 4,000,000 to 8,000,000 clams (in round numbers), depending on whether the largest or the smallest count of 1919 young is used as the basis. Six miles would therefore represent from 25,000,000 to 48,000,000 clams. To this must be added the young on the beach at Morro which, though not examined with the exactness of the above, supports a hardly inferior fishery of adults and might double the above estimate.

These figures are almost incredible, but several facts show that they are not unreasonable. On one occasion while making a cross-section a graphic picture of the abundance of the young was encountered. The intertidal zone had been exposed for a long time by a very low tide and, due perhaps to this cause, the exact position of many of the clams could be made out. Above the siphons of some a tiny hole appeared; above many a slight mound was formed, and these in the area of greatest concentration mentioned above were so close as to touch one another. Not every clam was so represented, as we determined by digging, yet the mounds and, in the distance the roughened areas formed by them, stretching along the level beach as far as we could see, brought home to us in a vivid fashion the abundance of the young. A portion of the beach at this time is shown in Fig. 15.

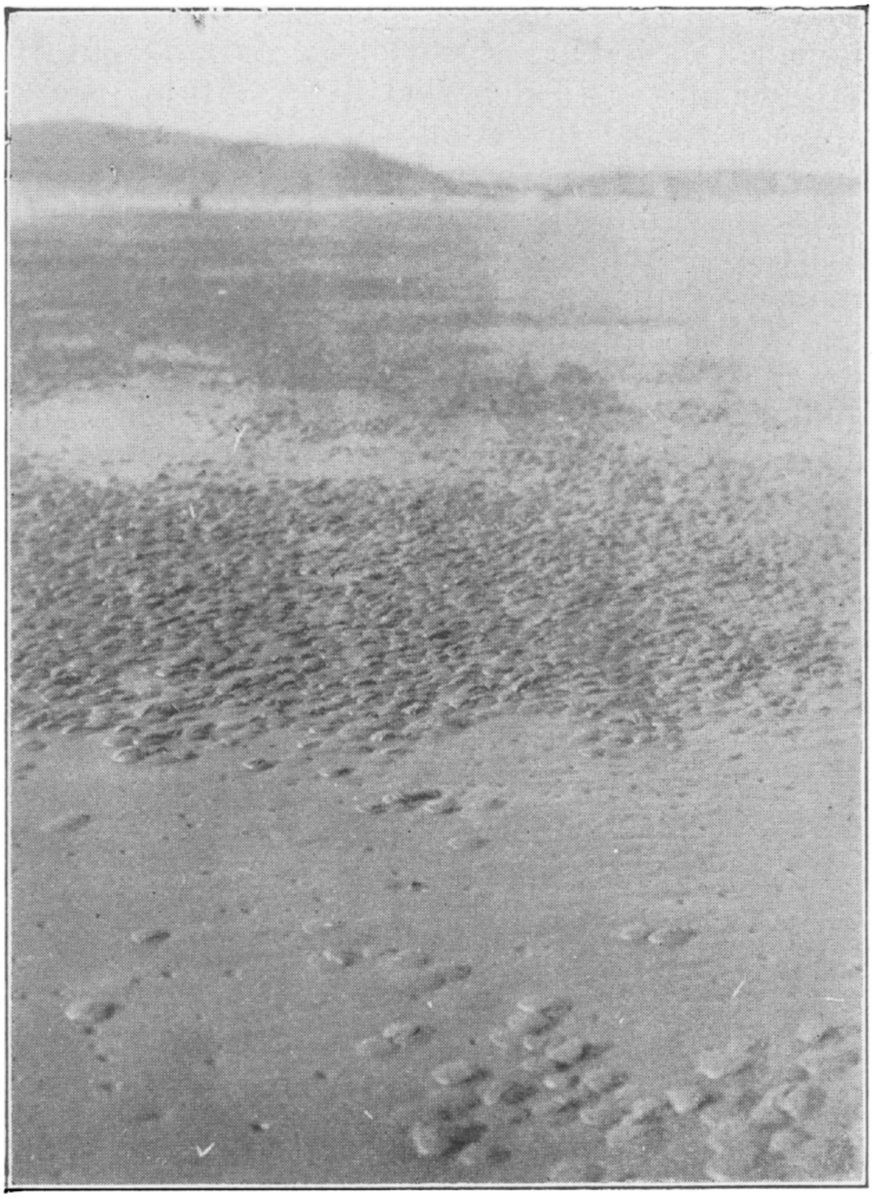


Fig. 15.

FIG. 15

The estimates indicate that there were approximately 50,000,000 young on the Pismo-Oceano beach in the fall of 1919, yet a single individual may produce more than this number of eggs, and the adults present on the beach would be capable of producing this number of young *under favorable conditions*. Or, to approach the question from a different angle: during the past six years we have records of the shipment of over 2,200,000 pounds of adult clams dug from the beaches at Pismo and Oceano and Morro, which at an average weight of one and one-third pounds apiece would mean over 1,600,000 individuals, and to these should be added those used locally. To support a fishery of this magnitude the number of young must be enormous.

6.12. Causes of variations in abundance

A consideration of the data just presented would naturally raise a variety of questions; what caused such great variation in the success of the various spawning years? Has this variation occurred in the past? What effect will this variation have on the future of the fishery? The causes of these fluctuations would be difficult to determine in detail but their general nature may be pretty closely surmised. They are not a direct reflection of changes in the abundance of adults, for if they had been reduced to a mere handful in 1917 and 1918 they could not have been restored to immense numbers in 1919 to disappear again in 1920 and 1921. We have previously pointed out that the larval stage is an unusually critical period in the life of this clam and that this fact appears to be correlated with the enormous egg-production of this species. It is probable that natural causes such as a cold summer, heavy rains or off-shore winds during the free-swimming stage, or other disasters might reduce the larvae to a mere fraction of their original numbers, and that such untoward happenings are more common than favorable circumstances. If this is true we may expect to find wide fluctuations in the abundance of the adult from year to year that are independent of overfishing and tend seriously to obscure the apparent depletion that has in general been observed.

6.13. Effect of abundance of adults on success of spawning

At the same time it is possible that the abundance of the adult does to some degree affect the success of the spawning season. The returns of only the past six seasons are available for the adult, and it is possible that the record of the first year (1916) is inadequate. This commercial catch by quarters is shown in Table 30 and Graph 17. If it reflects the conditions at all satisfactorily it is clear that during the winter of 1917–18 and the following spring and summer the clams were by far more abundant than at any other time during the entire period. This is the gross total catch and is somewhat difficult of exact analysis. It is first complicated by two changes in the legal bag limit; from 50 to 36 per day in July, 1919, and from 36 to 15 per day in July, 1921. No attempt has been made to determine

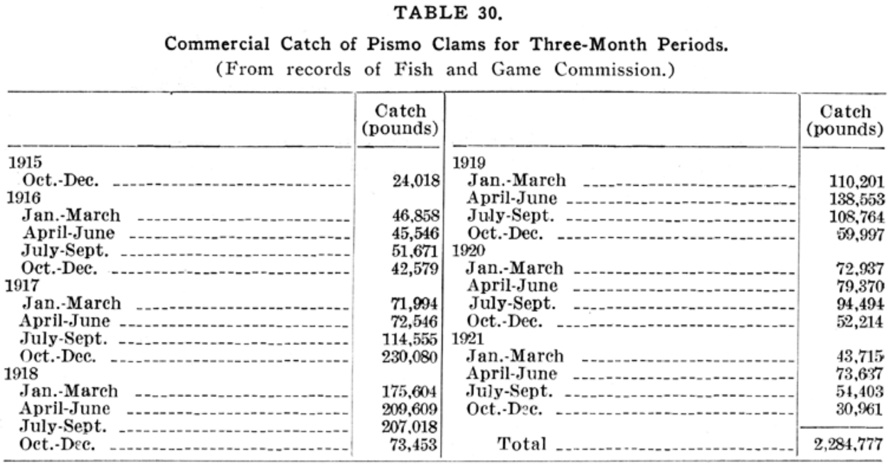


TABLE 30.

Commercial Catch of Pismo Clams for Three-Month Periods.

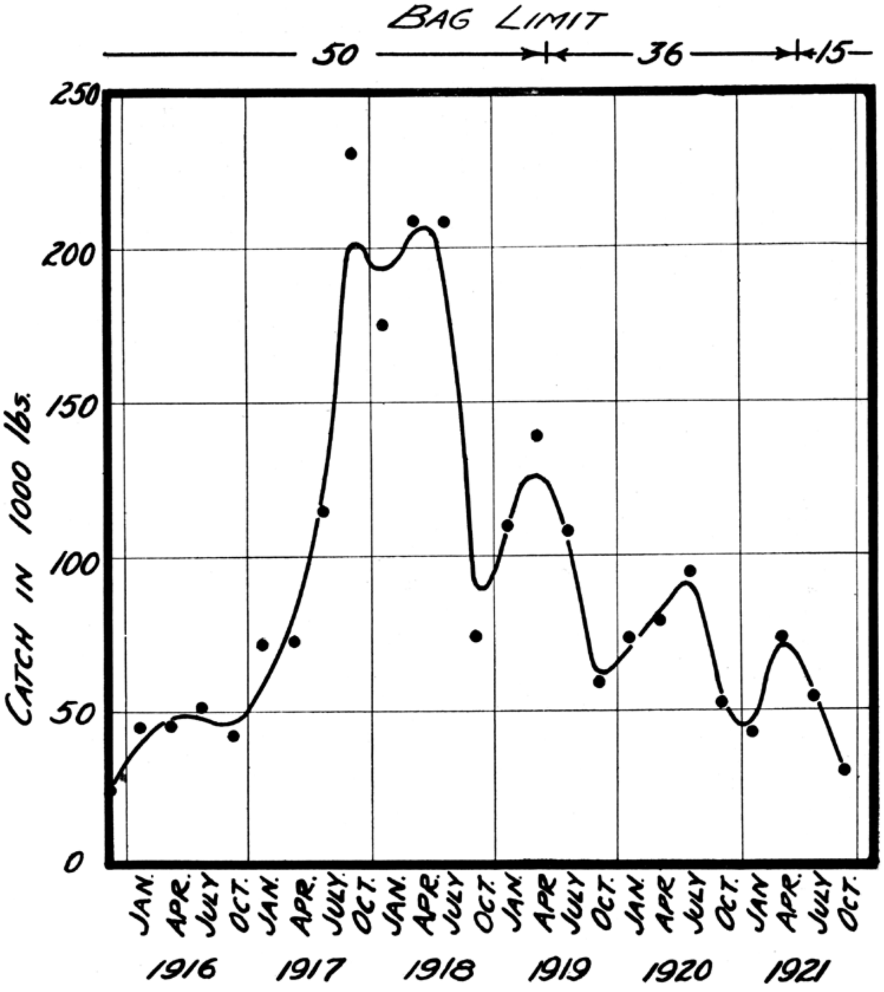
(From records of Fish and Game Commission.)

	Catch (pounds)		Catch (pounds)
1915		1919	
Oct.-Dec.	24,018	Jan.-March	110,201
1916		April-June	138,553
Jan.-March	46,858	July-Sept.	108,764
April-June	45,546	Oct.-Dec.	59,997
July-Sept.	51,671	1920	
Oct.-Dec.	42,579	Jan.-March	72,937
1917		April-June	79,370
Jan.-March	71,994	July-Sept.	94,494
April-June	72,546	Oct.-Dec.	52,214
July-Sept.	114,555	1921	
Oct.-Dec.	230,080	Jan.-March	43,715
1918		April-June	73,637
Jan.-March	175,604	July-Sept.	54,403
April-June	209,609	Oct.-Dec.	30,961
July-Sept.	207,018		
Oct.-Dec.	73,453	Total	2,284,777

Table 30.

Commercial Catch of Pismo Clams for Three-Month Periods. (From records of Fish and Game Commission.)

from the number of diggers the catch per man. Clamming requires little gear and, if profitable, readily attracts casual diggers, while the bag limit restricts the individual catch. The number of licenses issued reflects, therefore, the abundance of clams, and the gross total catch is more significant than the catch per man. From these figures it might be expected that the spawning of 1918 would have been the largest and that of 1919 next. That this is not the case may tend to show that the number of adults is not the deciding factor, or it may be that the greater age and size of the new group of adults appearing at this time gave a greater egg-producing power in 1919. At any rate the approximate coincidence of the great abundance of adults in 1917–18 and of young in 1919 can hardly have been chance.



GRAPH 17. Amounts of commercial catch of the Pismo clam for three-month periods, from 1916 to 1921, inclusive, from records of the California Fish and Game Commission.

