THE RELATIVE GROWTH AND MORTALITY OF THE PACIFIC RAZOR CLAM (*SILIQUA PATULA*, DIXON), AND THEIR BEARING ON THE COMMERCIAL FISHERY [1]

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CONTENTS

INTRODUCTION

The present paper is a continuation of previous work on the economically important mollusks of the Pacific coast of North America. The earlier studies of the senior author on the bivalves of California led to the development of a method of determining age and thus made possible an accurate study of growth. The seasonal growth shown for the Pismo clam has since been substantiated in other species, for example, in *Anodonta*, Thiel (1928) found practically no increase in length during the entire winter. This method of age determination based on the annual rings of the shell was later successfully applied to the Alaska razor clam (fig. 1) which was showing signs of depletion (Weymouth, McMillin, and Holmes, 1925). In the present report the accumulated data on the growth of this species over a wide range of latitude has been analyzed in greater detail. It is clear that in all parts of the coast, where the razor clam is fished commercially, supervision is necessary to maintain this valuable resource. It has become equally clear that the course of growth, breeding habits, and the like vary so widely in different parts of the coast that the regulations must be adapted to the district. Thus in Alaska the set of the young clams seems never to be more than a fraction of that on the Washington beaches, and the growth is much slower. For example, the clams reach the breeding size in two years at Copalis on the Washington coast but require four years at Swickshak, Alaska. The smaller set and slower growth of the clams make the northern beds less resistant to heavy fishing

and slower to return to productivity when depleted. The importance of this knowledge for protective regulations as well as for its intrinsic biological interest makes desirable the analysis here attempted.

THE GENUS SILIQUA

The primary purpose of the present paper is an analysis of the growth data now accumulated for the Pacific razor clam. The first question to be considered is that of the homogeneity of the material studied. The Pacific razor clam belongs to the genus *Siliqua* of the family *Solenidæ*. This genus includes at least 12 species found along the shores of the entire North Pacific from Lower California north to Bering Sea and south on the Asiatic side to the Malay Archipelago. The type of the genus (*Siliqua radiata*) extends into the Indian Ocean and two species are found on the North Atlantic coast from the Arctic down to Cape Hatteras. In the initial report we briefly discussed the systematic relations of certain of these species (Weymouth, McMillin, and Holmes, 1925). More intensive work has convinced us of the validity of our former conclusions. Briefly, we consider that there are four species of *Siliqua* on the west coast of North America: *S. media*, found in Bering Sea and Arctic Ocean; *S. alta*, in Cook Inlet and westward to Bering Sea and Siberia; *S. patula*, from the Aleutian Islands to Pismo, Calif.; and *S. lucida*, from Monterey, Calif., to Lower California. All authorities agree that *S. media* and *S. lucida* are distinct species. The present view differs from that of Dall (1899) in two respects. *S. patula* var. *nuttallii* and typical *S. patula*, which he considers connected by gradiations, we are unable to separate on reliable criteria and are forced, therefore, to deny to *nuttallii* even subspecific rank. *S. patula* var. *alta* considered by Dall as a variety of *S. patula*, we find undoubtedly entitled to specific rank. A more detailed discussion of these species and their relationships is to be presented elsewhere.

We have arrived at the above conclusions after extensive observations on razor-clam beds from San Diego to the Bering Sea. We have dug and handled large numbers of animals and have carefully measured over 6,000 shells, the majority of these measurements being made under laboratory conditions. In addition to the data on form to be presented later, there are differences in the living animal which clearly indicate that *S. alta* represents a distinct species.

The most notable character in *S. alta* is the pigmentation. All exposed parts of the mantle, siphon, and foot are colored by a chocolate-brown pigment which immediately distinguishes it from *S. patula*, which is entirely without this coloration. The siphons of *S. alta* are short and thickly studded with tubercles which become longer near the opening. The siphons of *S. patula* are less closely fused and have a distinct tendency to separate near the openings, the exhalant siphon being the longer. They also lack the tubercles and do not have as long tentacles about the siphon openings. *S. alta* is found higher on the beach and owing to its short siphon lies nearer the surface. These differences and the distinctive pigmentation in *S. alta* make it possible for the commercial clam diggers to recognize these two species readily and to avoid taking *S. alta*.

DIFFERENTIAL GROWTH RATIOS IN SILIQUA PATULA AND S. ALTA

Since the shape of the shell is an important specific character in the genus *Siliqua*, an analysis of the variations in form of the material studied was necessary. Accordingly, not only the length but also, in many cases, the width and the distance
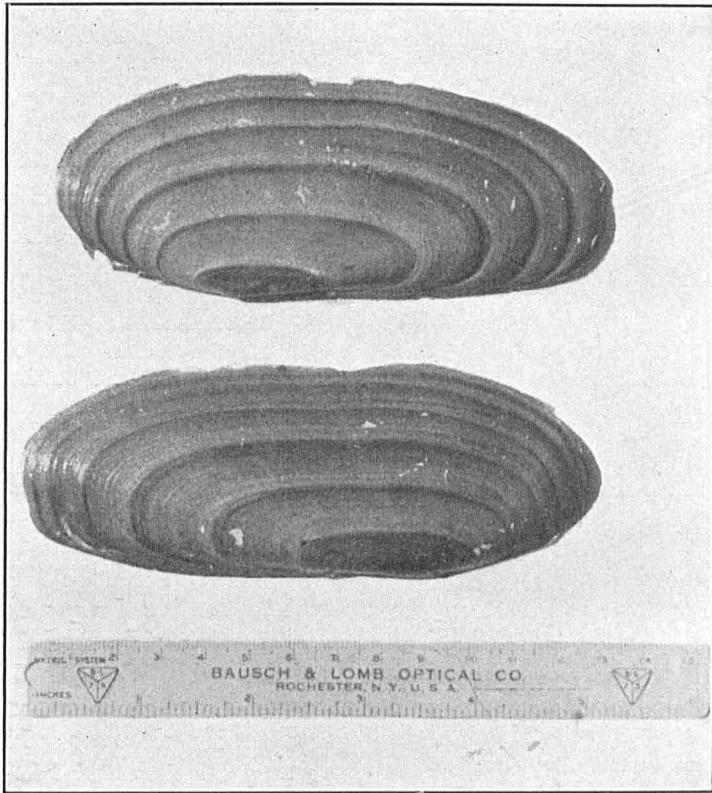
Figure 1.—*Siliqua patula* Dixon (photo by O. W. Richards)

from the umbo to the posterior end of the shell were measured. In a smaller number of cases the ventricosity or transverse diameter, the length of the ligament bed, and other dimensions were determined but these proved less useful.

Although the form of animals, as, for example, the head length and size of eye in fish, have been used in systematic work, too little attention has been paid to the variability and the changes of form with age. In recent years Huxley and some of his students (1924, 1927, 1927a) have made a series of notable studies of animal form. They have found that in most cases the relation between part and whole may be represented by the formula

$$y = bx^k,$$

where y is the length (or weight) of the part, and x that of the whole.
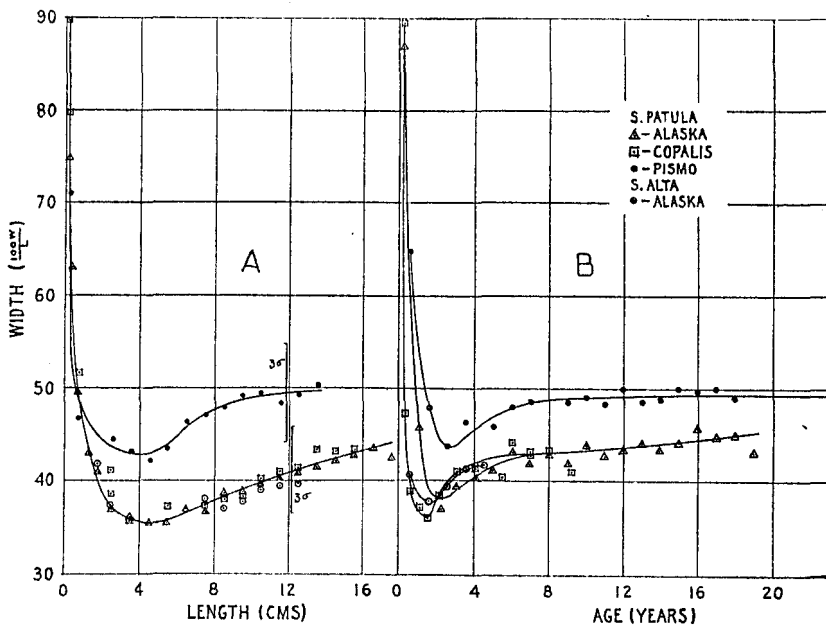
FIGURE 2.—Average percental width of S. patula from California, Washington, and Alaska, S. alta from Alaska. A, For each centimeter of length; and B, for each year of age

If a constant relation of this type persists throughout life we may distinguish two cases. In one the exponent k is unity and the formula becomes

$$y = bx;$$

that is, the part bears a constant relation to the whole, and the form does not change with size. This, Huxley calls "isogonic" growth. On the other hand, k may be greater or less than unity, indicating that the part is increasing or decreasing in relation to the whole, a type of growth called by Huxley "heterogonic." Of course, neither condition may exist through life, but the differential growth ratio may change.

