PALEOECOLOGICAL IMPLICATIONS OF THE MINERALOGY, STRUCTURE, AND STRONTIUM AND MAGNESIUM CONTENTS OF SHELLS OF THE WEST COAST SPECIES OF THE GENUS *MYTILUS*

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James Robert Dodd

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ABSTRACT

Large specimens of *M. californianus*, *M. edulis edulis*, and *M. edulis diegensis* show a positive correlation with temperature in the percent aragonite in their shells. Shell thickness and probably other unknown factors also affect the shell mineralogy of *M. californianus*. Shell size and salinity are the most important factors affecting the mineralogy of *M. edulis edulis* and *M. edulis diegensis*. The shell structure of *M. californianus* is temperature dependent. A method making possible the quantitative determination of paleotemperatures from shell structure is devised. The age of specimens of *M. californianus* can be determined from shell structure making possible the estimation of growth rates, which are in part a function of temperature. The magnesium and strontium contents of the outer prismatic layer of the west coast species of *Mytilus* are positively correlated with temperature. The strontium content is affected by the size of the specimen but is independent of salinity in the samples in this study. The strontium content of the nacreous layer shows a negative correlation with temperature. Shell structure, strontium content, shell mineralogy, and growth rates are used to determine paleotemperatures for fossils from four localities in the upper Pleistocene of California and Baja California and one locality in the lower Pleistocene of California. These methods indicate that the temperatures were much like the present temperatures at these localities.

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TABLE OF CONTENTS

TITLE PAGE

INTRODUCTION 1

MYTILUS SHELL STRUCTURE 6

- Literature Review 6
- Methods of Shell Structure Study 6
- Structural Units of *Mytilus* Shells 8
- Periostracum 8
- Outer Prismatic Layer 12
- Nacreous Layer 15
- Inner Prismatic Layer 17
- Relationships between Layers 20

SHELL MINERALOGY 24

- Literature Review 24
- Sample Preparation 25
- Percent Aragonite in Seasonal Collections of *Mytilus* 27
- Model Growth Series 31
- Growth Series in *M. californianus* 38
- Growth Series in *M. edulis diegensis* from Corona del Mar 43
- Growth Series in *M. edulis diegensis* from Avila Beach 45
- Geographic Variation of Percent Aragonite in Small Specimens of *M. californianus* 47
- Geographic Variation in Percent Aragonite in Small Specimens of *M. edulis edulis* and *M. edulis diegensis* 49
- Geographic Variation of Percent Aragonite in Larger Specimens of *M. edulis edulis* and *M. edulis diegensis* 52

TITLE PAGE

Geographic Variation in Percent Aragonite in Larger Specimens of *M. californianus* 54

Variation with Temperature of Percent Aragonite in *M. californianus* 61

Variation of Percent Aragonite in *M. californianus* with Oxygen Isotope Temperature 66

Relationship between Shell Thickness and Mineralogy at Corona del Mar 68

Relationship between Shell Thickness and Mineralogy at other Locations 72

Variation of Shell Mineralogy with Salinity in *M. edulis edulis* 77

Variation of Shell Mineralogy with Salinity in *M. edulis diegensis* 79

Variation of Shell Mineralogy between Microenvironments 81

Unknown Factors Affecting Shell Mineralogy in *Mytilus* 82

Mytilus Specimens Grown in Aquariums 83

Miscellaneous Observations on Specimens Grown in Aquariums 85

SHELL STRUCTURE VARIATION 88

Determining Percent Aragonite in Thin Section 88

Variation with Latitude of Percent Aragonite in Section 92

Structural Types 96

Variation of Mean Structural Type with Temperature 99

Geographic Variation in Growth Rates in *M. californianus* 99

Structural Variation in *M. edulis diegensis* and *M. edulis edulis* 103

Growth rates in *M. edulis edulis* and *M. edulis diegensis* 104

TITLE PAGE

STRONTIUM AND MAGNESIUM CONTENTS 106

Literature Review 106

Spectrographic Techniques 108

Seasonal Variation in Strontium and Magnesium Content of the Outer Prismatic Layer of *Mytilus* 109

Correlation between Temperature and Spectrographically Determined $MgCO_3$ and $SrCO_3$ 113

X-ray Fluorescence Analysis Technique 117

Correlation between Temperature and $SrCO_3$ as Determined by X-ray Fluorescence 120