Graph 17. Amounts of commercial catch of the Pismo clam for three-month periods, from 1916 to 1921, inclusive, from records of the California Fish and Game Commission

7. MORTALITY OF THE ADULT AND OF THE YOUNG AND ITS RELATION TO CONSERVATION

7.1. Mortality of the adult

A further analysis of the situation may be possible through a consideration of the age composition of theadult catch. For this, use may be made of the data for length and age already presented. In Table 31 are given the numbers of clams of each age and this is also shown in Graph 18. It will be seen that the numbers increase up to seven years and thereafter show a rapid and fairly uniform decline. If reference is made to the curve of length on age it will be seen that this peak corresponds to the period at which legal size is reached. Apparently a new "crop" will make itself felt

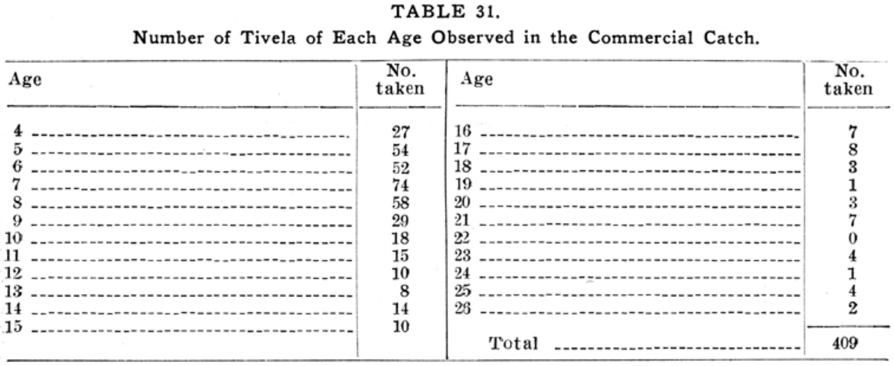
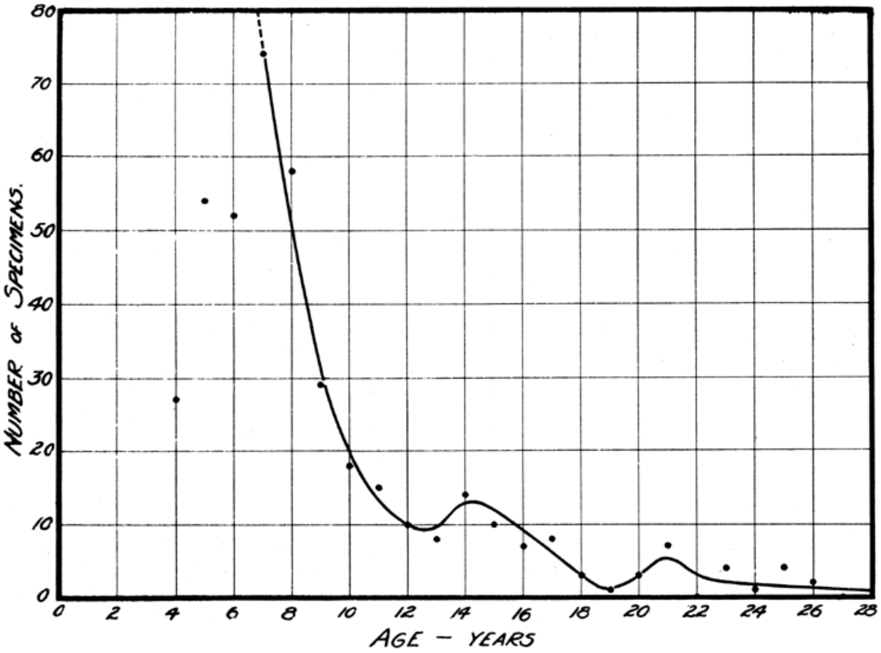


TABLE 31.

Number of Tivela of Each Age Observed in the Commercial Catch.

Age	No. taken	Age	No. taken
4	27	16	7
5	54	17	8
6	52	18	3
7	74	19	1
8	58	20	3
9	29	21	7
10	18	22	0
11	15	23	4
12	10	24	1
13	8	25	4
14	14	26	2
15	10	Total	409

Table 31. Number of Tivela of Each Age Observed in the Commercial Catch



GRAPH 18. Survival curve of adult *Tivela*, showing the numbers of adults at each age among 409 specimens examined.

Graph 18. Survival curve of adult Tivela, showing the numbers of adults at each age among 409 specimens examined at about seven years, though the ages of six and eight contribute heavily, and that when fully exposed to the fishing as well as the natural causes of mortality the numbers of each year-class melt away with great rapidity. Accordingly, we might expect to find a successful breeding year about seven years previous to 1917–18. This is approximately satisfied by the reports of some of the clam-diggers that the summer of 1913 saw a heavy set of small clams. This would require the contribution to come chiefly from five and six-year-old clams, which is not impossible if the intervening period had been one favorable for growth.

In the further downward course of this curve which, as we see, represents approximately the mortality of the adult, a crest will be noticed at 14 to 15 years. This would point back toward a good spawning year about 1905, but for this we have no independent evidence. The further irregularities of the curve are probably not significant though one is tempted to see in the rise at 21 years a continuance of the approximately seven-year rhythm (1919, 1913, 1905, 1899). It is not beyond the bounds of possibility that we have here a series of self-perpetuating cycles comparable to the "big run" of the Frazer River sockeye salmon.

If one were to risk prophesy it would be that an increased number of adults might be expected in 1924, 1925, and 1926, *provided that the young receive adequate protection in the meantime*.

7.2. Importance of conservation of young

Before analyzing the causes of mortality in the young, I wish to show why this phase of the life-history is of peramount importance. The numbers of the Pismo clam have been materially reduced during the past fifteen or twenty years. The testimony of many eye-witnesses establishes its former abundance on the beaches of the southern half of the state, even in the absence of detailed statistics. A general depletion, moreover, may be considered as proven by its commercial importance and the legal attention which it has received. of the four or five species of mollusks of commercial importance in this state, Tivela has contributed the second or third largest total, a sure sign of former abundance and an equally sure sign of a heavy strain on the fishery. In only a few species of mollusks has there been such a demand for protective legislation as in the case of the Pismo clam, and in none a more striking example of repeated requests for increased stringency.

While general depletion is clearly established, I wish to discriminate sharply between this condition and the trend of the fishery during a short period such as one or two years. To fail in this must inevitably lead to unwarranted fears and equally unwarranted complacency, and to an unstable and short-sighted policy of protection. We have seen the great variations in the success of various spawning years and that this must and does cause a corresponding fluctuation in the abundance of adults. A decrease of the catch in any season should not, therefore, be taken as proof of imminent destruction of a fishery, nor should increase be taken as proof that the sea is "inexhaustible," and that the clams are "coming back." If the periods of natural fluctuation are long, and we have evidence of periods approximating seven years, it is clear that our records must cover two or three times this number of years to give a true picture of the trend of the catch. Since the records of the Fish and Game Commission began in 1916 this is not yet possible. Pending the time when such information will be available, we must continue to collect data which in the light of the present facts of the life-history will ultimately permit a satisfactory analysis and lead to a stable and sane policy of conservation. For the present we must be content to take account of stock in a more superficial fashion, and attempt such reasonable protection as will safeguard the fishery in the meantime.

Does the adult require more protection? The present drastic bag limit of fifteen clams per day leaves open no further step except complete closure of the fishery for a period of years. I doubt that such a step is yet necessary. The cost of a commercial digger's license and the digger's time will hardly be repaid by a daily shipment of fifteen clams unless the retail price is materially advanced. Since this is already high, a further advance would reduce the demand, and it is not probable that a large commercial catch will continue. The adult would seem to be adequately protected.

What body of breeding animals is assured? Two groups of clams are protected: by law, those less than 4¾ inches in total length; and by nature, those in water deeper than five or six feet. These latter can not be reached by diggers and constitute a breeding reserve. Unfortunately, though we know that such a group exists, we can not even roughly estimate its numbers. However, there are indications that it is but a small fraction of the adult population.

Accurate data for determining at what size or age general spawning begins are lacking. Some undoubtedly mature specimens as small as 10 cm. (4 inches) have been examined. Others smaller than this have been noted in which large eggs were present, and it may prove that some of these are capable of spawning. A length of 10 cm. corresponds on the average to an age of five years, though in some cases it may be reached at four years. How large a percentage of the clams mature at this size is not clear. In theory, breeding may occur undisturbed until a length of 4¾ inches is reached, after which the numbers of the clams, as we have just seen, will be rapidly reduced by commercial fishing. The animals thus protected are not the most valuable breeders, since the number of eggs produced is approximately proportional to the weight of the clam, yet they would insure a small production of young *were they accorded the protection assumed by the legal size limit of* 4¾ *inches*.

7.3. Mortality of the larvae and of the young.

Oil

We are thus brought back forcibly to the pivotal point of the whole question of conservation in the Pismo clam—*the mortality of the young*. The larval mortality is undoubtedly enormous, but the causes are, with one exception, beyond our control. That one cause is oil, a cause of mortality added by man to the already numerous ones provided by nature. Port Harford (Port San Luis) is a shipping point of importance for oil and in loading tankers there are various ways in which oil escapes to the sea water. Some of these are preventable, as for instance the pumping overboard of bilge water containing large quantities of oil. Others are less easily controlled, as the breaking of loading hoses. In these various ways the water at the northern end of the Pismo-Oceano beach receives from time to time considerable amounts of oil which the prevailing wind distributes southward along the entire beach. It has recently been shown by Gutsell (1921) in a summary of the effects of oil and tar pollution of waters that a number of very active poisons are present in such waste and that it has a mechanical action in that the film formed at the surface greatly diminishes the oxygen supply. The action is said to be greatest on surface organisms, which would of course include the free-swimming larvae of Tivela. While direct proof of the destruction of the larvae is lacking, this is not the case with the young. The writer has already put on record an instance of extensive destruction of the young by oil. (Weymouth, 1919). The habitat of the young is particularly exposed to the effect of oil brought in on the surface of the waves, but older individuals at levels never bare are not immune, as the heavier components of the oil may after a time separate and sink. In several cases adults taken well below low tide have been observed in which the shell was smeared with oil.

7.4. Physical causes of mortality

The physical causes of mortality in the young are not numerous. Severe storms at times wash them out of the sand and cast them up to die on the higher beach, but this is an infrequent occurrence. Cold weather may also cause heavy losses. The only recent instance of this was in the winter of 1921–22. The exposed position of the young in the intertidal zone permitted the conjunction of low tides and a heavy frost to do much damage. It is doubtful if many clams were "frozen to death," as certain species at least are known to endure very low temperatures, but near the freezing point their muscular activity is too slight to keep up the constant fight against wave action and many were washed out. Beaten up and down the beach, and too inactive to keep the shells closed, they fell victims in large numbers to the gulls and pelicans. A similar case of the destructive action of frost in the European cockle is recorded by Scott (1910).

7.5. Natural enemies

The natural enemies of the young are better known than those of the larvae. Gulls may often be seen feeding on the injured or the very small individuals where clams have been dug, and they have been observed to drop small clams from the air in order to break the shells. There is no evidence that the gulls can obtain undisturbed clams; those eaten had been turned out by the clammers or by wave action. This agrees with Walton's observations on the cockle of the English coast (1920a). Scoters and other water birds have often been seen feeding in the surf where young clams are found and some of the fishermen claim to have found many small clams in the crops of "surf-ducks." Various fish are known to feed on clams, for instance, the ray upon the soft-shell in San Francisco Bay, but no evidence has been found that fish feed upon the Pismo clam. Starfish are known to be destructive to oysters and other bivalves, but very few have been encountered on this sandy beach. In one case coming under the writer's notice, the starfish was attacking a razor clam. Various marine snails destroy clams by drilling through the shell, usually near the umbo, and eating out the soft parts. The shell of the adult Tivela is so hard and thick as to render it proof against this form of attack, and though shells have been found which the snails have attempted to drill, none have been encountered in which they have been successful. The very young are, however, less protected and perforated shells have been found, though they are far less common than in several other species. In the adult the exposed siphonate end is sometimes the attachment point of a particular species of hydroid (Clytia bakeri), which, however, does not harm its host. A species of slender red boring worm often attacks the shells of old individuals at this same exposed point, but though their holes weaken the shell it seems improbable that they do further harm. In fact, after the Pismo clam has reached a length of an inch or more it seems better fitted to resist its natural enemies than the majority of clams, and though found in a particularly exposed habitat it is well adapted to the conditions it encounters and finds them, as we have seen, conducive to growth.

It will be seen that though there is a heavy larval mortality, the natural enemies of the young and the adult are neither numerous nor formidable; the correctness of this conclusion is borne out by the abundance of clams found in the early days on all the beaches in the southern part of the state. There can be no doubt that man is by far the most dangerous enemy. The intertidal zone, which, as we have seen, presents many natural advantages, is the most directly exposed to man, and man's activities have practically removed the adult from this region. A small fraction of the adults continue to thrive in water where they are with difficulty accessible to man, but every new generation of young must settle between the tides and run the gauntlet before any of them reach even comparative shelter.

It may be of interest in passing to note that apparently the Indians did not use the Pismo clam to any great extent, as far as can be told from an examination of kitchen middens near Oceano. In one mound examined there were numbers of young Tivela but no adults; no young or adults were noted in any other mounds. Other species were more favored, in particular the bent-nosed clam (Macoma) which, strangely enough, is not now found in any numbers in this locality. Possibly they were obtained from some lagoon since drained or silted up by changes at the mouths of neighboring creeks.

7.6. Inadequacy of present protection of young

In theory the present size limit of 4¾ inches should completely protect the young under discussion. But in practice it does not. On this point I speak from personal observation. At present the drain on the young, none of which can legally be taken, is more of a menace to the species than is the commercial fishery, in spite of the extent of the latter. Complete closure of the commercial fishery will not long protect the Pismo clam if the young continue to be taken at the present rate. In part the destruction of the young is the result of carelessness or ignorance of the conditions and of the law which these conditions have made necessary. The clams lie open to anyone who scratches in the sand when the tide is low, and the small clams are undeniably tender and toothsome. Many tourists stopping at the beach would not molest the young clams if they understood that the preservation of the species were bound up in the protection of these young.

Unfortunately there is another group, chiefly local residents, who, though knowing both the conditions and the law, are selfishly devoid of any feeling of responsibility toward the future inhabitants of the state, and daily contribute to the extermination of this bivalve to furnish profitable clam dinners. How rapidly they are accomplishing this destruction can be seen from a typical case. One sack found on the beach contained 365 clams, or over 24 times the bag limit of clams, and of these not more than a half dozen were of legal size. Add to this that the great majority were too small to have spawned and had therefore never contributed to the future supply, and it will take little imagination to see the future of this valuable and distinctive clam.

8. RECOMMENDATIONS

In view of the facts set forth in the foregoing report it is respectfully recommended to the Board of Fish and Game Commissioners:

1. That the present laws fixing a size and a bag limit be retained unchanged at least until such time as we have more adequate information concerning the natural fluctuations in abundance and possible depletion.

2. That adequate protection be afforded the young. This should include a campaign of education aimed particularly at the summer tourist and camper, through newspapers and by posting the beach; a more rigorous enforcement of existing laws; and a vigorous policy regarding the wastage of oil at and near Port Harford.

3. That, in order to follow the actual conditions of the species, in addition to the collection of the data on the commercial shipments, a census of the young by the method of cross-sectioning the beach be carried out at least once each year.