WIDTH

In order to present the length-width relation in the clam, we have calculated the percental width of the shells in a series of 1,330 individuals of S. patula and S. alta. These results are given in Tables 1 and 2 and presented graphically in Figure 2.

Growth is clearly not isogonic. The young of both species are nearly round, but undergo a rapid change in shape as they grow, becoming greatly elongated. This reduction in width continues until the shell is about 5 centimeters in length, when *S. patula* has a width of about 36 per cent and *S. alta* a width of 42 per cent. During the remainder of the life of the clam the shell becomes wider until in the oldest specimens of *S. patula* the width measures 42 per cent of the length and in *S. alta* about 50 per cent.

Treated by Huxley's method of plotting the logarithm of the width on the logarithm of the length we obtain a consistent picture, k is at first less than unity (0.6) and gradually increases, reaching a value of 1 at five or six years (minimum of the above curve) and finally attaining a value of about 1.2. It will be noticed further that specimens from all parts of the coast have the same proportional width of shell. One exception is recorded: The largest shells from Pismo, Calif., show a tendency to be narrower than those from other localities. This difference, however, but slightly exceeds the probable error and is, therefore, of doubtful significance but may be interpreted as an effect of age on the proportional width. This would be comparable to our findings on sexual maturity, which occurs at essentially the same length on different parts of the coast, although at widely different ages (Weymouth, McMillin, and Holmes, 1925). Nevertheless a minor effect of age on sexual maturity can be traced, and it would be reasonable to expect a similar effect on relative width.

TABLE 1.—*Average width of Siliqua patula from California, Washington, and Alaska, and of Siliqua alta from Alaska, for each centimeter of length*

| Length in centimeters | S. patula | | | | | | S. alta | |
| | Alaskan | | Copalis | | Pismo | | | |
	100 W/L	Number of specimens	100 W/L	Number of specimens	100 W/L	Number of specimens	100 W/L	Number of specimens
17.0–17.2	42.5	2						
16.0–16.9	43.6	14						
15.0–15.9	42.9	19	43.5	2				
14.0–14.9	42.1	29	43.3	8				
13.0–13.9	41.5	21	43.4	28			50.3	12
12.0–12.9	41.0	18	41.5	34	39.7	23	49.3	62
11.0–11.9	40.5	18	41.1	37	39.5	36	48.4	31
10.0–10.9	39.9	44	40.3	9	39.0	8	49.5	16
9.0–9.9	38.8	55	38.2	12	37.8	54	49.3	14
8.0–8.9	38.7	31	38.1	13	38.1	33	47.9	15
7.0–7.9	36.9	33	37.5	7	38.0	10	47.2	10
6.0–6.9	36.8	21					46.5	10
5.0–5.9	35.3	12					43.5	17
4.0–4.9	35.3	20	37.3	6			42.2	21
3.0–3.9	36.0	16	35.8	4			43.2	9
2.0–2.9	36.9	33	38.5	8	37.2	38	44.5	7
1.5–1.9	41.0	24	41.0	11	41.9	79		
1.0–1.4	43.1	101					46.8	17
0.5–0.9	49.6	67	51.6	14			51.0	7
0.3–0.4	63.0	12	63.2	3				
0.1–0.2	75.0	7	79.8	3				
0.0–0.1			89.6	3			71.0	2

TABLE 2.—*Average width of Siliqua patula from California, Washington, and Alaska, and of Siliqua alta from Alaska, for each year of age*

Age, years	S. patula						S. alta	
	Kukak		Copalis		Pismo			
	100 W/L	Number of speci-mens	100 W/L	Number of speci-mens	100 W/L	Number of speci-mens	100 W/L	Number of speci-mens
23							49.0	1
19	43.0	2						
18	45.0	2					49.0	2
17	44.8	3					50.0	3
16	45.8	9					49.7	9
15	44.2	33					50.0	14
14	43.5	21					48.8	14
13	44.2	29					48.6	17
12	43.4	37					50.0	12
11	42.8	29					48.5	14
10	44.0	27					49.2	7
9	42.0	6	42.0	4			48.7	3
8	43.0	6	43.3	12				
7	42.9	19	43.3	10			48.8	5
6	43.2	14	44.3	5			48.2	3
5	41.2	3	41.0	10	[1] 41.8	1	46.0	7
4	40.2	39	41.7	22	[1] 41.3	8	[1] 46.5	28
3	39.5	123	41.0	39	[1] 39.4	60	[1] 43.9	42
2	38.2	13	38.6	39				
1.5			36.0	6	37.9	97	48.0	24
1	45.8	2	37.2	11				
0.5			39.0	6	40.8	117	65.0	4
0.2			47.5	27				
0.1	87.1	6	89.6	3				

[1] Ring measurement: For correct age subtract one-half year.

In the foregoing comparisons of the form of *Siliqua patula* and *S. alta* we have used the average of each group. For the length of 11 and 12 centimeters sufficient material is available to show the variability. Here it is found that some specimens of *S. patula* were wider than some of *S. alta*. There is an overlapping between the two distributions which is found to amount to 6 specimens in 200, or 3 per cent of the entire number of clams of these lengths. There can be no doubt of a significant difference in relative width.

POSITION OF UMBO

By measuring the distance from the umbo to the posterior end of the shell, and expressing this as a per cent of the total length of the shell a numerical value for the location of the umbo is obtained. For *S. patula* from all parts of the coast this ratio is constant at any given length. During the period of rapid growth of the clam the umbo shifts toward the posterior end, indicating a relatively greater growth of the anterior end. After a length of 10 centimeters has been reached, the proportion of the length of shell on either side of the umbo is constant. (Table 3.)

Comparable data are available for *S. alta* larger than 10 centimeters. In this species the umbo is more anterior than in *S. patula*. The anterior position of the umbo in *S. alta*, together with the narrower anterior end of the shell, gives it a distinctive appearance by which it can easily be separated from *S. patula*.

TABLE 3.—*Position of the umbo at each centimeter of length for Siliqua patula and Siliqua alta*

Length	Position of umbo		Length	Position of umbo		Length	Position of umbo	
	S. patula	S. alta		S. patula	S. alta		S. patula	S. alta
Centimeters			*Centimeters*			*Centimeters*		
0.0–0.9	71.43		6.0	70.38		12.0	67.33	74.44
1.0	70.75		7.0	70.25	74.50	13.0	67.73	74.67
2.0	72.83		8.0	69.20	72.50	14.0	68.65	76.00
3.0	72.67		9.0	68.00	72.00	15.0	67.70	
4.0	71.67		10.0	67.86	74.25	16.0	68.25	
5.0	71.00		11.0	67.17	74.29	17.0	67.25	

DIRECTION OF RIB

One very noticeable character of the shell is the direction of the rib. If the shell is opened until the two valves lie in the same plane, the two ribs of *Siliqua alta* form nearly a straight line, but those of *S. patula* lie at a distinct angle. The direction of the rib from the umbo was measured by placing the dorsal margin of the shell on the table and reading from a protractor the angle between the table anterior to the umbo and the posterior margin of the rib. The results show a small individual variation which can not be correlated with age or size. In *S. patula* the angle is between 69° and 84°, in *S. alta* between 84° and 90°.

From this study we are convinced that there are four species of the genus *Siliqua* on the west coast of North America. These include, in addition to *S. media* and *S. lucida*, generally recognized, *S. alta* and *S. patula*. The only species considered in the present growth study is *S. patula*.

An additional conclusion applicable to other animals may be drawn from this study of body proportions. It is useless for comparative purposes to state the ratio between the measurements of any two parts of the body, such as length and width of the shell in the present case, or the head and the body length of a fish, unless the total size or age is also given. The variation of these ratios with size and age can not be foretold but must be determined for each species; they are, in the razor clam, so considerable that they can not be ignored. The greatest variation occurs in clams below 5 centimeters in length; but if we disregard these, the larger ones still are widely variable. If we deal with what may justly be considered "adult" specimens, the change in proportional width of either *S. alta* or *S. patula* with size is as great as the differences between the species. In other words, while specimens of the same length show an average difference in width which no one would hesitate to call specific, large specimens of *S. patula* may be selected giving the same average width as those of small *S. alta*. This fact should be borne in mind by systematists in framing specific descriptions.

SILIQUA PATULA

VARIABILITY

The variability of each age class of clams has been measured in terms of "D" or interdecile range (Kelley, 1921) as the most appropriate measure to accompany the median. This may readily be visualized as the range in length of the central 80 per cent of each frequency distribution.

This value for all ages and localities is given in Table 8. For four typical localities Figure 3 shows "D" plotted on length. It will be seen that the absolute variability rises to a maximum after which it again declines to become fairly constant

in the larger sizes (12 to 16 centimeters). The maxima fall at widely different ages but at a common length of 5 to 8 centimeters. The highest absolute variability therefore corresponds in general to the period of most rapid growth but in all cases occurs somewhat after the inflection.