Effect of Shell Size on $SrCO_3$ Content 123

Variation of $SrCO_3$ Content with Salinity 127

Seasonal Variation Series from Single Shells 129

$SrCO_3$ Content of Other Layers 135

PALEOECOLOGICAL INTERPRETATIONS 138

Comparison of Paleotemperature Methods 138

Review of California Upper Pleistocene Faunas 141

Use of *M. californianus* for Paleotemperature Interpretations 144

M. californianus Fossils from Rosarito Beach 145

M. californianus Fossils from Torrey Pines 150

M. californianus Fossils from Newport Bay 154

M. californianus Fossils from Cayucos 158

M. edulis edulis Fossils from San Francisco 163

Oxygen Isotope Analysis of Fossils 165

Oxygen Isotope Analyses of Portions of *M. californianus* Fossils 166

TITLE PAGE

CONCLUSION 171

REFERENCES 176

APPENDIX I 186

APPENDIX II 214

LIST OF FIGURES

FIGURE PAGE

1. Collecting localities of modern shells 4
2. Collecting localities of fossil shells 5
3. Orientation of sections and terms used in describing sections 9
4. Diagrammatic representation of the relationship between layers in *M. californianus* 10
5. Seasonal variation in the percent aragonite in specimens of varying sizes of *M. californianus* 29
6. Seasonal variation in the percent aragonite in specimens of varying sizes of *M. edulis diegensis* 29
7. Variation in mean temperature of shell deposition with season 33
8. Model growth series 36
9. Rate of increase in length in *M. californianus* 39
10. Growth series of *M. californianus* from Corona del Mar 40
11. Growth series of *M. edulis diegensis* from Corona del Mar 44
12. Growth series of *M. edulis diegensis* from Avila Beach 46
13. Geographic variation in shell mineralogy in small specimens of *M. californianus* 48
14. Geographic variation in shell mineralogy in small specimens of *M. edulis edulis* and *M. edulis diegensis* 50
15. Geographic variation in shell mineralogy in larger specimens of *M. edulis edulis* and *M. edulis diegensis* 53
16. Growth series of *M. californianus* from Hoh 55
17. Growth series of *M. californianus* from Waldport 55
18. Growth series of *M. californianus* from Westport 56
19. Growth series of *M. californianus* from Avila Beach 58

FIGURE PAGE

20. Growth series of *M. californianus* from La Jolla 59

21. Geographic variation in shell mineralogy in large specimens of *M. californianus* 62

22. Variation of the shell mineralogy of *M. californianus* with temperature 63

23. Semi-logarithmic plot of the variation of the shell mineralogy of *M. californianus* with temperature 65

24. Variation of the shell mineralogy in *M. californianus* with temperature as determined by oxygen isotope analysis 67

25. Log weight vs. log length of *M. californianus* from Corona del Mar 70

26. Effect of shell thickness on shell mineralogy in *M. californianus* from Corona del Mar 71

27. Growth series of *M. californianus* from Corona del Mar with correction for effect of shell thickness 73

28. Effect of shell thickness on shell mineralogy in *M. californianus* from La Jolla 74

29. Variation of salinity at collecting time and shell mineralogy of *M. edulis edulis* from the Washington area 78

30. Variation of salinity at collecting time and the shell mineralogy of *M. edulis diegensis* from the San Francisco area 80

31. Effect of orientation of the section on the percent aragonite in longitudinal section 90

32. Comparison of x-ray determined percent aragonite with percent aragonite in longitudinal section of the opposite valves of the same individual 91

33. Variation with latitude of percent aragonite in longitudinal section 93

34. Variation in percent aragonite in longitudinal section with mean annual temperature of the collecting locality 95

35. Variation of mean structural type with mean annual temperature of collecting locality 100

FIGURE PAGE

36. Growth rate of M. californianus at selected stations 102

37. Variation with collecting date of mole percent $MgCO_3$ in the calcite rims of M. edulis diegensis from Corona del Mar 111

38. Variation with collecting date of mole percent $SrCO_3$ in the outer calcite rims of M. edulis diegensis from Corona del Mar 112

39. Variation with estimated mean temperature for two weeks at collecting time of mole percent $SrCO_3$ in the outer calcite rims of M. edulis diegensis 115

40. Variation with estimated temperature for two weeks at collecting time of mole percent $MgCO_3$ in the outer calcite rims of M. edulis diegensis 116

41. Effect of sample size on x-ray fluorescence analyses of Sr content 119

42. Variation with temperature of mole percent $SrCO_3$ in the outer prismatic layer of Mytilus 121

43. Variation with length of specimen of the $SrCO_3$ content of the outer prismatic layer 124

44. Idealized representation of the relationship between $SrCO_3$ content and temperature in Mytilus 126

45. Variation with salinity in mole percent $SrCO_3$ in the outer prismatic layer of M. edulis edulis 128

46. Location of samples used in seasonal variation studies of the $SrCO_3$ content of individual shells 130

47. Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a specimen of M. californianus from Pacific Grove 131

48. Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a specimen of M. californianus from Corona del Mar 134

49. Variation with temperature of mole percent $SrCO_3$ in the nacreous layer of Mytilus 136

50. Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. californianus from Rosarito Beach 147

FIGURE PAGE

51. Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Torrey Pines 152

52. Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Newport Bay 156

53. Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Cayucos 161

LIST OF TABLES (Appendix I)

TABLE PAGE

1. X-ray Determination of the Percent Aragonite in *M. californianus* Collected Seasonally from Corona del Mar, California 187

2. X-ray Determination of the Percent Aragonite in *M. edulis diegensis* Collected Seasonally from Corona del Mar, California 188

3. X-ray Determination of the Percent Aragonite in Specimens of *M. californianus* Collected at Corona del Mar on October 29, 1959 189

4. X-ray Determination of the Percent Aragonite in Specimens of *M. edulis diegensis* Collected at Avila Beach on October 16, 1959 190