4. That, in order to relieve the strain not only on the Pismo clam but upon other native species of mollusks, steps be taken to foster the cultivation of clams. For this purpose, as the writer pointed out in the previous report, the soft-shell clam (Mya) is by far the best fitted. There exist, in a number of bays along the California coast, acres of suitable tide land which can be made highly productive, and since the "farming" of this species has been developed on the east coast for a number of years, it would not be an experiment here. The first step in building up such an industry is the fixing of the legal status of such grounds and the establishment of a system of leasing which will assure to a person engaged in clam culture a definite and dependable control similar to that which the oystermen have over their grounds. Such an industry would prove profitable to those taking it up, would supply to the markets a valuable and appetizing food, and would materially reduce the strain of the commercial fishery on forms like the Pismo clam in which, from the habits, "farming" is impossible. The writer considers this the most constructive suggestion arising from the work which he has carried out on the mollusks of the state and that it merits careful consideration.

9. SUMMARY

Owing to the diversity of the subjects treated in the present paper, and the fact that it may prove of interest to workers in various fields, this summary is presented in three sections. The first deals with the general life-history of the Pismo clam as determined by this work, the second deals with the depletion of the fishery and the bearing of the facts of the life-history on the problems of conservation, the third deals with the physiology of growth as shown in this species and a comparison of certain of its features with those observed in other forms.

9.1. A. Facts of Life History

1. The Pismo clam (Tivela stultorum) is one of the most important edible bivalves of California. It is found along the entire coast south of Monterey Bay and extends into Mexico, but at present reaches its greatest abundance in San Luis Obispo County on the Morro and Pismo-Oceano beaches.

2. It spawns in late summer, during July, August, and September.

3. After a short free-swimming larval stage the young settle in the sand between high and low tide level and take up a life similar to that of the adult. They are at this time protected from wave action by the presence of a thread-like byssus anchoring them to sand grains.

4. They grow rapidly during the fall until about November when growth slackens and finally ceases for the season. Their average length at this time (the first winter) is about 2.2 cm. (# inch), while 80 per cent are included between the lengths of 1.6 cm. and 2.8 cm. (# and 1 1/16; inch).

5. Growth is resumed in the spring about March or April and continues until the following November, when they average (second winter) 4.5 cm. (1¾ inch), 80 per cent being included between 3.5 cm. and 5.4 cm. (1# to 2# inches).

6. During the winter pause in growth a mark is formed at the margin of the shell (see p. 35 for figure and fuller account) and from these annual marks the age may be determined accurately in the great majority of cases.

7. By means of these annual marks the lengths and weights at various ages have been determined. These are given in Tables 16, 17, 18, and 23, and in Graphs 7 and Graph 13.

8. The legal length of 4¾ inches (12.07 cm.) corresponds on the average to an age of 7 years. Eighty per cent of those of legal size are from 5½ to 8½ years of age; a few extreme cases may be as young as 4 or as old as 11 years.

9. Corresponding to this slow growth, a great age is attained by some individuals; 33 specimens examined showed an age of 18 years or over, and 6 specimens had reached 25 years.

9.2. B. Abundance and Protection

1. The Pismo clam is much less abundant than formerly. An exact analysis of the catch in relation to the intensity of fishing and the extent of natural fluctuation in abundance is not yet possible, *but there can be no doubt of a general depletion*. That it was present in immense numbers where it is now obtained with great difficulty is clear from the testimony of many eye-witnesses. That those people

in the best position to observe are convinced that it is decreasing is proved by the legal limits of size and bag which have been set and repeatedly reduced at the request of the people of San Luis Obispo County.

2. Its slow growth and the unusually heavy mortality in the larval stages due to the exposed situations in which it lives makes its restoration in case of depletion much more difficult and much more slow than that of other bivalves such as the oyster or the soft-shell clam.

3. It is not adapted to artificial propagation or to culture as are the oyster and soft-shell and hence no improvement is to be looked for from hatchery work or "farming."

4. The Pismo clam is enormously fertile at times, but the success of different seasons is strikingly uneven; for example, the number of young hatched in 1919 that survived the larval stage and established themselves in the sand is estimated at from 30,000,000 to 40,000,000, but the young hatched in 1918 amount to only about 5 per cent of this figure, and the young hatched in 1920, 1921, and 1922 combined have never exceeded 5 per cent of the total.

5. From a consideration of these facts it is probable that the Pismo clam can maintain itself if properly protected, but owing to its slow growth and the uncertainties of spawning and of larval life no sudden effects can be expected, while many natural fluctuations in abundance may be looked for. To accomplish any results the efforts at protection must be consistently maintained over a long period of years. The progress and success of such work should be followed by a study of the abundance of the young and the statistics of the catch as suggested on p. 85 and p. 95.

6. The protection at present afforded the adult is probably adequate, but should not be relaxed. The protection afforded the young by the present size limit is in theory sufficient, but in fact the law is so generally violated by both residents and tourists as to make it a dead letter. Because of the slow growth and natural mortality among the young this loss of immature clams before they reach the spawning age constitutes a more serious menace than it would in the case of most bivalves, and unless it is stopped will inevitably lead to speedy depletion and ultimate practical extinction. Even complete closure of the fishery will not afford protection to the species if the young are not in practice, as well as in theory, given satisfactory protection.

9.3. C. Main Features of Growth Physiology

1. From a study of approximately 1700 young Pismo clams during two years it is proven that growth shows a distinct seasonal rhythm, being most rapid in summer and very slow in winter.

2. That this type of seasonal growth is not peculiar to this species but is a widespread and fundamental phenomenon is shown by an examination of the literature; a similar seasonal rhythm has been found in other mollusks and in a variety of diverse organisms including many plants, crustacea, fish, and even man.

3. The possible factors, external and internal, causing this seasonal rhythm are discussed and it is shown that temperature, both directly and indirectly, is one of the most important influences.

4. Because of this difference in rate of growth during different times of year the shell shows permanent structural traces of the seasons, the most prominent of which are the annual rings. It is here established that one of these is formed each winter and therefore the rings are accurate indicators of age.

5. From a study of the annual rings in adult shells data have been obtained on the total length of the clam at each age and these are presented in the form of a growth curve which shows graphically the length and rate of growth at each age.

6. Because of the long life of this clam the mean length at any age is the average of growth under the environmental conditions of so many different years that the curve of life-growth is uninfluenced by the chance succession of favorable and unfavorable seasons.

7. Because the life includes so many seasonal cycles the life-growth curve is free from a serious source of confusion present in forms like the insects, in which, during the one or two years of life, the life-growth and the seasonal growth can not be distinguished.

8. For these reasons the life-growth curve represents not only a particularly accurate and reliable norm for this species but a curve of marked theoretical interest as presenting life-growth in an unusually pure form. Similar norms for many diverse species would be desirable for two reasons: they might form the basis for an analysis of the factors influencing growth and their comparison might show whether, as has been claimed, there exists a single generalized type of life-growth curve.

9. A life-growth curve may be fitted to the data on length at each age in the Pismo clam by the general formula $y = a - bc^x$ in which y is the length, x the age, and b and c constants (see p. 56 for these values). It is also shown that this formula may be applied to certain other species.

10. The ratios between length, height, and thickness in this clam are shown to be constant at all sizes studied; as in the other bivalves and fish for which we have data, the shape does not materially change after the larval period. Mammals and birds on the other hand change materially in shape during growth.

11. The weight is shown to be approximately proportional to the cube of the length as in other animals; exact figures show that the weight increases somewhat more rapidly than the third power (3.157) of the length, due apparently to increased thickness of the individual valves with increased age.

12. The weights at each age (determined from the length-weight ratio) are given; from these a life-growth curve in terms of weight has been constructed.

10. BIBLIOGRAPHY

In the following list no attempt has been made to compile a complete bibliography either on growth or on bivalves. In it are included only those papers actually referred to in this report. Some of the articles listed were not available and are known to the writer only through abstracts or quotations of later authors; such are marked "not examined."

Barney, R. L. and Anson, B. J. 1920. Life history and ecology of the pigmy sunfish, Elassoma zonatum. Ecology, Vol. 1, No. 4, October, pp. 241–256.

Belding, David L. 1909. A report upon the mollusk fisheries of Massachusetts, Boston.

1910. A report upon the scallop fishery of Massachusetts, Boston.

1912. A report upon the quahaug and oyster fisheries of Massachusetts. Boston.

1916. Report on the clam fishery. Fiftieth annual report of the Commissioners of Fisheries and Game (Mass.). Public Document No. 25, pp. 93–234.

Biedermann. 1902. Untersuchungen über Bau und Erstehung der Molluskenschalen. Jena. Zeitschr. Naturw., Bd. 36, pp. 1–160.

Brunow, Hanns. 1911. Der Hungerstoffwechsel des Flusskrebses (Astacus fluviatilis). Zeitschr. allg. Physiol., Bd. 12, pp. 215–276.

Calderwood, W. L. 1908. The life of the salmon. London.

Clark, Janet H. 1922. The physiological action of light. Physiological Reviews, Vol. 2, pp. 277–309.

Clark, W. M. 1920. The determination of hyrdogen ions. Baltimore.

Coville, V. 1921. Influence of cold in stimulating the growth of plants. Annual report of the Smithsonian Institution for 1919, pp. 281–291.

Crozier, W. J. and Hecht, Selig. 1914. Correlations of weight, length, and other body measurements in the weakfish, Cynoscion regalis. Bulletin, U. S. Bureau of Fisheries, Vol. 33, 1913, pp. 141–147. Document No. 800.

Crozier, W. J. 1914. The growth of the shell in the lamellibranch, Dosinia discus Reeve). Zool Jahrb., Abt. f. Anat., Bd. 38, pp. 577–584.

1918a. Growth and duration of life of Chiton tuberculatus. National Academy of Sciences, Vol. 4, November, pp. 322–325. (Contributions from the Bermuda Biological Station, Vol. V, No. 96.)

1918b. Growth of Chiton tuberculatus in different environments. National Academy of Sciences, Vol. 4, November, pp. 325–328. (Contributions from the Bermuda Biological Station, Vol. 5, No. 97.)

Daffner, Franz. 1902. Das Wachstum des Menschen (2d ed.) Leipzig, Wilhelm Engelmann.

Edmondson, Charles H. 1920. Edible mollusca of the Oregon coast. Occasional Papers of the Bishop Museum, Vol. 7, No. 9, Honolulu, H. I.

1922. Shellfish resources of the northwest coast of the United States. Appendix III to the report of the U. S. Commissioner of Fisheries for 1922, Bureau of Fisheries Document No. 902.

Fraser, C. McLean. 1917. On the scales of the spring salmon. Contributions to Canadian Biology, 1915–16. Supplement to the Sixth annual report of the department of Naval Service, Fisheries branch. Ottawa.

Gilbert, C. H. 1913. Age at maturity of the Pacific coast salmon of the genus Oncorhynchus. Bulletin, U. S. Bureau of Fisheries, Vol. 32, for 1912.

Gutsell, J. S. 1921. Danger to fisheries from oil and tar pollution of waters. Appendix VII to the Report of the U. S. Commissioner of Fisheries for 1921, Bureau of Fisheries Document No. 910.

Hazay, J. 1881. Die Molluskenfauna von Budapest. III. Biol. Teil, in Malakozool. Blatter. Kassel. Not examined.

Heath, Harold. 1913. Investigation of the clams of California. State of California, Fish and Game Commission, Fish Bulletin No. 1, pp. 27–28.

1916. California clams. California Fish and Game, Vol. 2, October, p. 175.

Hecht, Selig. 1916. Form and growth in fishes. Journal of Morphology, Vol. 27, pp. 379–400.

Hess, Alfred F. and Gutman, P. 1921. The cure of infantile rickets by sunlight as demonstrated by a chemical alteration of the blood. Proc. Soc. Exper. Biol. and Med., Vol. 19, pp. 31–34.

Hess, Alfred F. and Lundagen, Marion A. 1922. Seasonal tide of blood phosphate in infants. Proc. Soc. Exper. Biol. and Med., Vol. 19, pp. 380–382.

Hessling, V. 1859. Die Perlmuscheln und ihre Perlen. Leipzig. Not examined.

Holt, L. Emmett. 1922. The diseases of infancy and childhood. New York, D. Appleton and Co.

Howard, Arthur Day. 1922. Experiments in the culture of fresh-water mussels. Bulletin, U. S. Bureau of Fisheries, Vol. 38, 1921–1922, pp. 63–87. Document No. 916.

Isely, Frederick B. 1914. Experimental study of the growth and migration of fresh-water mussels. Appendix III to the Report of the U. S. Commissioner of Fisheries for 1913, Bureau of Fisheries Document No. 792.

Israël, W. 1911. Najadologische Miscellen. Nachrichtsblatt der deutschen malakozoologischen Gesellschaft, pp. 10–17. Not examined.

Keeble, Frederick. 1910. Plant animals. Cambridge University Press.

Kellogg, James L. 1910. Shell-fish industries. New York, Henry Holt and Co.

Lefevre, George, and Curtis, Winterton C. 1912. Studies on the reproduction and artificial propagation of fresh-water mussels. Bulletin, U. S. Bureau of Fisheries, Vol. 30 for 1910. Document No. 756.

Lindsay, B. 1913. On periodicity of growth in the shells of molluscs. 9*e* Congrès intern. de Zool. tenu à Monaco. Section 1*re*, pp. 266–268. Rennes, 1914.

List, Theodor. 1902. Die Mytiliden des Golfes von Neapel. (Fauna und Flora des Golfes von Neapel). Berlin, R. Friedländer & Sohn.

Malling-Hansen, Pasteur R. 1886. Perioden im Gewicht der Kinder und in der Sonnenwärme. Kobenhagen. Not examined.

Massy, Anne L. 1914. Notes on the evidence of age afforded by the growth rings of oyster shells. Fisheries, Ireland, Scientific Investigations, 1913, p. 12, pl. 11.

Meyer, Arthur William. 1914. Curves of prenatal growth and autocatalysis. Arch. f. Entwicklungs-mechanik, Bd. 40, pp. 497–524.