If the relative variability is calculated, a different picture is obtained. The interdecile range expressed as a per cent of the median $\left(\dfrac{100\,D}{Mi}\right)$ is very large in the younger stages, for example at a length of 0.35 centimeter it is over 200. From these high values it falls throughout the available life history until in large clams it is less than 15 per cent of the length.
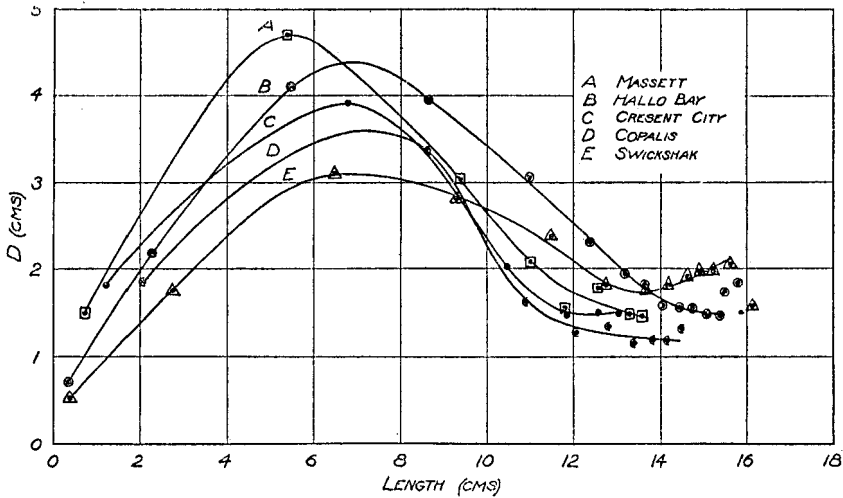

FIGURE 3.—The variability (D) of each length of clams from five localities

SEXUAL DIFFERENCES

In the curves here presented the sexes have not been considered separately except in three localities. The shells of the two sexes are indistinguishable, and hence identification requires the examination of fresh material in which the eggs or sperm may be recognized by a hand lens. In order to see if sexual differences in size or weight were apparent, growth curves were constructed for three localities. At Swickshak 152 males and 150 females between the lengths of 7.50 and 12.25 centimeters were measured. During the period of most rapid growth the differences were too slight and inconsistent to be of significance in spite of the fact that at this time such differences are greatest.

A series of 115 males and 113 females were available from Hallo Bay (Table 4); and since greater and more consistent differences were found in these than in other material, the two curves are reproduced in Figure 4. At the first winter the males average slightly the larger. During the period of most rapid growth, in this case from 2 to 9 years, the males are the shortest and the curves then again cross, the two sexes having the same length during the tenth, eleventh, and twelfth years after which again the males are longer, though the differences are less marked than in the period of rapid growth. Incidentally the mortality of the females is higher as shown by the fact that the males outnumber them from 8 years on, and that from 16 to 19 years only males are represented, although the numbers are small.

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TABLE 4.—*Median lengths of males and females from Hallo Bay to correspond with Figure 4*

Ring number	Males Length	Males Number of specimens	Females Length	Females Number of specimens	Ring number	Males Length	Males Number of specimens	Females Length	Females Number of specimens	Ring number	Males Length	Males Number of specimens	Females Length	Females Number of specimens
	Cm.		Cm.			Cm.		Cm.			Cm.		Cm.	
1	0.39	37	0.32	54	8	13.56	97	13.76	95	15	15.85	15	15.67	12
2	2.07	111	2.48	115	9	14.05	93	14.07	89	16	15.62	8	15.50	2
3	5.05	113	6.22	116	10	14.44	88	14.46	84	17	15.74	4		
4	8.01	113	9.21	116	11	14.77	73	14.77	65	18	16.31	3		
5	10.59	112	11.33	116	12	15.13	57	14.98	54	19	16.74	2		
6	12.21	111	12.59	116	13	15.42	42	15.28	35					
7	13.10	105	13.27	106	14	15.60	28	15.42	24					

Whether the greater difference in the size of the males and females in this series is peculiar to the locality or whether the method of taking the shells did not give an accurate sample, it is impossible to determine. The shells were taken from two lots of
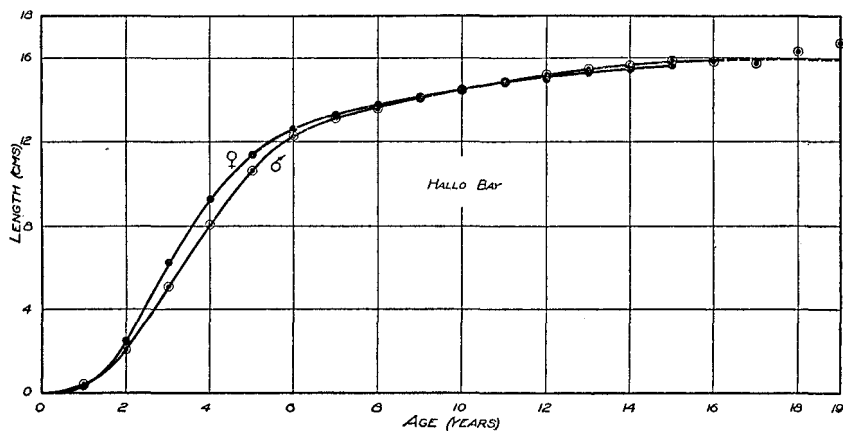

FIGURE 4.—Growth curves for males and females taken in Hallo Bay, Alaska. Age is indicated as ring number; to determine actual age subtract one-half year

clams which may have come from different localities. One sample contained over one-half males and the other a larger number of females, so the significance is doubtful. However, these results are similar to those of Copalis, Wash., although the differences are more marked. The curves in the latter case cross and recross in a similar manner at corresponding periods in their life cycle. Differences in the growth curves of the sexes in mollusks have been described by Chamberlain, who found the course of growth to vary between sexes of fresh-water mussels [2] (1931). In this case, however, the sex is indicated by the shape of the shells, and one can easily determine the sex of the animal from its appearance, while in razor clams weights and proportional measurements of the shell do not show sexual differences. Since the number of each sex is approximately equal, it is assumed that a composite curve calculated from growth records of both sexes, if taken in a limited habitat, is adequate for growth study.

MORTALITY

One striking feature in the study of clams from all parts of the coast is the difference in age found between northern and southern beds. No clams over 5 years old

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[2] Thesis, Stanford University.

have been found at Pismo, Calif. The Washington beds produce clams up to 9 years of age, while the commercial catch in Alaska contains a large number of 13-year-old clams and ages up to 19 years have been recorded. In order that any valid comparison of age may be made it is necessary that mortality data in the form of survival curves be available.

TABLE 5.—*Survival table showing numbers of clams still living at each age for each 100 clams forming first ring, and age of 5 per cent survival for each locality*

Year	Pismo	Crescent City	Channel	Sink	Copalis	Massett	Controller Bay	Karls Bar	Swickshak	Hallo Bay
1	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
2	92.0	98.0	97.3	97.3	98.5	98.7	99.0	98.3	97.6	98.3
3	53.7	93.6	91.1	96.4	91.3	95.8	99.0	97.0	97.6	96.2
4	10.5	88.1	62.8	88.6	83.6	93.4	99.0	96.5	89.6	96.2
5	1.7	79.3	30.4	76.5	71.1	71.8	97.8	94.4	84.3	95.8
6		60.3	11.9	29.6	53.8	54.7	89.1	87.3	80.4	95.3
7		20.9	9.2	2.6	37.1	47.7	71.8	86.0	76.9	88.7
8		4.4	1.1	1.8	17.2	33.0	48.2	54.3	72.0	80.7
9		.6			3.8	12.2	15.9	24.0	62.5	76.9
10						2.0	7.4	14.6	58.6	72.2
11							6.1	9.7	44.8	58.0
12							3.7	5.8	27.2	46.7
13							1.2	3.2	9.5	32.3
14								1.3	1.8	21.8
15								1.3	.4	11.4
16								1.3		3.0
17								1.3		1.3
18										1.3
19										.9
Age (years) of 5 per cent survival	4.4	7.9	7.0	7.0	8.8	9.6	11.0	12.0	13.4	15.6

This need we were forced to supply from age-frequency data from the different beds. We have assumed, as did Lea for the herring (1924), that the frequency of the older ages represents a practical survival curve for that locality and have supplied the earlier portion by comparison with those based on the most adequate data. In the resulting curves for each locality, we located the smallest survival that could be accurately determined, which proved to be 5 per cent. This we have arbitrarily taken as the maximum age. (See Table 5.) The comparison of different localities is discussed in a later portion of this paper.

GROWTH

The data on the growth of the razor clam here presented were collected over a period of years from 1923 to 1928. We consider them unique in that the growth of a single species is recorded from 10 different localities, making possible a comparison of the general course of growth under the widely differing environments involved in 2,400 miles of coast and 25° of latitude. We propose to consider (1) certain significant general tendencies common to all localities and to other animals, and (2) certain less significant differences due to the environment.

As explained in former papers (Weymouth, 1923, 1923a; Weymouth, McMillin, and Holmes, 1925), the seasonal growth of the clam leaves its record in the shell as a series of age marks so that it is possible to measure not only the length of the shell at the time it was taken, but also its actual length at each previous winter of its life. We have thus available a complete record of the growth of the individual usually only obtained if the animal is reared and observed throughout life. Therefore, the norms of growth which we present are not based solely upon the size of the individuals

gathered at a certain time but chiefly upon the median values of a large series of records of individuals throughout their entire lives.

The number of measurements each representing the length of a clam at a known age is such as to inspire confidence in the statistical results. Although many others have been measured, 13,797 lengths have been used in the growth curves here considered.

LENGTH AS A MEASURE OF SIZE

Length has been selected as the basis of this growth study because, in the present case, we consider it the best measure of size. Calipers with which accurate measurements of length may be made rapidly are easily used in the field where equally accurate scales can not be carried. The weight of clams varies widely, owing to two causes. The sinuses of the foot and the mantle cavity hold a variable amount of water which may or may not be lost at the time of digging. The sexual products of the clam comprise 10 to 30 per cent of the total weight, and further error in weight is introduced by seasonal fluctuations in the amount of spawn developed. Not only are solid structures, such as shell and bone, incapable of reversal so that a decrease of length in contrast to weight does not normally occur, but growth in length persists under unfavorable circumstances when it can only take place at the expense of weight, as Podhradsky and Kostomarov (1925) have shown in starving carp. Because less error is involved in its determination and because it is a more conservative and persistent process, increase in length is not only the more convenient but also the more significant biological measure of growth.

LOCALITIES STUDIED

As an aid in the consideration of the growth curves from various beds, the name and location, together with a brief description of each place, are here included:

Pismo, Calif., (lat. 35° 11′ N.).—The beach is of considerable extent and represents a normal habitat—a wide pure sand beach exposed to surf. Pismo represents the practical southern limit of this species; although occasional shells are found farther south, these were not abundant enough for growth data.

Crescent City, Calif., (lat. 41° 45′ N.; 500 miles from Pismo).—The bed just south of the city is of fine and coarse sand with some fine gravel; the beach is broad and exposed to surf. We consider it a normal habitat.

Copalis, Wash., (lat. 46° 58′ N.; 860 miles from Pismo).—This is an extensive and surf-washed beach of pure sand which, as we shall see, must be considered particularly favorable. The "Channel" and the "Sink" at Copalis are two local habitats selected because distinctly atypical. The "Channel" bed is located on the entrance to Grays Harbor, where there are strong currents and the beach is steep and gravelly. The "Sink" bed is near the mouth of a lagoon cut off by the formation of a bar consequent to the building of a jetty. It lacks surf and there is much mud in the sand.

Massett, British Columbia (lat. 53° 20′ N.; 1,380 miles from Pismo).—On Queen Charlotte Island between Massett Inlet and Rose Spit the beach is broad and of pure sand. Although not directly exposed to surf, all northerly wind causes small breakers over the beds. It is the only bed of commercial importance in British Columbia. Specimens were taken the second year of commercial operation.

The Alaskan beds are on or adjacent to the Gulf of Alaska and their relative position requires a word of explanation. The coast of the gulf trends north and west, reaching the most northern position near Cordova; after which it sweeps again to the south and west, so that the beds on Shelikof Straits (Swickshak and Hallo Bay) lie about 2° farther south than those near Cordova (Controller Bay and

Karls Bar). The isotherms follow in general the sweep of the gulf but the beds in Shelikof Straits lie north of the mean annual isotherm of 40° F. which passes approximately through those near Cordova. For this reason we have used the position along the coast measured in miles rather than the latitude as indicating the geographical position.

Controller Bay, Alaska (lat. 60°; 2,040 miles from Pismo).—This bay is a broad shallow body of water, with much of the bottom exposed at low tide. The upper part of the bay is covered with fine glacial mud, and the outer bars are of sand with some glacial mud. During the summer the Bering River empties a large amount of glacial drainage into the bay, making the water cold and filled with muddy silt. We consider Controller Bay a very unfavorable habitat. The beds will not support commerical operations.

The clams furnishing the Karls Bar growth curve were taken from a small portion of the beds in Orca Inlet near Cordova (lat. 60° 27′ N.; 2,105 miles from Pismo). The soil is fine sand with some glacial silt. The bed is not exposed to the surf; and, although it differs greatly from the southern beds, it is typical of the Alaskan clam-producing areas. The beds in this vicinity have been dug for 12 years, but the area from which these specimens were taken had not been previously exploited.

Swickshak, Alaska (lat. 58° 5′ N.; 2,405 miles from Pismo).—This bed is on the north of Shelikof Straits opposite Kodiak Island. The beach is of fine sand and volcanic ash and is more exposed to surf than most of the northern beds. This bed was first dug in 1923 and our material was taken during that year and in 1924.

Clams are taken in Hallo Bay (lat. 58° 5′ N.; 2,425 miles from Pismo) on the northern shore where it is protected by the island in the bay. The beach is of sand, volcanic ash, and glacial mud. The shells were taken from among the first clams dug in that place.

QUANTITATIVE TREATMENT OF DATA

We may define growth as increase in size and take, in the present case, length as a measure of size. Quantitative data on the length of the clam will be considered. This may be presented as absolute growth; that is, average total size at each age or the gross annual increments. Or we may show the relative growth rate; that is, the proportional or percental gains at each age. The graphic representation of growth may be cast, therefore, in two contrasting pictures, both of which contribute to an understanding of growth.

Absolute growth.—We shall first consider absolute growth. In Figures 4, 5, and 6 are presented norms of growth for 10 localities; the corresponding medians are given in Table 8. These are plotted in the usual fashion; that is, they are the regressions of length on age, or average length for each age-group. The converse regression, age on length, is closely similar in early life, but differs significantly in the later years (Weymouth, McMillin, and Rich, 1925).

The length of the first ring varies roughly with the latitude of the beds from which the clams are taken, ranging from one-third of a centimeter in the north to 2 centimeters in the south. These differences appear to result from the higher temperature in the south which favors a more rapid growth and, permitting an earlier spawning, furnishes a longer growing season.

Following the formation of the first ring, growth is rapid. In the southern beds, over two-thirds of the length is reached during the first growing season. In the north growth is slower and a comparable increase requires over four years. In the northern forms it will be noted that the curve of absolute growth rises slowly at

first but with an increasing slope up to a certain point, followed by a decreasing slope during the remainder of the curve. This inflection, or point of change from increasing to decreasing slope was not noticed in our early growth studies on the Washington beds. Ultimately a method of fitting, to be discussed later, convinced us
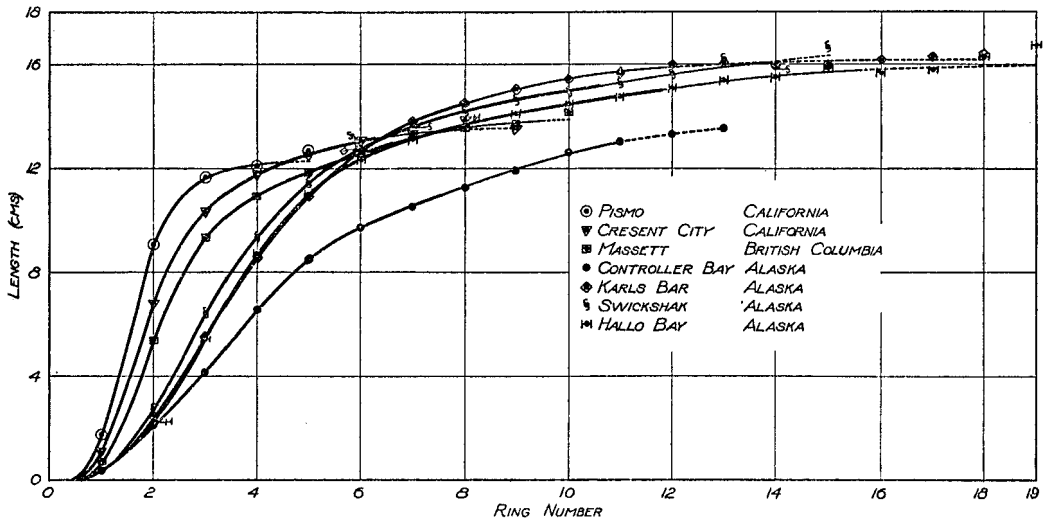

FIGURE 5.—Growth curves from seven localities in California, Oregon, British Columbia, and Alaska. Ages are indicated by ring number; to determine actual age subtract one-half year

that an inflection is present in all, and the curves of absolute growth have been so drawn. The inflection, on the average, is at 22.36 per cent of the maximum age and 32.75 per cent of the total length. There is no obvious correlation between these ages and lengths and any other features of the growth curves as maximum age, maximum length, relative growth rate, or the like.

Following the inflection, the rate of growth decreases regularly until a final adult length characteristic of the locality is reached. This varies from 12 to 16 centimeters, the slower-growing northern clams reaching in general the greatest size and having the longest life.