Mitchell, Philip H. 1914. The oxygen requirements of shellfish. Bulletin, U. S. Bureau of Fisheries, Vol. 32, 1912, pp. 209–222.

Morse, Edward S. 1919. Observation on living lamellibranchs of New England. Proc. Boston Soc. Nat. His., Vol, 35, No. 5, July, pp. 139–196.

Mossop, Bessie K. E. 1921 A study of the sea mussel (Mytilus edulis L.) Contributions to Canadian Biol., 1921, No. 2.

1922. The rate of growth of the sea mussel (Mytilus edulis L.) at St. Andrews, New Brunswick; Digby, Nova Scotia; and in Hudson Bay.

Nelson, Thurlow C. 1921a. Aids to successful oyster culture. 1. Procuring the seed, N. J. Agricultural Exp. Stations, Bulletin No. 351. New Brunswick, N J.

1921b. Report of the dept. of biology of the N. J. Agricultural College Exp. Station for 1920. Trenton, N. J.

Petersen, 1908. Report of the Danish Biological Station, Vols. 15 and 18, p. 31. Copenhagen. Not examined.

Pfund, A. H. 1917. The colors of mother-of-pearl. Journal of the Franklin Institute, Vol. 183, pp. 453–464.

Porter, W. T. 1920. The seasonal variation in the growth of Boston school children. Am. Jour. of Physiol., Vol. 52, p. 121–131.

1922. The relative growth of individual Boston school boys. Am. Jour. Physiol., Vol. 61, p. 311–325.

Rassbach, Richard. 1912a. Zur Kenntnis der Schalenregeneration bie der Teichmuschel (Anodonta cellensis). Zool. Anz., Bd. 39, No. 1, pp. 35–38.

1912b. Beiträge zur Kenntnis der Schale und Schalenregeneration von Andonta cellensis Schröt. Zeitsch. f. Wiss. Zool., Bd. 103, pp. 363–448.

Rich, Willis H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento Rivers. Bulletin, U. S. Bureau of Fisheries, Vol. 37, 1919–1920. Document No. 887.

Rubbel, A. 1911. Uber Perlen und Perlbildung bie Margaritana margaritifera. Zool. Jahr., Abt. f. Anat., Bd. 32, pp. 287–366.

1913. Beobachtungen über das Wachstum von Margaritana margaritifera. Zool. Anz., Bd. 41, pp. 156–162.

Scofield, N. B. 1921. Report of the department of Commercial Fisheries. Twenty-sixth biennial report, Fish and Game Commission, State of California, 1918–1920, p. 63.

Scott, Andrew. 1910. Note on the Flookburgh cockle beds. Report (18th) for 1909 on the Lancashire Sea-Fisheries Laboratory at U. of Liverpool, pp. 186–192. Liverpool.

Shann, Edward. 1910. Some notes on the life-history and rate of growth in Gobius minutus. Annals and Magazine of Natural History, Ser. 8, Vol. 5, pp. 217–239.

Shapley, Harlow. 1920. Thermokinetics of Liometopum apiculatum. Proc. National Academy of Sciences, Vol. 6, p. 204.

Snyder, J. O. 1921. Three California marked salmon recovered. California Fish and Game, Vol. 7, No. 1, pp. 1–6.

1922. The return of marked king salmon grilse. California Fish and Game, Vol. 8, No. 2, p. 102.

Stafford, Joseph. 1913. The Canadian Oyster. Commission of Conservation, Ottawa.

1917. The native oyster of British Columbia. Report of the Commissioner of Fisheries for British Columbia for 1916, p. S88.

1918. The native oyster of British Columbia. Report of the Commissioner of Fisheries for British Columbia for 1917, p. Q91.

Thompson, D'Arcy Wentworth. 1917. On growth and form. Cambridge.

Thompson, Will F. 1917. Temperature and the albacore. California Fish and Game, Vol. 3, No. 4, pp. 153–159.

Thompson, Will F. and Thompson, Julia Bell. 1919. The spawning of the grunion. State of California, Fish and Game Commission, Fish Bulletin No. 3.

Thompson, Will F. 1920. California Fish and Game, Vol. 6, No. 4, October.

Walton, C. L. 1920a. A contribution to the ecology of some cockle beds. Report (28th) for 1919 on the Lancashire Sea-Fisheries Laboratory at U. of Liverpool, pp. 34–46. Liverpool.

1920b. Notes on the shell of Cardium edule. Report (28th) for 1919 on the Lancashire Sea-Fisheries Laboratory at U. of Liverpool and the sea-fish hatchery at Piel, pp. 47–50. Liverpool.

Weinland, Ernst. 1919. Beobachtungen über den Gaswechel von Anodonta cygnea. Zeitsch. f. Biol., Bd. 69, pp. 1–86.

Wesenberg-Lund, C. 1912. Über einige eigentumliche Temperaturverhaltnisse in der Litoralregion der baltischen Seen u. s. w. Internal. Revue d. ges. Hydrobiol. u. Hydrog. Vol. 5, p. 287.

Weymouth, F. W. and Richardson, C. H. 1912. Observations on the habits of the crustacean Emerita analoga. Smithsonian Miscellaneous Collection, Vol. 59, No. 7, pp. 1–13.

Weymouth, F. W. 1918. Contributions to the life-history of the Pacific Coast edible crab. (Paper No. 3.) Report of the Commissioner of Fisheries for British Columbia for 1917, pp. Q81–Q90.

1919. A case of destruction of Pismo clams by oil. California Fish and Game, Vol. 5, p. 174.

1921a. The edible clams, mussels and scallops of California. State of California, Fish and Game Commission, Fish Bulletin No. 4.

1921b. The abundance of young Pismo clams. California Fish and Game, Vol. 7, April, p. 103.

Whipple, G. C. 1896. Some experiments on the growth of diatoms. Technology Quarterly, Vol. 9, pp. 145–168. Not examined.

11. APPENDIX.

Tables of Original Frequency Distributions

In the following tables are given the frequency distributions—the raw data—on which are based the means, medians, standard deviations, deciles, and other statistical measures presented by the tables in the body of the report when such data is not there included. For convenience, each table bears the same number as the text-table prefixed by "A".

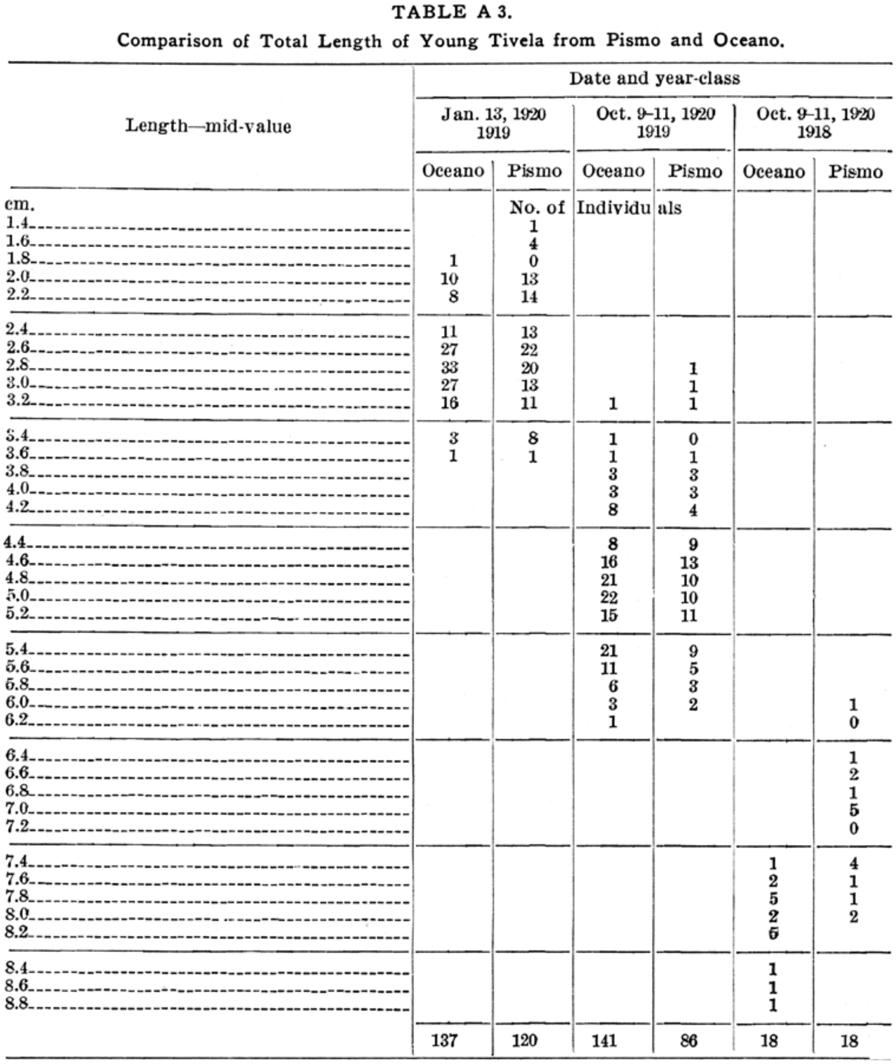


TABLE A 3.

Comparison of Total Length of Young Tivela from Pismo and Oceano.

Length—mid-value	Date and year-class					
	Jan. 13, 1920 1919		Oct. 9–11, 1920 1919		Oct. 9–11, 1920 1918	
	Oceano	Pismo	Oceano	Pismo	Oceano	Pismo
cm.		No. of	Individu	als		
1.4		1				
1.6		4				
1.8	1	0				
2.0	10	13				
2.2	8	14				
2.4	11	13				
2.6	27	22				
2.8	33	20		1		
3.0	27	13		1		
3.2	16	11	1	1		
3.4	3	8	1	0		
3.6	1	1	1	1		
3.8			3	3		
4.0			3	3		
4.2			8	4		
4.4			8	9		
4.6			16	13		
4.8			21	10		
5.0			22	10		
5.2			15	11		
5.4			21	9		
5.6			11	5		
5.8			6	3		
6.0			3	2		1
6.2			1			0
6.4						1
6.6						2
6.8						1
7.0						5
7.2						0
7.4					1	4
7.6					2	1
7.8					5	1
8.0					2	2
8.2					5	
8.4					1	
8.6					1	
8.8					1	
	137	120	141	86	18	18

Table A 3.
Comparison of Total Length of Young Tivela from Pismo and Oceano

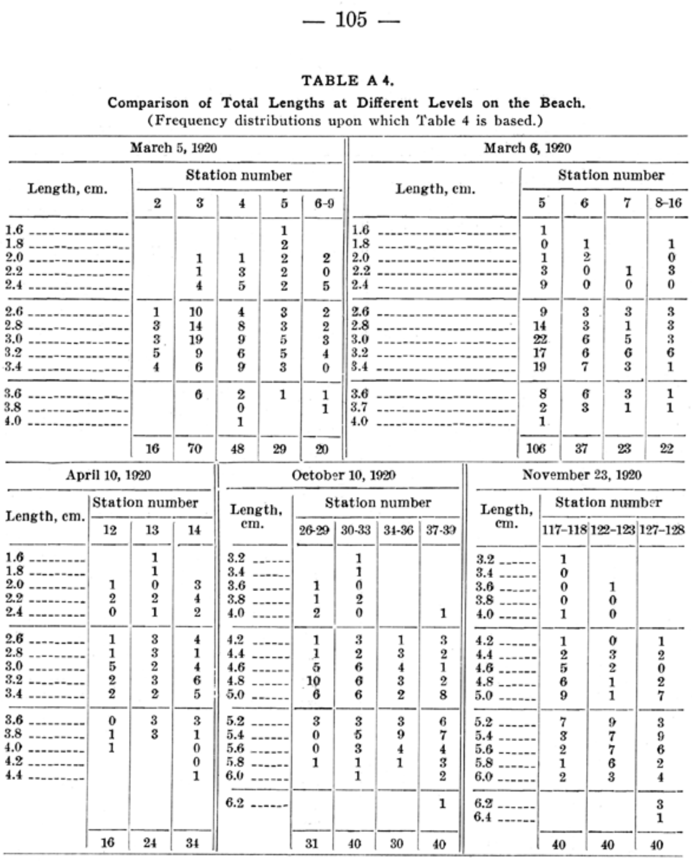


TABLE A 4.

Comparison of Total Lengths at Different Levels on the Beach.
(Frequency distributions upon which Table 4 is based.)

March 5, 1920

Length, cm.	Station number				
	2	3	4	5	6-9
1.6				1	
1.8				2	
2.0		1	1	2	2
2.2		1	3	2	0
2.4		4	5	2	5
2.6	1	10	4	3	2
2.8	3	14	8	3	2
3.0	3	19	9	5	3
3.2	5	9	6	5	4
3.4	4	6	9	3	0
3.6		6	2	1	1
3.8			0		1
4.0			1		
	16	70	48	29	20

March 6, 1920

Length, cm.	Station number			
	5	6	7	8-16
1.6	1			
1.8	0	1		1
2.0	1	2		0
2.2	3	0	1	3
2.4	9	0	0	0
2.6	9	3	3	3
2.8	14	3	1	3
3.0	22	6	5	3
3.2	17	6	6	6
3.4	19	7	3	1
3.6	8	6	3	1
3.7	2	3	1	1
4.0	1			
	106	37	23	22

April 10, 1920

Length, cm.	Station number		
	12	13	14
1.6		1	
1.8		1	
2.0	1	0	3
2.2	2	2	4
2.4	0	1	2
2.6	1	3	4
2.8	1	3	1
3.0	5	2	4
3.2	2	3	6
3.4	2	2	5
3.6	0	3	3
3.8	1	3	1
4.0	1		0
4.2			0
4.4			1
	16	24	34

October 10, 1920

Length, cm.	Station number			
	26-29	30-33	34-36	37-39
3.2		1		
3.4		1		
3.6	1	0		
3.8	1	2		
4.0	2	0		1
4.2	1	3	1	3
4.4	1	2	3	2
4.6	5	6	4	1
4.8	10	6	3	2
5.0	6	6	2	8
5.2	3	3	3	6
5.4	0	5	9	7
5.6	0	3	4	4
5.8	1	1	1	3
6.0		1		2
6.2				1
	31	40	30	40

November 23, 1920

Length, cm.	Station number		
	117-118	122-123	127-128
3.2	1		
3.4	0		
3.6	0	1	
3.8	0	0	
4.0	1	0	
4.2	1	0	1
4.4	2	3	2
4.6	5	2	0
4.8	6	1	2
5.0	9	1	7
5.2	7	9	3
5.4	3	7	9
5.6	2	7	6
5.8	1	6	2
6.0	2	3	4
6.2			3
6.4			1
	40	40	40

Table A 4.
Comparison of Total Lengths at Different Levels on the Beach. (Frequency distributions upon which Table 4 is based.)