To show the rate of absolute growth we may plot the annual increments, or differences between successive total lengths, on the age. (Fig. 7.) This shows an increase of rate which reaches a maximum at the point of inflection of the total length curve. This maximum may fall early in life; and, since the smallest time interval available is the year, its location may only be approximated by this method.
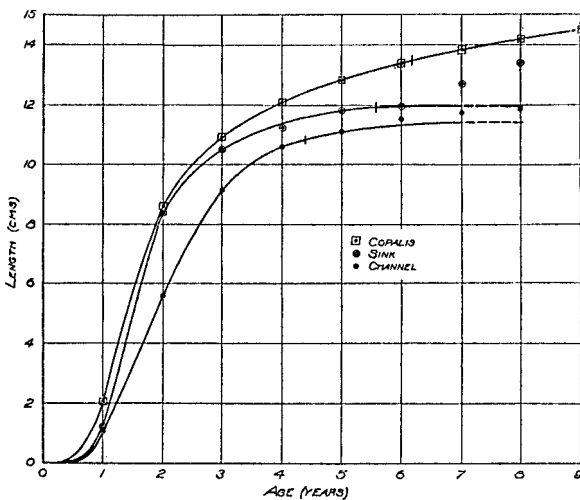

FIGURE 6.—Growth curves for three localities in Washington. Ages are indicated by ring number; to determine actual age subtract one-half year

Following the maximum, the rate declines throughout life and for a time closely approximates a descending geometric series; that is to say, each yearly growth is a certain percentage of the preceding. This relation was first pointed out by Pütter

(1920) and subsequently for the Pismo clam (Weymouth, 1923a), by Brody (1923), and by Munford (1926) for the growth of various domestic mammals.   This relation however fails in old age when the growth is greater than would be predicted on this basis.

Relative   growth.—To picture   the   relative   or percental growth, recourse may   be   had   to   the   ratio diagram   as   used   by   the economist. Here equal proportional   or   percental changes   are   represented   by equal   vertical   distances. Such a diagram is obtained if   we   plot   the   logarithms of the total length on age, as in Figures 8 and 10.   Such a curve rises most steeply at first, and the slope continually   declines   throughout

FIGURE 7.—Absolute growth curve of clams from Hallo Bay, Alaska, with the first differential

life.   Or, as before, we may plot the percental yearly gains which show a continually decreasing increment during the period for which we have data.   (Figs. 8 and 9.)

Comparison of absolute and relative treatments.—With these two methods of presentation before us, let us contrast the pictures.   The differences lie chiefly in early   life;   the   slow growth of old age differs little whether regarded from the absolute or the relative viewpoint. The early growth, however, appears in a very different light when presented by   these   contrasted methods.   As   stated above,   the   absolute growth of small clams is slow.   This later becomes   more   rapid   with its   maximum   at   the point of inflection, after which it again declines. The relative growth, on the other hand, is most rapid at the youngest

FIGURE 8.—Ratio diagram of growth of clams from Hallo Bay, Alaska, with the first differential

ages for which we have records and steadily declines with time.   Obviously, as with other statistical procedures, both pictures are true and necessary to complete presentation.   Which, however, represents the more significant point of view?   Unless

we are to forget the purpose of quantitative work we must emphasize that method which agrees with the greater number and the more significant qualitative, in the present case biological, facts.

The most significant difference between the two viewpoints relates to the rate of growth. Many physiological processes are considered on a relative basis. To use a familiar example, the metabolic rate is measured by the oxygen consumption or the heat production per unit of time per unit of weight or of body surface. This is obviously necessary to permit the comparison of rates in animals of widely differing sizes. Minot early recognized and clearly stated the biological significance of the relative growth rate which he expressed, as a first approximation, on a percental basis
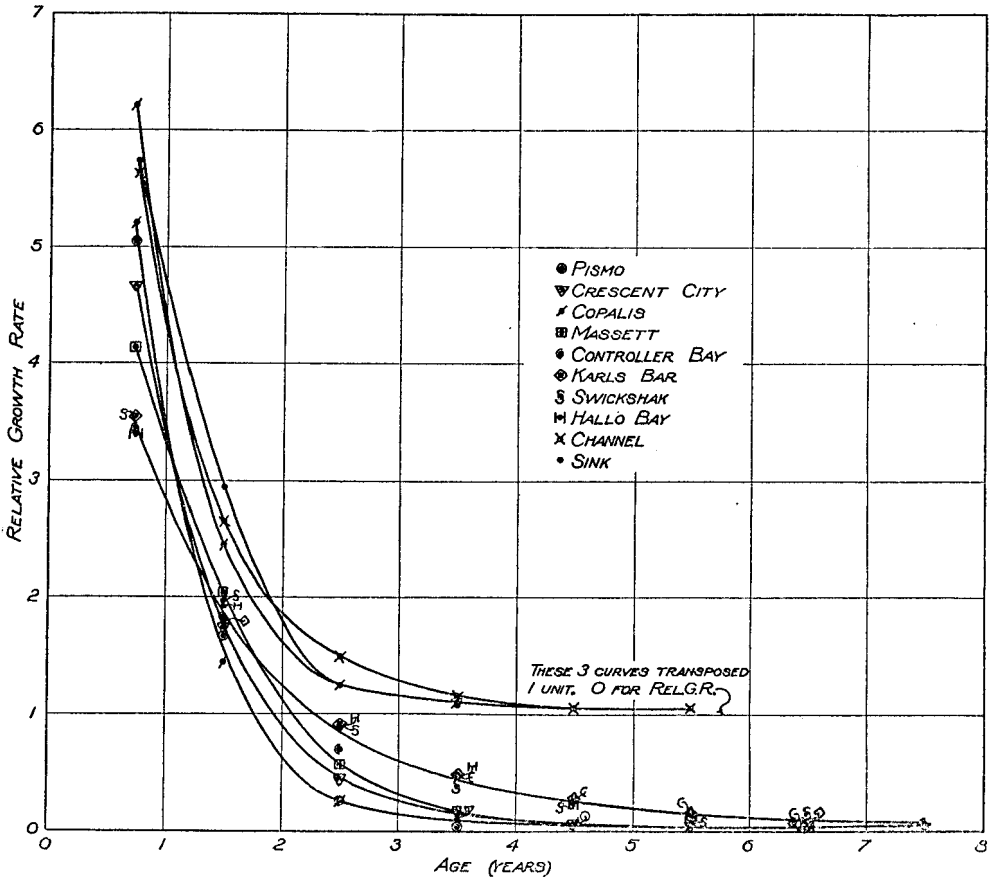
FIGURE 9.—Relative growth rate of clams from 10 localities plotted on age

(1891, 1908). A number of authors have followed Minot in this. It will be sufficient to cite Meyer (1914), Murray (1925), and Schmalhausen (1929), who considers the relative rate $\left(\dfrac{dy}{dt} \cdot \dfrac{1}{y} \right)$ as "die wahre Wachstumsgeschwindigkeit."

If, following the above investigators, we consider the relative rate, the clams show the most rapid growth at the youngest age for which we have data. An example will make this clear. On the Swickahak beach the gross growth in length during the first growing season is 0.38 centimeter, in the twelfth growing season 0.36 centimeter. If we consider these as absolute increments they are essentially the same, but as in the first case the growth is made from the egg with a diameter of

about 0.01 centimeter and in the second from a clam already 12.25 centimeters long, the relative growths are approximately 340 and 2 per cent, and the growth during the first summer is 170 times as fast as in the twelfth.

The definition of rate is important not only in early growth but also at the time of inflection on the absolute growth curve. Is the inflection as significant as its universal presence in the absolute growth curve would indicate, or as negligible as its complete absence from the relative growth curve would suggest? Brody (1927) claims several points of significance for the inflection, namely: (1) Maximum velocity of growth, (2) age of puberty, (3) lowest specific mortality, (4) equivalence in age of different animals. It is true that the inflection represents the greatest gross increase for a unit of time, but, as we shall show later, this is a mathematical fact of no biological significance. In the growth curves of man and rat the inflection roughly corresponds with the age of puberty, but Brody also shows on the same page growth curves of eight other species in which the inflection does not correspond to puberty. In the clam the inflection occurs at lengths from 3.17 to 5.81 centimeters, whereas sexual maturity does not occur until a size of about 10 centimeters is reached. (Weymouth, McMillin, and Holmes, 1925.)

The age of the inflection in man is the age of lowest specific mortality; but, since mortality data on other animals are not available, this generalization relating the inflection with specific mortality is unwarranted. As a "point of reference for the determination of equivalence of age in different animals" the inflection is a convenient working basis, but this has no influence on its possible biological significance.

Robertson (1923) claims no biological significance for the inflection but looks upon it as dividing the growth curve into two portions which Brody has designated the "self-accelerating" and "self-inhibiting" phases. These terms imply that the specific growth activity of the protoplasm increases up to the time of the inflection and thereafter declines. But this is not true; as many authors from Minot to Schmalhausen have pointed out, the intensity of growth due to an increasing proportion of inactive material in the organism and other causes is continually decreasing, a condition clearly shown by the relative growth rate of the clam (fig. 9) which falls without detectable change through the period of inflection on the absolute curve. The occurrence of a maximum gross addition which does not represent "die wahre Wachstumsgeschwindigkeit" will be clear from a moment's analysis.

An animal growing at a constantly decreasing relative rate will, if starting at a rate initially very high, show for a time an increasing absolute rate, each increment being, as in ordinary compound interest, larger than the preceding. But the falling relative rate will after a time more than offset the increasing body size; and the total gains will slacken and, having passed through a maximum, finally become progressively less, thus showing an inflection in the absolute rate. Viewed in this light, the inflection becomes a mere mathematical consequence of the course of growth and not a point which a priori might correspond to any physiological stage.

A hypothetical illustration may show how an inflection results from a constantly decreasing growth rate. Table 6 shows the increase of a small principal at compound interest, the rate of which is initially very high but steadily decreasing. For a time the income (annual increments) will be larger each year, but there will come a time when interest rate is so reduced that the income becomes smaller each year. The income will then be comparable to the absolute growth rate, showing an increase to a maximum followed by a decrease; a graph of the principal will be comparable to an absolute growth curve and show an inflection.

TABLE 6.—*The increase of a principal at compound interest when the interest rate is decreasing by 20 per cent each unit of time*

Prin-cipal	Interest rate	Income	Prin-cipal	Interest rate	Income	Prin-cipal	Interest rate	Income	Prin-cipal	Interest rate	Income
	Per cent			*Per cent*			*Per cent*			*Per cent*	
$0.31	152.6	$0.47	$27.72	25.6	$7.10	$70.63	5.4	$3.80	$87.02	1.1	$0.96
.78	122.1	.95	34.82	20.5	[1] 7.14	74.43	4.3	3.21	87.98	.90	.79
1.74	97.7	1.71	41.96	16.4	6.88	77.04	3.4	2.67	88.77	.72	.64
3.45	78.1	2.69	48.84	13.1	6.41	80.31	2.8	2.21	89.41	.58	.52
6.15	62.5	3.85	55.25	10.5	5.80	82.52	2.2	1.81	89.92	.48	.43
10.00	50.0	5.00	61.05	8.4	5.13	84.33	1.8	1.48	90.35	.37	.33
15.00	40.0	6.00	66.18	6.7	4.45	85.81	1.4	1.21	90.68	.29	.26
21.00	32.0	6.72									

[1] Inflection.

We are thus forced to conclude that the significant biological aspects of growth are not adequately shown by the plot of absolute size on age. Such curves indicate
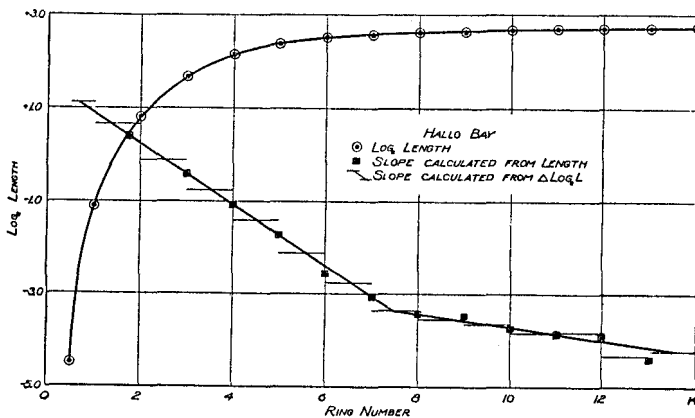
FIGURE 10.—Ratio diagram of growth of clams from Hallo Bay, Alaska, from larval stage to 14 years of age, with the slope of the growth rate calculated by two methods: Squares from the formula

$$\frac{1}{L} \cdot \frac{dL}{dt} = \frac{L_2 - L_1}{L_1} \cdot \frac{r \log_e r}{r-1} \text{ when } L = \text{length}$$

and

$$r = \frac{L_1(L_4 - L_1)}{L_4(L_2 - L_1)}$$

and horizontal lines from the graph of $\log_e (\triangle \log_e L)$

a slow growth at those early ages when each unit of protoplasm is actually putting forth a maximum of energy in the construction of new tissue. They further represent the most rapid growth as occurring at the "inflection" whereas it has been shown above that an increasing body size and a decreasing growth rate per unit mass at this age make a maximum contribution of new tissue. Therefore, if we analyze gross growth into its capacity and intensity factors we find that the rate is constantly decreasing and that the inflection neither corresponds to a biological epoch nor represents a real quantitative landmark.

A GROWTH FORMULA BASED ON RELATIVE RATE

Having emphasized the importance of relative growth, we may consider it more in detail. If we examine the curves of relative growth rate (fig. 9), it will be noticed that the descent is regular, suggesting the logarithmic-exponential relation. A plot

of the logarithm of the relative rate of growth on time, over the range of sizes for which we have data, closely approximates a straight line. (Fig. 10.) Therefore,

$$P_L = \frac{d \log L}{dt} = \text{relative growth rate}$$

$$\log P_L = a - kt$$

where a = initial relative growth

          k = rate of decline

          t = time.

$$\frac{d \log L}{dt} = e^{a-kt}$$

$$= Ae^{-kt} \qquad\qquad \text{where } A = e^a$$

$$\log L = \frac{A}{-k} e^{-kt} + b$$

$$= b - ce^{-kt} \qquad\qquad \text{where } c = \frac{A}{k}$$

$$L = e^{b - ce^{-kt}}$$

$$= Be^{-ce^{-kt}} \qquad\qquad \text{where } B = e^b$$

This formula, which is that of a Gompertz curve, fits the growth curve of the clams from all localities from the first winter to extreme old age when the observed values tend to be high. Although expressed in a different form, it contains the same idea as advocated by Minot who claimed that the percental growth decreased throughout life in the animals studied by him; namely, the guinea pig, rabbit, and man. To use his terminology we might say that the percental growth rate declines at a constant percental rate. This growth formula was developed in ignorance of the work of Wright and Davidson, the latter now associated with the writers. Wright suggested (1926) and Davidson developed and later applied with Wright's assistance, a formula essentially the same as that here given to the growth of cattle (1928). This is the first case, however, in which it has been applied to a growth curve including an inflection.

DIFFERENCES OF GROWTH IN DIFFERENT LOCALITIES

We have presented the general features common to all our growth curves which, as we have stated above, are representative of growth in 10 localities ranging from Pismo, Calif., to Hallo Bay, Alaska—a distance of over 2,500 miles along the Pacific coast and 25 degrees of latitude. It remains to consider the differences in growth of clams as influenced by the great differences of environment encountered in this unusually wide range.

To analyze these differences, we selected for comparison a large number of constants derived from the growth curves. These we have studied by means of scatter diagrams and in many cases have calculated the coefficients of correlation between selected constants. As a result we have chosen five constants as the most significant for comparison and have presented their values in Table 7 and the coefficients of correlation in Figure 11.

As representative of age and length the maxima, as defined above, were selected as most significant. The growth rate, while a single feature, shows such characteristic relation between its initial and its later course that two constants were necessary to represent it. Those selected were the initial relative growth rate and the rate at two

years. These constants have been compared with the geographical position as represented by the distance in statute miles along the coast from Pismo.

TABLE 7.—*Growth constants of Siliqua patula for the localities considered*

	Pismo	Crescent City	Channel	Sink	Copalis	Massett	Controller Bay	Karls Bar	Swickshak	Hallo Bay
Latitude	35° 11'	41° 45'	46° 58'	46° 58'	46° 58'	53° 20'	60°	60° 27'	58° 5'	58° 5'
Distance from Pismo miles	0	500	860	860	860	1,380	2,040	2,105	2,405	2,425
5 per cent survival age [1] years	4.40	7.90	7.00	7.00	8.85	9.55	11.00	12.05	13.40	15.65
5 per cent survival length centimeters	12.05	13.40	11.40	12.00	14.40	13.70	13.00	15.95	16.00	15.70
Average growth centimeters	2.74	1.69	1.63	1.72	1.63	1.43	1.18	1.32	1.19	1.00
Initial relative growth rate	5.05	4.67	4.59	4.69	5.21	4.14	3.43	3.53	3.53	3.39
Relative growth rate, 2 years	0.25	0.43	0.49	0.23	0.23	0.56	0.68	0.90	0.85	0.88

[1] Given as ring number. To calculate actual age subtract one-half year.

It is obvious that a satisfactory analysis is impossible at present. The physico-chemical factors represented by the environment are imperfectly known for even the most studied points on the Pacific coast; and for 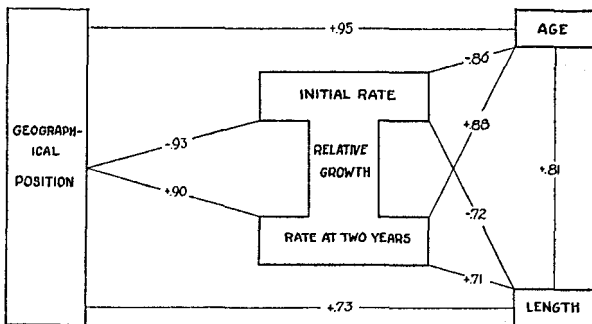many of our localities we have no information whatever as to temperature, salinity, hydrogen-ion concentration, plankton, or any other of the agencies known to influence physiological processes. We may safely infer that the temperatures on the southern beds are higher and the season of higher temperatures is longer than in the north, but we can not put this into quantitative form.