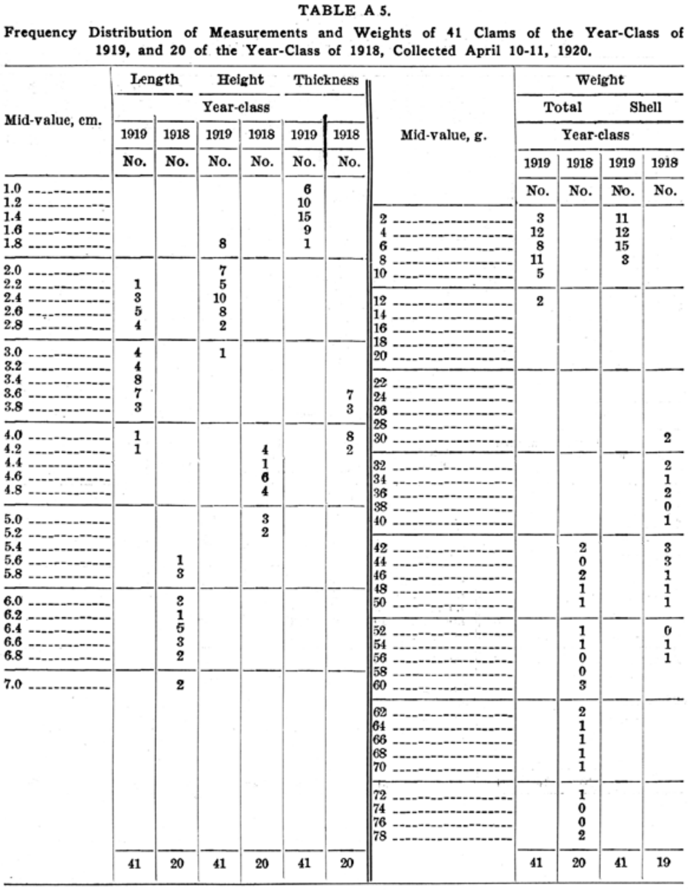


TABLE A 5.

Frequency Distribution of Measurements and Weights of 41 Clams of the Year-Class of 1919, and 20 of the Year-Class of 1918, Collected April 10-11, 1920.

Mid-value, cm.	Length		Height		Thickness	
	Year-class					
	1919	1918	1919	1918	1919	1918
	No.	No.	No.	No.	No.	No.
1.0					6	
1.2					10	
1.4					15	
1.6					9	
1.8			8		1	
2.0			7			
2.2	1		5			
2.4	3		10			
2.6	5		8			
2.8	4		2			
3.0	4		1			
3.2	4					
3.4	8					
3.6	7					7
3.8	3					3
4.0	1					8
4.2	1			4		2
4.4				1		
4.6				6		
4.8				4		
5.0				3		
5.2				2		
5.4						
5.6		1				
5.8		3				
6.0		2				
6.2		1				
6.4		5				
6.6		3				
6.8		2				
7.0		2				
	41	20	41	20	41	20

Mid-value, g.	Weight			
	Total		Shell	
	Year-class			
	1919	1918	1919	1918
	No.	No.	No.	No.
2	3		11	
4	12		12	
6	8		15	
8	11		3	
10	5			
12	2			
14				
16				
18				
20				
22				
24				
26				
28				
30				2
32				2
34				1
36				2
38				0
40				1
42		2		3
44		0		3
46		2		1
48		1		1
50		1		1
52		1		0
54		1		1
56		0		1
58		0		
60		3		
62		2		
64		1		
66		1		
68		1		
70		1		
72		1		
74		0		
76		0		
78		2		
	41	20	41	19

Table A 5.
Frequency Distribution of Measurements and Weights of 41 Clams of the Year-Class of 1919, and 20 of the Year-Class of 1918, Collected April 10–11, 1920

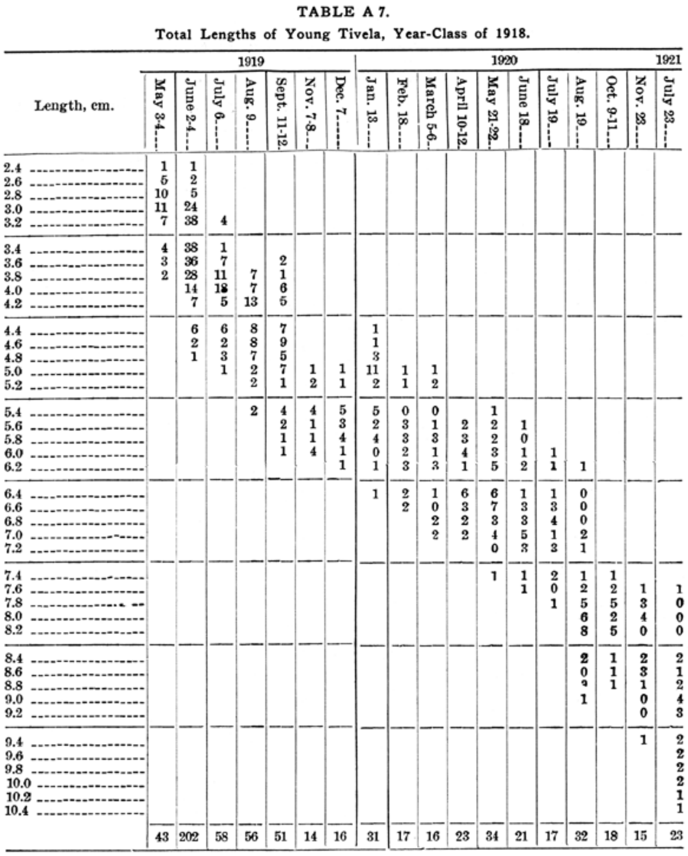


TABLE A 7.
Total Lengths of Young Tivela, Year-Class of 1918.

Length, cm.	1919							1920										1921
	May 3-4	June 2-4	July 6	Aug. 9	Sept. 11-12	Nov. 7-8	Dec. 7	Jan. 13	Feb. 18	March 5-6	April 10-12	May 21-22	June 18	July 19	Aug. 19	Oct. 9-11	Nov. 23	July 23
2.4	1	1																
2.6	5	2																
2.8	10	5																
3.0	11	24																
3.2	7	38	4															
3.4	4	38	1															
3.6	3	36	7		2													
3.8	2	28	11	7	1													
4.0		14	18	7	6													
4.2		7	5	13	5													
4.4		6	6	8	7			1										
4.6		2	2	8	9			1										
4.8		1	3	7	5			3										
5.0			1	2	7	1	1	11	1	1								
5.2				2	1	2	1	2	1	2								
5.4				2	4	4	5	5	0	0		1						
5.6					2	1	3	2	3	1	2	2	1					
5.8					1	1	4	4	3	3	3	2	0					
6.0					1	4	1	0	2	1	4	3	1	1				
6.2							1	1	3	3	1	5	2	1	1			
6.4								1	2	1	6	6	1	1	0			
6.6									2	0	3	7	3	3	0			
6.8										2	2	3	3	4	0			
7.0										2	2	4	5	1	2			
7.2												0	3	3	1			
7.4												1	1	2	1	1		
7.6													1	0	2	2	1	1
7.8														1	5	5	3	0
8.0															6	2	4	0
8.2															8	5	0	0
8.4															2	1	2	2
8.6															0	1	3	1
8.8															3	1	1	2
9.0															1		0	4
9.2																	0	3
9.4																	1	2
9.6																		2
9.8																		2
10.0																		2
10.2																		1
10.4																		1
	43	202	58	56	51	14	16	31	17	16	23	34	21	17	32	18	15	23

Table A 7.
Total Lengths of Young Tivela, Year-Class of 1918

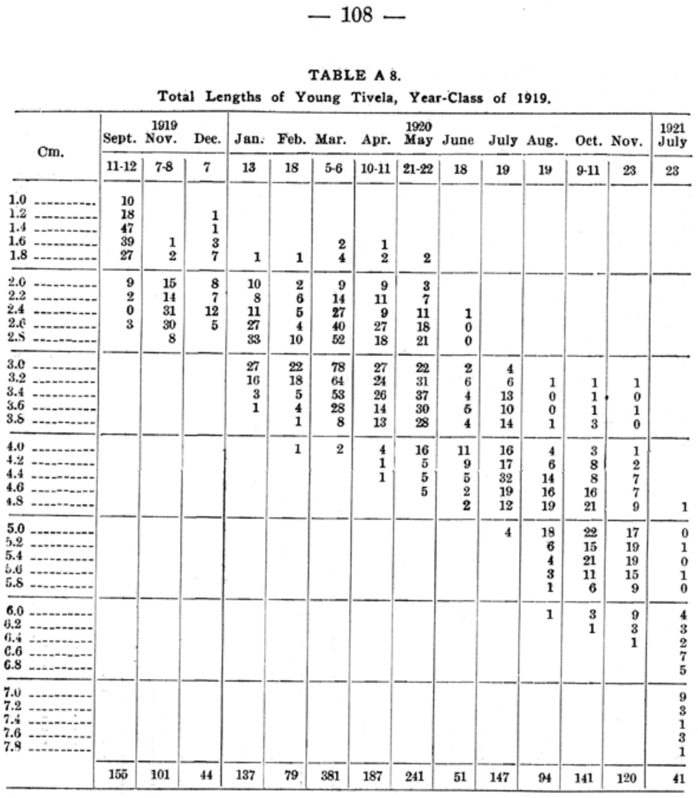


TABLE A 8.

Total Lengths of Young Tivela, Year-Class of 1919.

Cm.	Sept.	1919 Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	1920 May	June	July	Aug.	Oct.	Nov.	1921 July
	11-12	7-8	7	13	18	5-6	10-11	21-22	18	19	19	9-11	23	23
1.0	10													
1.2	18		1											
1.4	47		1											
1.6	39	1	3			2	1							
1.8	27	2	7	1	1	4	2	2						
2.0	9	15	8	10	2	9	9	3						
2.2	2	14	7	8	6	14	11	7						
2.4	0	31	12	11	5	27	9	11	1					
2.6	3	30	5	27	4	40	27	18	0					
2.8		8		33	10	52	18	21	0					
3.0				27	22	78	27	22	2	4				
3.2				16	18	64	24	31	6	6	1	1	1	
3.4				3	5	53	26	37	4	13	0	1	0	
3.6				1	4	28	14	30	5	10	0	1	1	
3.8					1	8	13	28	4	14	1	3	0	
4.0					1	2	4	16	11	16	4	3	1	
4.2							1	5	9	17	6	8	2	
4.4							1	5	5	32	14	8	7	
4.6								5	2	19	16	16	7	
4.8									2	12	19	21	9	1
5.0										4	18	22	17	0
5.2											6	15	19	1
5.4											4	21	19	0
5.6											3	11	15	1
5.8											1	6	9	0
6.0											1	3	9	4
6.2												1	3	3
6.4													1	2
6.6														7
6.8														5
7.0														9
7.2														3
7.4														1
7.6														3
7.8														1
	155	101	44	137	79	381	187	241	51	147	94	141	120	41

Table A 8.
Total Lengths of Young Tivela, Year-Class of 1919

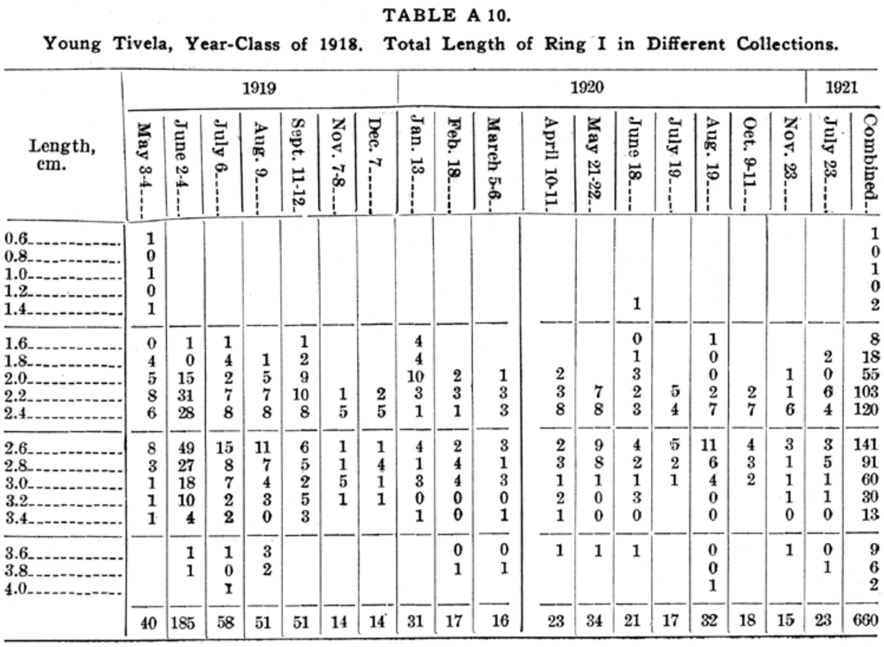


TABLE A 10.

Young Tivela, Year-Class of 1918. Total Length of Ring I in Different Collections.

Length, cm.	1919							1920											1921	
	May 3-4	June 2-4	July 6	Aug. 9	Sept. 11-12	Nov. 7-8	Dec. 7	Jan. 13	Feb. 18	March 5-6	April 10-11	May 21-22	June 18	July 19	Aug. 19	Oct. 9-11	Nov. 23	July 23	Combined
0.6	1																		1
0.8	0																		0
1.0	1																		1
1.2	0																		0
1.4	1												1						2
1.6	0	1	1		1			4					0		1				8
1.8	4	0	4	1	2			4					1		0			2	18
2.0	5	15	2	5	9			10	2	1	2		3		0		1	0	55
2.2	8	31	7	7	10	1	2	3	3	3	3	7	2	5	2	2	1	6	103
2.4	6	28	8	8	8	5	5	1	1	3	8	8	3	4	7	7	6	4	120
2.6	8	49	15	11	6	1	1	4	2	3	2	9	4	5	11	4	3	3	141
2.8	3	27	8	7	5	1	4	1	4	1	3	8	2	2	6	3	1	5	91
3.0	1	18	7	4	2	5	1	3	4	3	1	1	1	1	4	2	1	1	60
3.2	1	10	2	3	5	1	1	0	0	0	2	0	3		0		1	1	30
3.4	1	4	2	0	3			1	0	1	1	0	0		0		0	0	13
3.6		1	1	3					0	0	1	1	1		0		1	0	9
3.8		1	0	2					1	1					0			1	6
4.0			1												1				2
	40	185	58	51	51	14	14	31	17	16	23	34	21	17	32	18	15	23	660

Table A 10.
Young Tivela, Year-Class of 1918. Total Length of Ring I in Different Collections

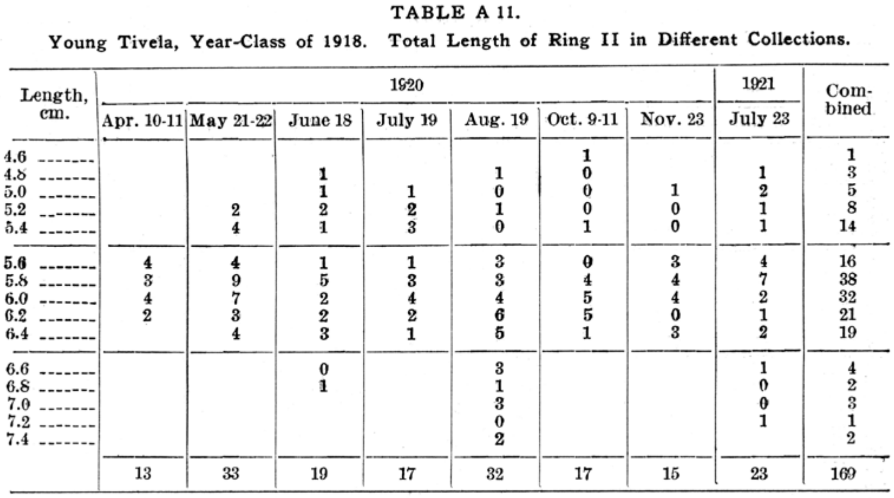
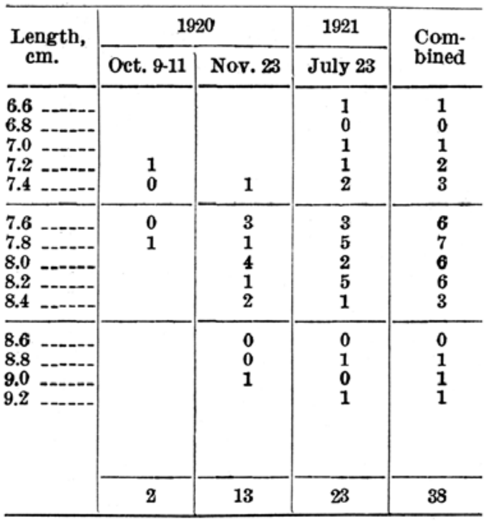


TABLE A 11.

Young Tivela, Year-Class of 1918. Total Length of Ring II in Different Collections.

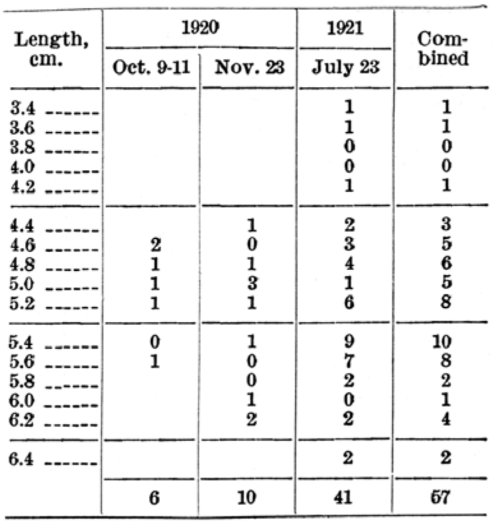
Length, cm.	1920							1921	Com-bined
	Apr. 10-11	May 21-22	June 18	July 19	Aug. 19	Oct. 9-11	Nov. 23	July 23	
4.6						1			1
4.8			1		1	0		1	3
5.0			1	1	0	0	1	2	5
5.2		2	2	2	1	0	0	1	8
5.4		4	1	3	0	1	0	1	14
5.6	4	4	1	1	3	0	3	4	16
5.8	3	9	5	3	3	4	4	7	38
6.0	4	7	2	4	4	5	4	2	32
6.2	2	3	2	2	6	5	0	1	21
6.4		4	3	1	5	1	3	2	19
6.6			0		3			1	4
6.8			1		1			0	2
7.0					3			0	3
7.2					0			1	1
7.4					2				2
	13	33	19	17	32	17	15	23	169

Table A 11.
Young Tivela, Year-Class of 1918. Total Length of Ring II in Different Collections



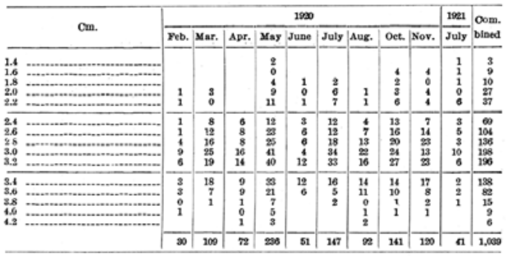
Length, cm.	1920		1921	Combined
	Oct. 9-11	Nov. 23	July 23	
6.6			1	1
6.8			0	0
7.0			1	1
7.2	1		1	2
7.4	0	1	2	3
7.6	0	3	3	6
7.8	1	1	5	7
8.0		4	2	6
8.2		1	5	6
8.4		2	1	3
8.6		0	0	0
8.8		0	1	1
9.0		1	0	1
9.2			1	1
	2	13	23	38

Table A 12.
Young Tivela, Year-Class of 1918. Total Length of Ring III in Different Collections



Length, cm.	1920		1921	Combined
	Oct. 9-11	Nov. 23	July 23	
3.4			1	1
3.6			1	1
3.8			0	0
4.0			0	0
4.2			1	1
4.4		1	2	3
4.6	2	0	3	5
4.8	1	1	4	6
5.0	1	3	1	5
5.2	1	1	6	8
5.4	0	1	9	10
5.6	1	0	7	8
5.8		0	2	2
6.0		1	0	1
6.2		2	2	4
6.4			2	2
	6	10	41	57

Table A 13.
Young Tivela, Year-Class of 1919. Total Length of Ring I in Different Collections



Cm.	1920									1921	Combined
	Feb.	Mar.	Apr.	May	June	July	Aug.	Oct.	Nov.	July	
1.4				2						1	3
1.6				0				4	4	1	9
1.8				4	1	2		2	0	1	10
2.0	1	3		9	0	6	1	3	4	0	27
2.2	1	0		11	1	7	1	6	4	6	37
2.4	1	8	6	12	3	12	4	13	7	3	60
2.6	1	12	8	23	6	12	7	16	14	5	104
2.8	4	16	8	25	6	18	13	20	23	3	136
3.0	9	25	16	41	4	34	22	24	13	10	198
3.2	6	19	14	40	12	33	16	27	23	6	196
3.4	3	18	9	33	12	16	14	14	17	2	138
3.6	3	7	9	21	6	5	11	10	8	2	82
3.8	0	1	1	7		2	0	1	2	1	15
4.0	1		0	5			1	1	1		9
4.2			1	3			2				6
	30	109	72	236	51	147	92	141	120	41	1,039

Table A 14.
Young Tivela, Year-Class of 1919. Total Length of Ring II in Different Collections

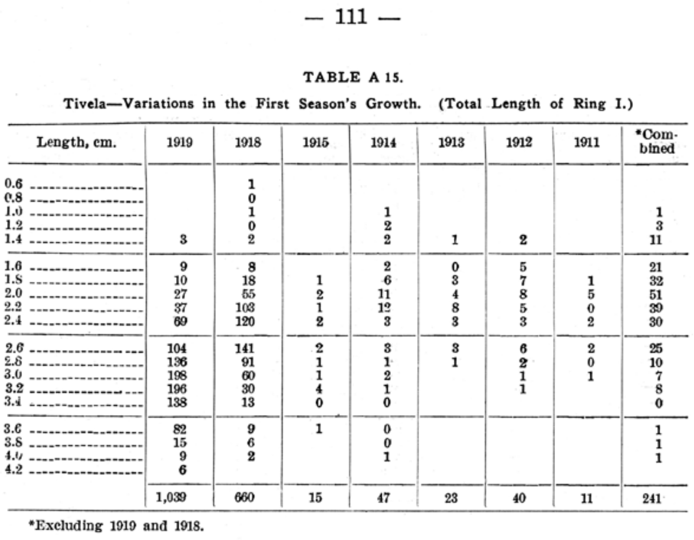


TABLE A 15.

Tivela—Variations in the First Season's Growth. (Total Length of Ring I.)

Length, cm.	1919	1918	1915	1914	1913	1912	1911	*Combined
0.6		1						
0.8		0						
1.0		1		1				1
1.2		0		2				3
1.4	3	2		2	1	2		11
1.6	9	8		2	0	5		21
1.8	10	18	1	6	3	7	1	32
2.0	27	55	2	11	4	8	5	51
2.2	37	103	1	12	8	5	0	39
2.4	69	120	2	3	3	3	2	30
2.6	104	141	2	3	3	6	2	25
2.8	136	91	1	1	1	2	0	10
3.0	198	60	1	2		1	1	7
3.2	196	30	4	1		1		8
3.4	138	13	0	0				0
3.6	82	9	1	0				1
3.8	15	6		0				1
4.0	9	2		1				1
4.2	6							
	1,039	660	15	47	23	40	11	241

*Excluding 1919 and 1918.

Table A 15.
Tivela—Variations in the First Season's Growth. (Total Length of Ring I.)

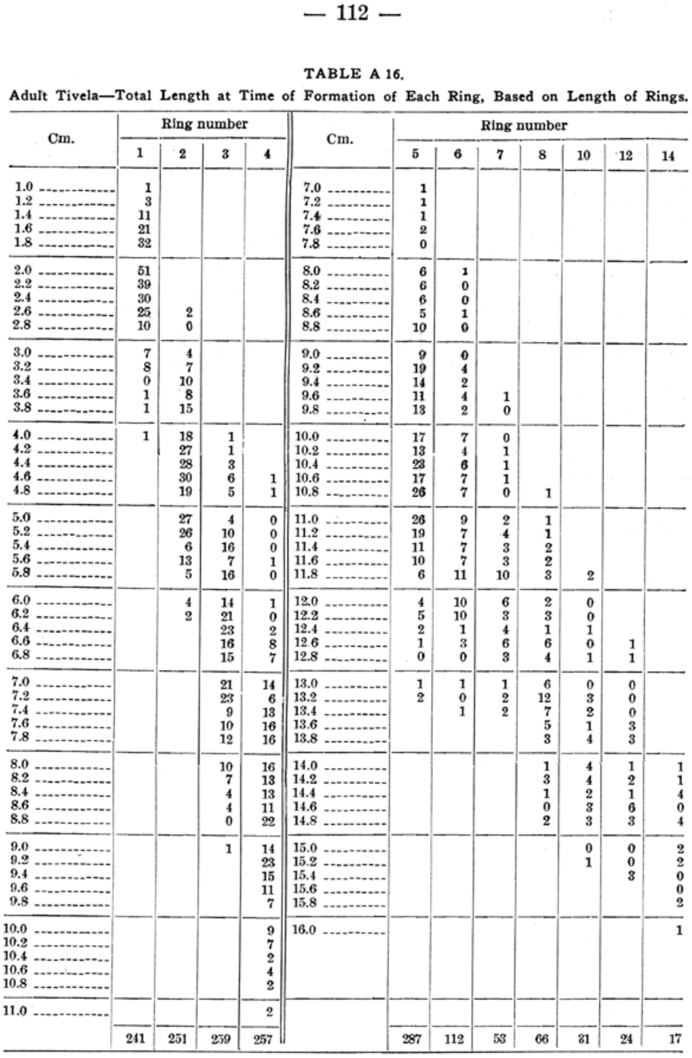


TABLE A 16.

Adult Tivela—Total Length at Time of Formation of Each Ring, Based on Length of Rings.