FIGURE 11.—Diagram of the five constants derived from growth curves with coefficients of correlation for each pair

The striking fact that many features of growth show such high correlation with the group of environmental features indicates that a satisfactory knowledge would reveal important laws of growth. For the present we can only record the suggestive observed relations which can not yet be analyzed.

The correlations obtained are given in Figure 11. For biological data these correlations are strikingly high, ranging from 0.71 to 0.95. The highest of these is between age and geographical positions in the sense that clams from the northern beds show the longest life or the lowest mortality. The next highest is the negative correlation between the initial growth rate and that at two years. Since these constants are two measures of the same thing, a close relation would be expected and the figure indicates that a high relative growth rate in early life is followed by a low growth rate in later life and vice versa.

In consequence, the correlations of the early and late growth rates with other constants show similar values but have opposite signs. The highest correlation of relative growth rate is with geographical location. The highest initial and lowest final values are found at Pismo, the southernmost locality. The next highest correlations are between relative growth rate and age. A low initial rate and high later rate are associated with long life.

The correlations of length with the other factors are the lowest. Large size is associated with great age, northern habitat, low early and high later relative growth rates. This lower correlation apparently reflects the fact that there is a lower percental variability in length than in any of the other factors.

To summarize, we may say that the complex of environmental features on the southern beds produces a more rapid initial relative growth rate which more rapidly falls to a lower final value, and that the clams reach a smaller final length and have a shorter life span than on the northern beds.

That these differing types of growth characteristic of the different localities are significant is indicated by their occurence in other cases. An example is furnished by the comparison of the growth of the two sexes at Hallo Bay, Alaska, where, as stated, slight sexual differences in size were observed. An inspection of Figure 4 will show that the females grow more rapidly at first, but that by the third or fourth year the more sustained growth of the males has placed them in the lead, and that they reach a greater final length and outlive the females on the average by more than a year. Chamberlain obtained for one species of fresh-water mussel a sexual difference in growth similar to that just described (1931). The results from other species of lamellibranchs are concordant. Thus in *Cardium* the differences of growth with latitude appear to parallel those found in the razor clam (Weymouth and Thompson, 1931). It is not here possible to examine other groups but recent work on the life history of the striped bass in California by Scofield[3] has shown a difference in growth between the sexes essentially similar to that in the razor clam.

Although the case is not comparable in detail, the findings of Gray (1928), who reared the eggs of *Salmo fario* at different temperatures, is interesting. Those developing at 15° C. grew far more rapidly but did not reach as great a weight as did those growing at 5° C. Gray points out that the yolk available for the metabolism of the embryo is limited, and must serve for both maintenance and growth. At the higher temperatures the life processes are pitched at a higher level and the fraction consumed in maintenance is greater, that available for growth is therefore less, hence the smaller size. Although there is no similar limitation of food material in the case of the clam, the observations are suggestive.

BIOLOGICAL FINDINGS AND THEIR BEARING ON FISHERY REGULATIONS

On the basis of the data presented in this and previous reports on the razor clam (McMillin, 1924, 1925, 1927, 1928; Weymouth, McMillin, and Holmes, 1925; Weymouth, McMillin, and Rich, 1931), the more significant biological findings may be summarized and their bearing on the question of fishery regulations pointed out.

BIOLOGICAL FINDINGS

These investigations have extended the applicability of the ring method of age determination to the razor clam. Work now in press (Weymouth and Thompson, 1931), has shown that the same relations hold for the cockle (*Cardium corbis*) and Chamberlain[4] has successfully applied the method to the fresh-water mussel (*Lampsilis*). There can be little doubt, therefore, that the ring method is of general validity for lamellibranchs and that in it we have a tool of great usefulness for the study of growth.

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[3] Manuscript in press. California Fish and Game Commission.
[4] Thesis, Stanford University.

These studies have furnished what is doubtless the largest body of invertebrate growth data as yet available. Since these growth data are uniquely regular it has permitted an analysis of certain features of growth not hitherto possible. This analysis has substantiated and extended the earlier findings of Minot, making possible a valuable mathematical formulation of the course of growth.

Many problems of growth and its relation to variability and longevity, as yet unsolved, may be confidently attacked by this method, and data are already at hand or will be obtained incidentally in the surveys hereafter proposed.

RAZOR-CLAM FISHERY AND ITS REGULATION

(a) Neither artificial propagation nor culture are feasible. Proper protective measures can maintain the present beds, but no extension can be expected. The forms suitable for "farming" on the Pacific coast are the oyster and soft-shelled clam (Mya). These may readily be extended to many bays now unproductive. The razor clam should and can be protected; it has, however, already spread to all suitable locations.

(b) With the knowledge of the rate of growth, the length of life, and the set at different latitudes now available, we may predict the resistance of various beds to commercial fishing. In the south the rate of growth is rapid; the life, short; and the set, heavy. In the north the rate is low; the life, long; and the set, light. Balancing these factors, the Washington beaches are undoubtedly the most resistant—a conclusion borne out by the history of the commercial fishery.

(c) *Evidences of overfishing.*—The validity of the method of age determination developed by the senior author is now well established. By its use the composition of the commercial catch may readily be ascertained. A fall in the relative abundance of the older age groups (with due allowance for dominant age classes) is the best evidence of danger from too intense fishing. This method of analysis has been applied by one of us (McMillin, 1925, 1927, 1928) to the Washington fishery, with such striking evidence of depletion that the State has finally passed protective measures including a size limit of 3½ inches and a bag limit of 3 dozen for the unlicensed digger. The fishery at Cordova is being followed by the same method and the size limit of 4½ inches set as a result of the first survey (Weymouth, McMillin, and Holmes, 1925) is proving an efficient protection. Measured areas, marked with permanent stakes, may be dug on successive days, and the same or similar areas examined each year. These areas are often avoided by the commercial diggers and are, therefore, not a completely satisfactory index of the general conditions of the beds, or contours of bottom may so change that successive records are not comparable. Nevertheless this method gives valuable supplementary evidence of the trend of the fishery.

(d) *Methods of protection.*—The protective measures available are closed seasons, closed areas, bag limits, and size limits. Additional experience in the application of these measures have supported the arguments advanced in a previous report (Weymouth, McMillin, and Holmes, 1925) in favor of the size limit. A bag limit has been set on the noncommercial digger for the Washington beaches, but has never been advocated for commercial operations. The closing of areas to digging would appear a useful method of protection, but experience has not proved it feasible. In the first place, the nature of the razor-clam beaches makes them difficult to post and police. Accurate description is often impossible because of absence of landmarks and the constant changing of the bars. This results in confusion and friction between war-

dens and diggers. The closed season so widely used elsewhere as a protective measure, if used alone, simply results in a shift of the time of intense digging and a concentration of effort in a shorter period. The total catch is not reduced, but its rapid handling leads to greater waste. This has been well illustrated on the Washington beaches.

The minimum size limit insures a reserve of breeding animals, and protects the clam at a time when it is increasing most rapidly in weight and therefore in economic value. The wastefulness of unrestricted digging has been emphasized by one of us (McMillin, 1927, 1928) in the case of the Washington beaches where, in 1928, the young not yet of spawning age constituted 42.5 per cent of the catch. Only the remarkable resilience of the clam populations on these beaches resulting from the heavy set and rapid growth have saved them from commercial extinction. Even with the protection now afforded these younger clams it will require time to rebuild the fishery. It was feared when the size limit was first proposed that its enforcement would be difficult, but this has not proved to be the case. The small clams, which are largely wasted in the canning operations because of the difficulty of cleaning them, are not wanted by the canners who have cooperated in enforcing the regulations. The size limit results in the practical closure of depleted areas. Beds which will not yield enough legal sized clams to repay the digger are carefully avoided.

(e) *Future work.*—It is recommended that surveys be made at least biennially of those regions where the razor-clam fishery is well developed to furnish material from which the age composition of the commercial catch may be found. If new regions are opened, these should be sampled at once in order that their subsequent history may be followed. Such surveys will show overfishing and permit the intelligent adjustment of regulations before conditions become acute and necessitate drastic action.

SUMMARY

The present paper is a continuation of previous studies of the Pacific razor clam undertaken for the Bureau of Fisheries.

The relationships of the most abundant and only commercially important species, *Siliqua patula*, are considered.

The variability, mortality, and sexual differences within the species are discussed.

Data on the growth of clams from 10 localities are presented, together with a discussion of methods employed and localities considered. Similarities shown by the growth data and the conception of growth to which they lead is given, and a critical examination of the graphic representation and terminology follows. The differences exhibited by the various localities are discussed.

Among legal restrictions on the fishery the importance of the size limit is again emphasized.

TABLE 8.—*Lengths of Siliqua patula at various localities*

PISMO

Ring No.	Median		P10		P90		Number of specimens	D
	Length	P. E.	Length	P. E.	Length	P. E.		
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*		
1	1.73	±0.024	1.27	±0.018	2.39	±0.030	272	1.12
2	9.07	±0.045	7.78	±0.083	9.80	±0.032	262	2.02
3	11.63	±0.016	10.51	±0.120	12.34	±0.050	153	1.83
4	12.10	±0.063	11.42	±0.038	12.66	±0.113	31	1.24
5	12.68						5	

CRESCENT CITY

Ring No.	Median		P10		P90		Number of specimens	D
1	1.19	±0.060	0.45	±0.023	2.26	±0.058	160	1.81
2	6.75	±0.093	5.21	±0.058	9.14	±0.085	178	3.93
3	10.35	±0.045	9.30	±0.070	11.93	±0.072	170	2.03
4	11.81	±0.046	11.11	±0.039	12.60	±0.059	160	1.49
5	12.58	±0.040	11.75	±0.096	13.29	±0.044	144	1.54
6	13.03	±0.040	12.32	±0.055	13.83	±0.063	110	1.51
7	13.32	±0.083	12.26	±0.150	14.16	±0.187	38	1.90
8	[1]13.84						8	
9	[1]13.51						1	

CHANNEL (COPALIS)

Ring No.	Median		P10		P90		Number of specimens	D
1	1.09	±0.055	0.49	±0.016	1.89	±0.029	167	1.40
2	5.59	±0.103	3.18	±0.111	7.66	±0.080	189	4.48
3	9.10	±0.100	6.49	±0.055	10.81	±0.067	177	4.32
4	10.54	±0.164	9.06	±0.112	11.48	±0.064	122	2.42
5	11.08	±0.086	10.19	±0.104	12.04	±0.052	59	1.85
6	11.50	±0.108	10.83	±0.097	12.28	±0.048	23	1.45
7	[1]11.89						8	
8	[1]11.89						2	

SINK (COPALIS)

Ring No.	Median		P10		P90		Number of specimens	D
1	1.21	±0.085	0.63	±0.017	2.12	±0.087	101	1.49
2	8.35	±0.055	6.84	±0.428	8.97	±0.025	112	2.13
3	[2]10.49	±0.040	9.31	±0.213	11.14	±0.106	111	1.83
4	11.18	±0.057	10.33		[2]11.94		102	1.70
5	11.78	±0.063	10.79		[2]12.48		88	1.69
6	[2]11.96	±0.050	[2]11.04		[2]12.68		34	1.74
7	[1]12.70						3	
8	[1]13.40						2	

COPALIS

Ring No.	Median		P10		P90		Number of specimens	D
1	2.04	±0.016	1.11	±0.040	2.98	±0.055	468	1.87
2	8.61	±0.043	6.37	±0.079	9.76	±0.023	457	3.39
3	10.87	±0.026	10.08	±0.038	11.72	±0.024	424	1.64
4	12.04	±0.020	11.40	±0.036	12.62	±0.020	388	1.28
5	12.81	±0.008	12.12	±0.046	13.48	±0.029	330	1.36
6	13.40	±0.020	12.85	±0.043	14.02	±0.013	250	1.17
7	13.84	±0.028	13.28	±0.053	14.48	±0.035	172	1.20
8	14.19	±0.050	13.70	±0.121	14.90	±0.052	80	1.20
9	14.50	±0.095	13.78		15.12		18	1.34

MASSETT, B. C.

Ring No.	Median		P10		P90		Number of specimens	D
1	0.70	±0.016	0.40	±0.017	1.88	±0.092	186	1.48
2	5.35	±0.159	3.32	±0.064	8.03	±0.096	201	4.71
3	9.35	±0.067	7.45	±0.094	10.51	±0.080	195	3.06
4	10.97	±0.055	9.88	±0.062	11.97	±0.093	190	2.09
5	11.78	±0.041	11.03	±0.049	12.60	±0.054	146	1.57
6	12.58	±0.060	11.77	±0.071	13.54	±0.107	112	1.80
7	13.27	±0.035	12.57	±0.200	14.07	±0.080	97	1.50
8	13.58	±0.034	12.68	±0.110	14.16	±0.083	67	1.48
9	13.69	±0.048	12.67	±0.067	14.45	±0.101	25	
10	[1]14.16						4	

[1] Mean.　　　　　　　　[2] Graphic.

TABLE 8.—*Lengths of Siliqua patula at various localities*—Continued

CONTROLLER BAY

Ring No.	Median		P_{10}		P_{90}		Number of specimens	D
	Length	P. E.	Length	P. E.	Length	P. E.		
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*		
1	0.34	±0.037	0.18	±0.044	0.53	±0.034	58	0.35
2	²2.12	±0.067	1.23	±0.036	2.83	±0.032	80	1.60
3	4.18	±0.062	3.10	±0.072	5.10	±0.062	80	2.00
4	6.52	±0.067	5.30	±0.091	7.84	±0.052	80	2.54
5	8.45	±0.046	7.39	±0.180	9.46	±0.072	79	2.07
6	9.71	±0.064	8.71	±0.034	10.75	±0.115	72	2.04
7	10.51	±0.064	9.55	±0.102	11.71	±0.076	58	2.16
8	11.25	±0.042	11.19	±0.126	12.31	±0.084	39	1.14
9	²11.90						13	
10	¹12.60						6	
11	¹13.00						5	
12	¹13.28						3	
13	¹13.51						1	

KARL BAR (CORDOVA)

Ring No.	Median		P_{10}		P_{90}		Number of specimens	D
1	0.38	±0.013	0.23	±0.014	0.58	±0.032	123	0.35
2	2.43	±0.037	1.82	±0.049	3.05	±0.041	148	1.23
3	5.49	±0.055	4.30	±0.099	6.80	±0.083	150	2.50
4	8.57	±0.092	7.30	±0.050	9.86	±0.099	150	2.56
5	10.92	±0.055	9.50	±0.055	12.24	±0.082	149	2.74
6	12.66	±0.055	11.67	±0.121	13.49	±0.040	146	1.82
7	13.78	±0.039	12.95	±0.078	14.54	±0.059	135	1.59
8	14.52	±0.049	13.58	±0.078	15.27	±0.052	133	1.69
9	15.03	±0.056	14.21	±0.062	15.77	±0.053	84	1.56
10	15.43	±0.071	14.74	±0.051	16.00	±0.064	37	1.26
11	15.63	±0.063					22	
12	15.95	±0.067					15	
13	16.05						9	
14	15.90						5	
15	¹15.95						2	
16	¹16.15						2	
17	¹16.25						2	
18	¹16.40						2	

SWICKSHAK BEACH

Ring No.	Median		P_{10}		P_{90}		Number of specimens	D
1	0.38	±0.010	0.24	±0.007	0.76	±0.026	238	0.52
2	2.73	±0.028	1.94	±0.035	3.69	±0.041	545	1.75
3	6.41	±0.076	4.70	±0.068	7.81	±0.080	275	3.11
4	9.28	±0.060	8.12	±0.051	10.94	±0.009	254	2.82
5	11.49	±0.058	10.30	±0.077	12.68	±0.065	239	2.38
6	12.74	±0.048	11.92	±0.048	13.76	±0.083	228	1.84
7	13.70	±0.040	12.74	±0.044	14.51	±0.062	218	1.77
8	14.19	±0.045	13.27	±0.072	15.11	±0.087	204	1.84
9	14.63	±0.051	13.67	±0.060	15.60	±0.052	177	1.93
10	14.94	±0.064	13.94	±0.065	15.93	±0.063	166	1.99
11	15.25	±0.054	14.29	±0.086	16.28	±0.055	127	1.99
12	15.61	±0.118	14.53	±0.082	16.61	±0.089	77	2.08
13	16.12	±0.046	15.19	±0.071	16.78	±0.033	17	1.59
14	¹15.96						5	
15	¹16.72						1	

HALLO BAY

Ring No.	Median		P_{10}		P_{90}		Number of specimens	D
1	0.34	±0.012	0.23	±0.022	0.59	±0.007	91	0.36
2	2.26	±0.048	1.11	±0.032	3.28	±0.050	226	2.17
3	5.42	±0.114	3.44	±0.047	7.56	±0.087	229	4.12
4	8.60	±0.138	6.67	±0.087	10.61	±0.087	229	3.97
5	10.96	±0.078	9.42	±0.059	12.49	±0.043	228	3.07
6	12.37	±0.049	11.13	±0.068	13.45	±0.044	227	2.32
7	13.17	±0.050	12.08	±0.080	14.04	±0.043	211	1.96
8	13.65	±0.045	12.72	±0.048	14.53	±0.056	192	1.81
9	14.06	±0.041	13.28	±0.056	14.88	±0.042	182	1.60
10	14.44	±0.045	13.63	±0.053	15.22	±0.048	172	1.59
11	14.75	±0.048	13.94	±0.053	15.51	±0.071	138	1.57
12	15.08	±0.063	14.30	±0.047	15.80	±0.061	111	1.50
13	15.38	±0.056	14.58	±0.063	16.07	±0.063	77	1.49
14	15.50	±0.081	14.71	±0.080	16.46	±0.147	52	1.75
15	15.80	±0.095	14.87	±0.211	16.73	±0.211	27	1.86
16	¹15.61						7	
17	¹15.74						4	
18	¹16.31						3	
19	¹16.74						2	

¹ Mean. ² Graphic.

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