Cm.	Ring number				Cm.	Ring number						
	1	2	3	4		5	6	7	8	10	12	14
1.0	1				7.0	1						
1.2	3				7.2	1						
1.4	11				7.4	1						
1.6	21				7.6	2						
1.8	32				7.8	0						
2.0	51				8.0	6	1					
2.2	39				8.2	6	0					
2.4	30				8.4	6	0					
2.6	25	2			8.6	5	1					
2.8	10	0			8.8	10	0					
3.0	7	4			9.0	9	0					
3.2	8	7			9.2	19	4					
3.4	0	10			9.4	14	2					
3.6	1	8			9.6	11	4	1				
3.8	1	15			9.8	13	2	0				
4.0	1	18	1		10.0	17	7	0				
4.2		27	1		10.2	13	4	1				
4.4		28	3		10.4	23	6	1				
4.6		30	6	1	10.6	17	7	1				
4.8		19	5	1	10.8	26	7	0	1			
5.0		27	4	0	11.0	26	9	2	1			
5.2		26	10	0	11.2	19	7	4	1			
5.4		6	16	0	11.4	11	7	3	2			
5.6		13	7	1	11.6	10	7	3	2			
5.8		5	16	0	11.8	6	11	10	3	2		
6.0		4	14	1	12.0	4	10	6	2	0		
6.2		2	21	0	12.2	5	10	3	3	0		
6.4			23	2	12.4	2	1	4	1	1		
6.6			16	8	12.6	1	3	6	6	0	1	
6.8			15	7	12.8	0	0	3	4	1	1	
7.0			21	14	13.0	1	1	1	6	0	0	
7.2			23	6	13.2	2	0	2	12	3	0	
7.4			9	13	13.4		1	2	7	2	0	
7.6			10	16	13.6				5	1	3	
7.8			12	16	13.8				3	4	3	
8.0			10	16	14.0				1	4	1	1
8.2			7	13	14.2				3	4	2	1
8.4			4	13	14.4				1	2	1	4
8.6			4	11	14.6				0	3	6	0
8.8			0	22	14.8				2	3	3	4
9.0			1	14	15.0					0	0	2
9.2				23	15.2					1	0	2
9.4				15	15.4						3	0
9.6				11	15.6							0
9.8				7	15.8							2
10.0				9	16.0							1
10.2				7								
10.4				2								
10.6				4								
10.8				2								
11.0				2								
	241	251	259	257		287	112	53	66	31	24	17

Table A 16.
Adult Tivela—Total Length at Time of Formation of Each Ring, Based on Length of Rings

TABLE A 17.

Adult Tivela—Total Lengths Based on Direct Measurements.

Cm.	Age										
	5.5	6	6.5	7	7.5	8	8.5	9	9.5	10	10.5
8.6	2										
8.8	0										
9.0	0										
9.2	0										
9.4	2										
9.6	1		1								
9.8	8		1								
10.0	2	1	1								
10.2	4	0	2								
10.4	3	0	2								
10.6	6	2	1	1							
10.8	0	0	2	0	1						
11.0	1	2	0	0	1						
11.2	2	0	1	0	0		1				
11.4	2	1	3	1	0		0				
11.6	2	0	5	0	1		0				
11.8	2	0	1	1	0		1		2		
12.0	3	0	1	1	2	1	0		0		
12.2	0	0	8	2	7	2	1		0		
12.4	0	0	2	0	5	2	4	2	0		1
12.6	3	1	6	1	5	3	7	1	2		0
12.8	2		2	1	9	0	5	1	2	1	1
13.0	1		0	0	6	1	5	2	1	0	1
13.2	0		0	0	8	4	8	1	3	0	2
13.4	0		2	1	2	0	7	1	2	0	4
13.6	1		1	0	4	1	4	0	3	0	0
13.8				0	4	2	2	0	3	0	1
14.0				0	0	1	1	1	6	0	3
14.2				0	1		0		1	0	1
14.4				1	0		1		1	0	1
14.6					1		1		0	1	2
14.8							0		0		0
15.0							0		1		0
15.2							1				0
15.4											0
15.6											1
	47	7	42	10	57	17	49	9	27	2	18

Table A 17.
Adult Tivela—Total Lengths Based on Direct Measurements

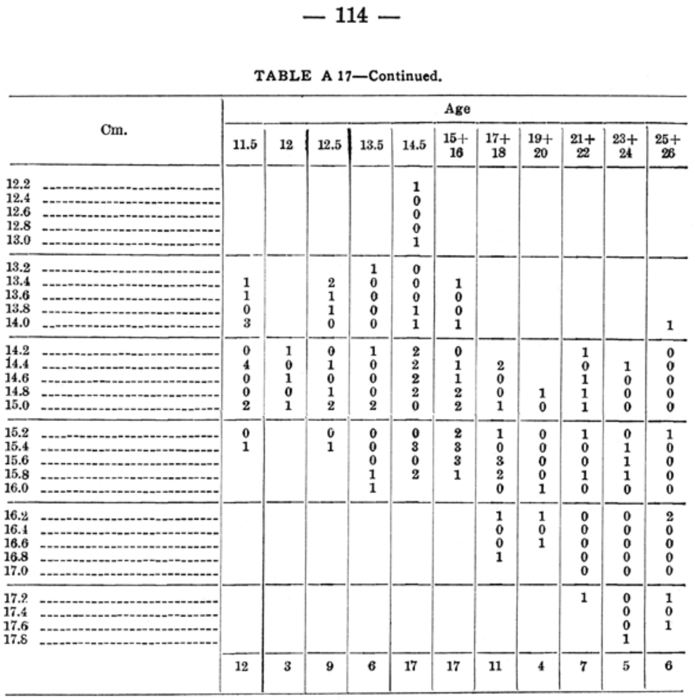


TABLE A 17—Continued.

Cm.	Age										
	11.5	12	12.5	13.5	14.5	15+ 16	17+ 18	19+ 20	21+ 22	23+ 24	25+ 26
12.2					1						
12.4					0						
12.6					0						
12.8					0						
13.0					1						
13.2				1	0						
13.4	1		2	0	0	1					
13.6	1		1	0	0	0					
13.8	0		1	0	1	0					
14.0	3		0	0	1	1					1
14.2	0	1	0	1	2	0			1		0
14.4	4	0	1	0	2	1	2		0	1	0
14.6	0	1	0	0	2	1	0		1	0	0
14.8	0	0	1	0	2	2	0	1	1	0	0
15.0	2	1	2	2	0	2	1	0	1	0	0
15.2	0		0	0	0	2	1	0	1	0	1
15.4	1		1	0	3	3	0	0	0	1	0
15.6				0	0	3	3	0	0	1	0
15.8				1	2	1	2	0	1	1	0
16.0				1			0	1	0	0	0
16.2							1	1	0	0	2
16.4							0	0	0	0	0
16.6							0	1	0	0	0
16.8							1		0	0	0
17.0									0	0	0
17.2									1	0	1
17.4										0	0
17.6										0	1
17.8										1	
	12	3	9	6	17	17	11	4	7	5	6

Table A 17—Continued.

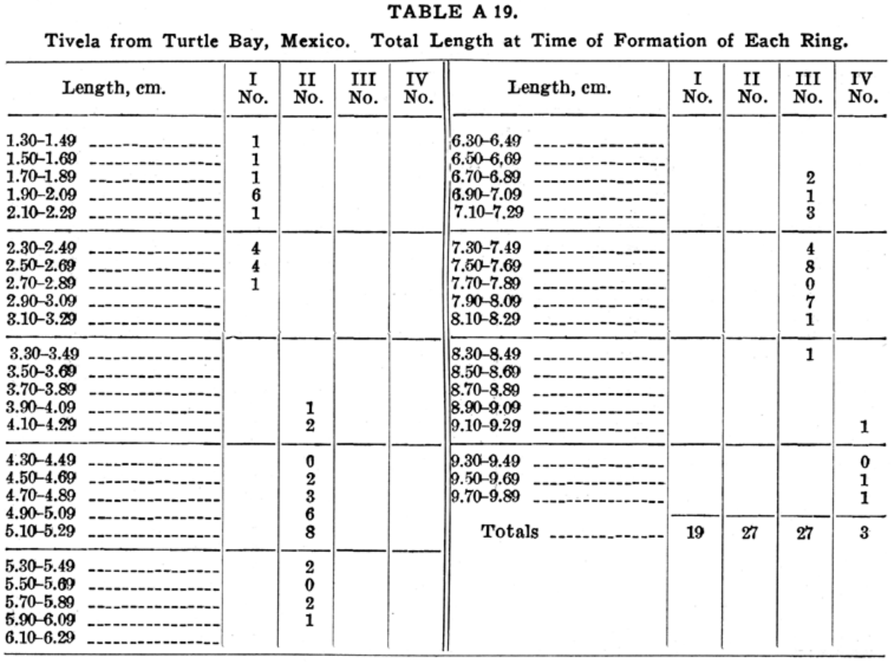


TABLE A 19.

Tivela from Turtle Bay, Mexico. Total Length at Time of Formation of Each Ring.

Length, cm.	I No.	II No.	III No.	IV No.
1.30–1.49	1			
1.50–1.69	1			
1.70–1.89	1			
1.90–2.09	6			
2.10–2.29	1			
2.30–2.49	4			
2.50–2.69	4			
2.70–2.89	1			
2.90–3.09				
3.10–3.29				
3.30–3.49				
3.50–3.69				
3.70–3.89				
3.90–4.09		1		
4.10–4.29		2		
4.30–4.49		0		
4.50–4.69		2		
4.70–4.89		3		
4.90–5.09		6		
5.10–5.29		8		
5.30–5.49		2		
5.50–5.69		0		
5.70–5.89		2		
5.90–6.09		1		
6.10–6.29				
6.30–6.49				
6.50–6.69				
6.70–6.89			2	
6.90–7.09			1	
7.10–7.29			3	
7.30–7.49			4	
7.50–7.69			8	
7.70–7.89			0	
7.90–8.09			7	
8.10–8.29			1	
8.30–8.49			1	
8.50–8.69				
8.70–8.89				
8.90–9.09				
9.10–9.29				1
9.30–9.49				0
9.50–9.69				1
9.70–9.89				1
Totals	19	27	27	3

Table A 19.
Tivela from Turtle Bay, Mexico. Total Length at Time of Formation of Each Ring

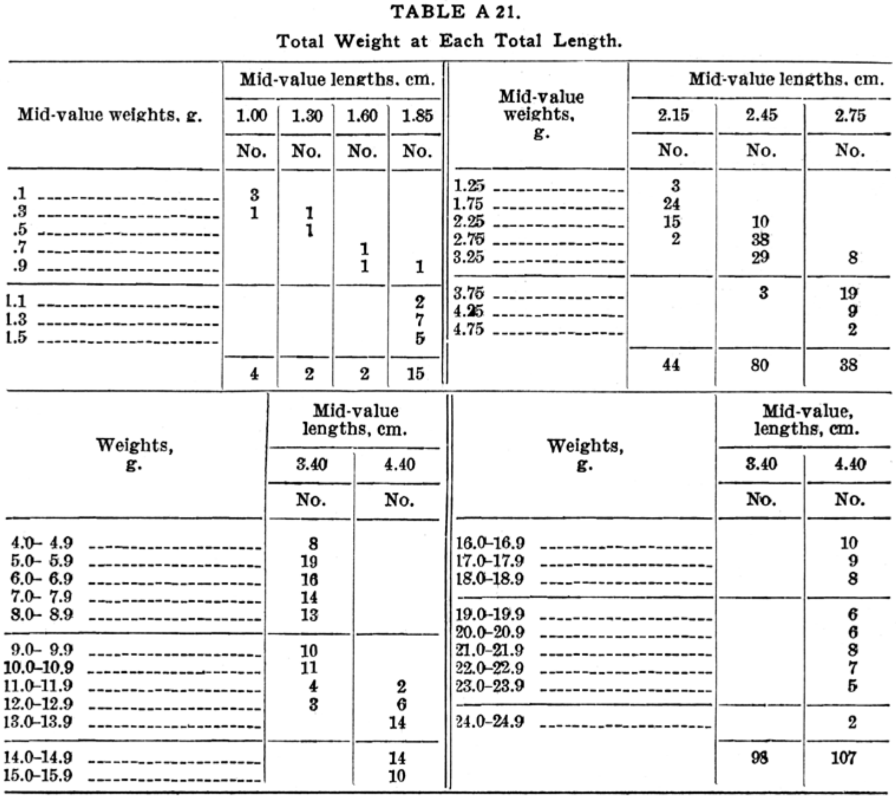


TABLE A 21.

Total Weight at Each Total Length.

Mid-value weights, g.	Mid-value lengths, cm. 1.00 No.	1.30 No.	1.60 No.	1.85 No.
.1	3			
.3	1	1		
.5		1		
.7			1	
.9			1	1
1.1				2
1.3				7
1.5				5
	4	2	2	15

Mid-value weights, g.	Mid-value lengths, cm. 2.15 No.	2.45 No.	2.75 No.
1.25	3		
1.75	24		
2.25	15	10	
2.75	2	38	
3.25		29	8
3.75		3	19
4.25			9
4.75			2
	44	80	38

Weights, g.	Mid-value lengths, cm. 3.40 No.	4.40 No.
4.0– 4.9	8	
5.0– 5.9	19	
6.0– 6.9	16	
7.0– 7.9	14	
8.0– 8.9	13	
9.0– 9.9	10	
10.0–10.9	11	
11.0–11.9	4	2
12.0–12.9	3	6
13.0–13.9		14
14.0–14.9		14
15.0–15.9		10
16.0–16.9		10
17.0–17.9		9
18.0–18.9		8
19.0–19.9		6
20.0–20.9		6
21.0–21.9		8
22.0–22.9		7
23.0–23.9		5
24.0–24.9		2
	98	107

Table A 21.
Total Weight at Each Total Length

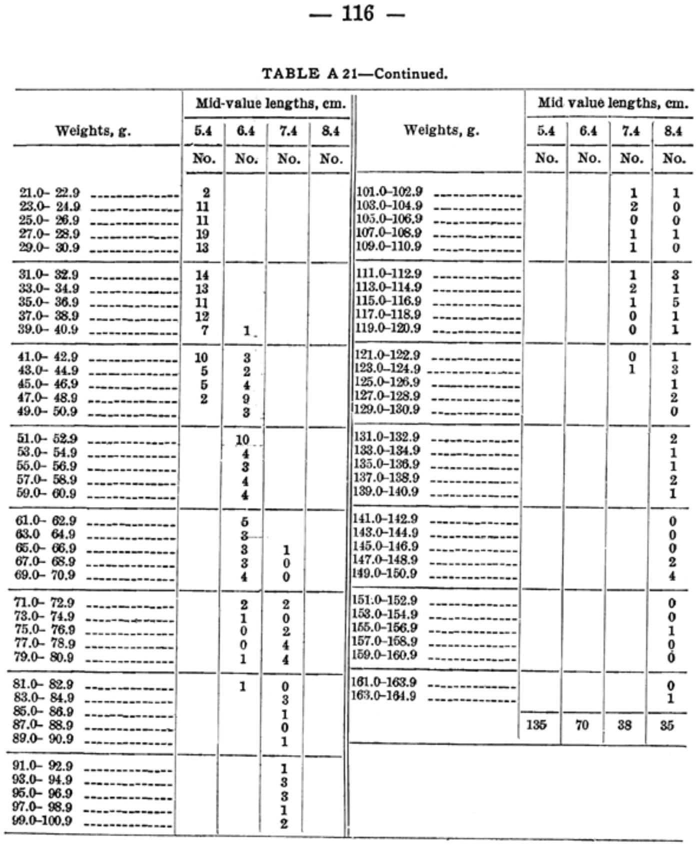


TABLE A 21—Continued.

Weights, g.	Mid-value lengths, cm.			
	5.4	6.4	7.4	8.4
	No.	No.	No.	No.
21.0- 22.9	2			
23.0- 24.9	11			
25.0- 26.9	11			
27.0- 28.9	19			
29.0- 30.9	13			
31.0- 32.9	14			
33.0- 34.9	13			
35.0- 36.9	11			
37.0- 38.9	12			
39.0- 40.9	7	1		
41.0- 42.9	10	3		
43.0- 44.9	5	2		
45.0- 46.9	5	4		
47.0- 48.9	2	9		
49.0- 50.9		3		
51.0- 52.9		10		
53.0- 54.9		4		
55.0- 56.9		3		
57.0- 58.9		4		
59.0- 60.9		4		
61.0- 62.9		5		
63.0 64.9		3		
65.0- 66.9		3	1	
67.0- 68.9		3	0	
69.0- 70.9		4	0	
71.0- 72.9		2	2	
73.0- 74.9		1	0	
75.0- 76.9		0	2	
77.0- 78.9		0	4	
79.0- 80.9		1	4	
81.0- 82.9		1	0	
83.0- 84.9			3	
85.0- 86.9			1	
87.0- 88.9			0	
89.0- 90.9			1	
91.0- 92.9			1	
93.0- 94.9			3	
95.0- 96.9			3	
97.0- 98.9			1	
99.0-100.9			2	
101.0-102.9			1	1
103.0-104.9			2	0
105.0-106.9			0	0
107.0-108.9			1	1
109.0-110.9			1	0
111.0-112.9			1	3
113.0-114.9			2	1
115.0-116.9			1	5
117.0-118.9			0	1
119.0-120.9			0	1
121.0-122.9			0	1
123.0-124.9			1	3
125.0-126.9				1
127.0-128.9				2
129.0-130.9				0
131.0-132.9				2
133.0-134.9				1
135.0-136.9				1
137.0-138.9				2
139.0-140.9				1
141.0-142.9				0
143.0-144.9				0
145.0-146.9				0
147.0-148.9				2
149.0-150.9				4
151.0-152.9				0
153.0-154.9				0
155.0-156.9				1
157.0-158.9				0
159.0-160.9				0
161.0-163.9				0
163.0-164.9				1
	135	70	38	35

Table A 21—Continued.

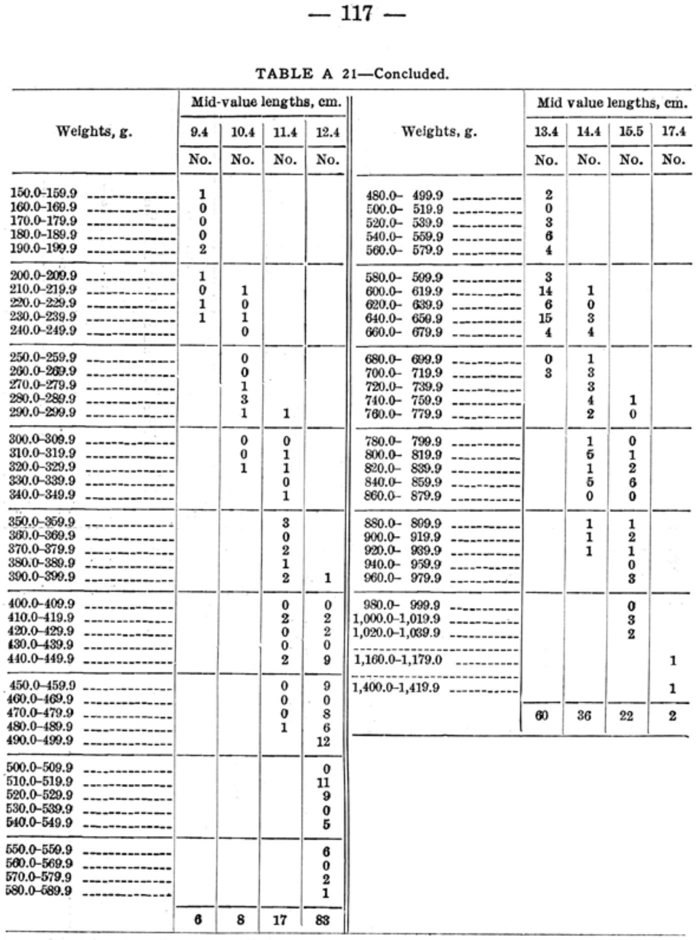


TABLE A 21—Concluded.

Weights, g.	Mid-value lengths, cm.			
	9.4	10.4	11.4	12.4
	No.	No.	No.	No.
150.0–159.9	1			
160.0–169.9	0			
170.0–179.9	0			
180.0–189.9	0			
190.0–199.9	2			
200.0–209.9	1			
210.0–219.9	0	1		
220.0–229.9	1	0		
230.0–239.9	1	1		
240.0–249.9		0		
250.0–259.9		0		
260.0–269.9		0		
270.0–279.9		1		
280.0–289.9		3		
290.0–299.9		1	1	
300.0–309.9		0	0	
310.0–319.9		0	1	
320.0–329.9		1	1	
330.0–339.9			0	
340.0–349.9			1	
350.0–359.9			3	
360.0–369.9			0	
370.0–379.9			2	
380.0–389.9			1	
390.0–399.9			2	1
400.0–409.9			0	0
410.0–419.9			2	2
420.0–429.9			0	2
430.0–439.9			0	0
440.0–449.9			2	9
450.0–459.9			0	9
460.0–469.9			0	0
470.0–479.9			0	8
480.0–489.9			1	6
490.0–499.9				12
500.0–509.9				0
510.0–519.9				11
520.0–529.9				9
530.0–539.9				0
540.0–549.9				5
550.0–559.9				6
560.0–569.9				0
570.0–579.9				2
580.0–589.9				1
	6	8	17	83

Weights, g.	Mid value lengths, cm.			
	13.4	14.4	15.5	17.4
	No.	No.	No.	No.
480.0– 499.9	2			
500.0– 519.9	0			
520.0– 539.9	3			
540.0– 559.9	6			
560.0– 579.9	4			
580.0– 509.9	3			
600.0– 619.9	14	1		
620.0– 639.9	6	0		
640.0– 659.9	15	3		
660.0– 679.9	4	4		
680.0– 699.9	0	1		
700.0– 719.9	3	3		
720.0– 739.9		3		
740.0– 759.9		4	1	
760.0– 779.9		2	0	
780.0– 799.9		1	0	
800.0– 819.9		5	1	
820.0– 839.9		1	2	
840.0– 859.9		5	6	
860.0– 879.9		0	0	
880.0– 899.9		1	1	
900.0– 919.9		1	2	
920.0– 939.9		1	1	
940.0– 959.9			0	
960.0– 979.9			3	
980.0– 999.9			0	
1,000.0–1,019.9			3	
1,020.0–1,039.9			2	
1,160.0–1,179.0				1
1,400.0–1,419.9				1
	60	36	22	2

Table A 21—Continued.

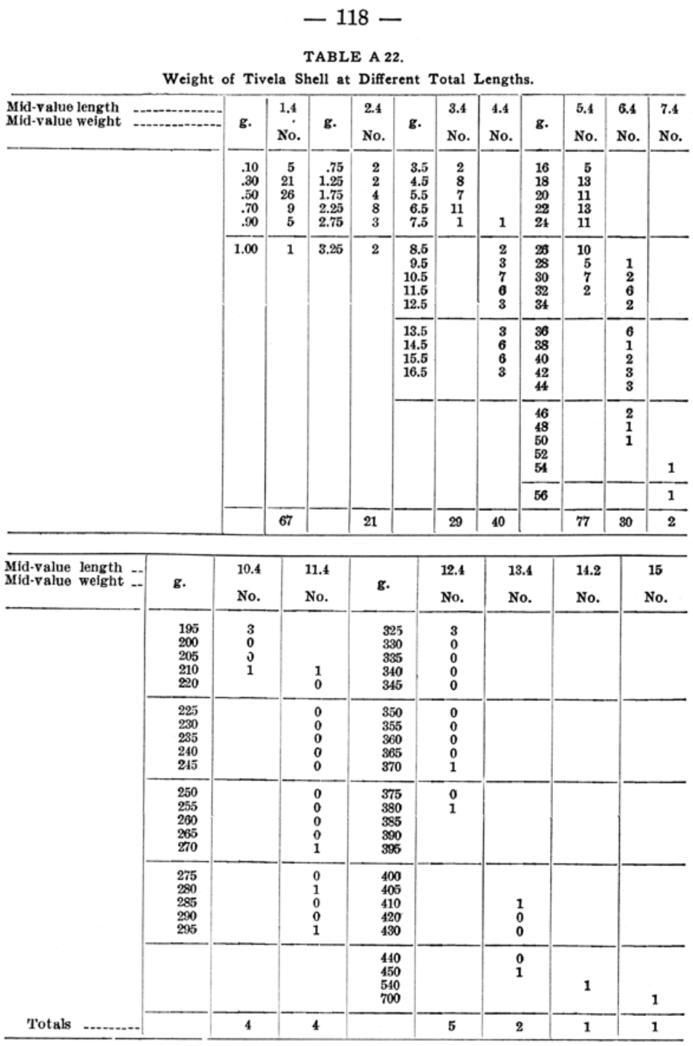


TABLE A 22.

Weight of Tivela Shell at Different Total Lengths.

Mid-value length		1.4		2.4		3.4	4.4		5.4	6.4	7.4
Mid-value weight	g.	No.	g.	No.	g.	No.	No.	g.	No.	No.	No.
	.10	5	.75	2	3.5	2		16	5		
	.30	21	1.25	2	4.5	8		18	13		
	.50	26	1.75	4	5.5	7		20	11		
	.70	9	2.25	8	6.5	11		22	13		
	.90	5	2.75	3	7.5	1	1	24	11		
	1.00	1	3.25	2	8.5		2	26	10		
					9.5		3	28	5	1	
					10.5		7	30	7	2	
					11.5		6	32	2	6	
					12.5		3	34		2	
					13.5		3	36		6	
					14.5		6	38		1	
					15.5		6	40		2	
					16.5		3	42		3	
								44		3	
								46		2	
								48		1	
								50		1	
								52			
								54			1
								56			1
		67		21		29	40		77	30	2

Mid-value length		10.4	11.4		12.4	13.4	14.2	15
Mid-value weight	g.	No.	No.	g.	No.	No.	No.	No.
	195	3		325	3			
	200	0		330	0			
	205	0		335	0			
	210	1	1	340	0			
	220		0	345	0			
	225		0	350	0			
	230		0	355	0			
	235		0	360	0			
	240		0	365	0			
	245		0	370	1			
	250		0	375	0			
	255		0	380	1			
	260		0	385				
	265		0	390				
	270		1	395				
	275		0	400				
	280		1	405				
	285		0	410		1		
	290		0	420		0		
	295		1	430		0		
				440		0		
				450		1		
				540			1	
				700				1
Totals		4	4		5	2	1	1

Table A 22.
Weight of Tivela Shell at Different Total Lengths

INDEX

Contribution No. 37 from the State Fisheries Laboratory. This paper represents part of a general program of the Fish and Game Commission of California for the investigation of the marine resources of the state. It has been made possible by the far-sighted policy and hearty support of Mr. N. B. Scofield, in charge of the Department of Commercial Fisheries, and is to be considered as a report, containing recommendations (p. ___), transmitted through him to the Board of Fish and Game Commissioners. It is also presented as a thesis to the Department of Zoology of Stanford University in partial fulfillment of the requirements for the degree of doctor of philosophy.

A complete acknowledgement of the assistance received from friends and associates is not possible here, but certain debts deserve specific mention. To Dr. Charles H. Gilbert, Professor of Zoology, Stanford University, to whom I owe the inspiration for, and the training in, this type of work, I am grateful for much helpful advice and criticism. It is not inappropriate here to point out that the type of investigation to which this paper is intended as a contribution owes its present standards and extent on the Pacific coast almost wholly to Dr. Gilbert, who directly, through his own research and indirectly through the work of his pupils, is responsible for most of our present knowledge concerning the economically valuable marine animals of this region. To certain of my friends who have been engaged with these problems I am especially indebted. Mr. Will F. Thompson has followed all stages of the present work from its inception and his advice, of which I have often availed myself, has been particularly helpful because of his clear understanding of the questions involved. Mr. Willis H. Rich of the United States Bureau of Fisheries, has offered many suggestions which have proved of material assistance, especially, as elsewhere acknowledged, in the study of growth. To my wife, Alice J. Weymouth, I am indebted for aid in many phases of the work; she has carefully revised the manuscript throughout and has prepared several of the drawings particularly those of the shell (figures 7, figure 8 and 11) based on a detailed study of its structure. The graphs were drawn by Mr. G. H. Payne.

The work was carried out in part, at the State Fisheries Laboratory, in charge of Mr. Will F. Thompson; in part, at the Hopkins Marine Station, to the director of which, Dr. W. K. Fisher, thanks are due for numerous courtesies; and in part, in the Laboratory of Physiology, Stanford University.

Lastly I wish to acknowledge the hearty and intelligent cooperation, without which the necessary material could not have been obtained, of various commercial clam diggers, particularly of Mr. J. A. Beckett and his son Mr. Farley Beckett of Oceano, California.