5. X-ray Determination of the Percent Aragonite in Small Specimens of *M. californianus* from the Pacific Coast of North America (collected between July 15, 1958 and August 3, 1958) 191

6. X-ray Determination of the Percent Aragonite in Small Specimens of *M. edulis* (both subspecies) from the Pacific Coast of North America (collected between July 15, 1958 and August 4, 1958) 192

7. X-ray Determination of the Percent Aragonite in Larger Specimens of *M. edulis diegensis* and *M. edulis edulis* from the Pacific Coast of North America 193

8. X-ray Determinations of Percent Aragonite in Larger Specimens of *M. californianus* from the Pacific Coast of the United States 194

9. Mean Temperatures of Growth as Determined by Oxygen Isotopic Analysis for *M. californianus* from Various Points along the Pacific Coast of North America 196

10. X-ray Determination of the Percent Aragonite in Specimens of *M. edulis edulis* from Washington and San Francisco Bay 197

11. X-ray Determination of the Percent Aragonite in Specimens of *M. californianus* and *M. edulis diegensis* from Corona del Mar Showing Microenvironmental Effects 198

TABLE PAGE

12. Percent Aragonite in Longitudinal Sections of Shells of M. californianus from the Pacific Coast of North America 199

13. Shell Structural Types in M. californianus from Southern California and Northern Baja California 201

14. Emission Spectrographic Determinations of Strontium and Magnesium in the Outer Two mm. of the Outer Prismatic Layer in M. edulis diegensis from the Kerckhoff Marine Laboratory at Corona del Mar, California 202

15. X-ray Fluorescence Determination of the Strontium Content in the Outer Prismatic Layer of Mytilus from Various Points along the California Coast 203

16. X-ray Fluorescence Determination of the Strontium Content in the Outer Prismatic Layer of Mytilus from the Open Coast at Corona del Mar 205

17. X-ray Fluorescence Determination of the Strontium Content in the Outer Prismatic Layer of M. edulis edulis from Locations with Reduced Salinity 206

18. X-ray Fluorescence Determination of the Strontium Content of Segments of the Outer Prismatic Layer Parallel to the Growth Lines of M. californianus 207

19. X-ray Fluorescence Determination of the Strontium Content of the Nacreous Layer of Mytilus 208

20. Structural Type of Fossil Specimens of M. californianus 209

21. X-ray Fluorescence Determination of the Strontium Content of Segments of the Outer Prismatic Layer Parallel to the Growth Lines of Fossil Specimens of M. californianus 210

22. Mineralogy of Fossil Specimens of Mytilus from the Pacific Coast of North America 212

23. Oxygen and Carbon Isotopic Analysis of Portions of the Outer Prismatic Layer of Fossil Specimens of Mytilus 213

LIST OF PLATES (Appendix II)

PLATE			PAGE
I	a	*Mytilus californianus*	215
	b	*M. edulis edulis*	
	c	*M. edulis diegensis*	
II	a	Thin section showing the outer prismatic layer and periostracum of *M. californianus*	216
	b	Peel showing calcite crystals of the outer prismatic layer	
	c	Peel containing calcite crystals of the outer prismatic layer (crossed Nicols)	
III	a	Outer prismatic layer of *M. edulis diegensis* (crossed Nicols)	217
	b	Transverse thin section of *M. californianus* (crossed Nicols)	
	c	Peel showing the inner surface of nacreous layer	
IV	a	Peel showing the inner prismatic layer of *M. californianus*	218
	b	Peel of the inner surface of the inner prismatic layer	
V	a	Peel showing the blocky aragonite layer	219
	b	Peel showing intertonguing of nacreous and inner prismatic layer in *M. californianus*	
VI	a	Longitudinal polished section of *M. edulis diegensis*	220
	b	Longitudinal polished section of *M. edulis edulis*	
	c	Interior of a valve of *M. californianus* showing the inner prismatic layer	
VII		Photographs and drawings of sections showing shell structural types	221
VIII		Photographs and drawings of sections showing shell structural types (con't.)	222

INTRODUCTION

The object of this study has been the development of quantitative techniques of paleotemperature and paleosalinity determination. Interest in quantitative ecological interpretation has grown rapidly since the development by Urey et al. (1951) of the oxygen isotopic technique of paleotemperature determination. Since that time, other geochemical techniques have been suggested (see especially Lowenstam, 1954a); but with a few exceptions (Lowenstam, 1959 and 1961; and Pilkey and Hower, 1960), these techniques have not been developed to the point of quantitative usefulness. It is important to have a variety of methods of quantitatively determining any paleoecological factor, not only to act as a check between methods, but also because not all methods will work in all cases.

In this study, three methods of quantitative paleotemperature determination have been developed for two species of one pelecypod genus found on the Pacific Coast of North America. They depend on strontium content of the outer prismatic layer, shell mineralogy, and shell structure.

Lowenstam (1954b) first showed that the relative amounts of calcite and aragonite in some invertebrates containing both of these minerals is at least in part a function of temperature. Variation in shell structure is indirectly an expression of variation in mineralogy of the shell. A number of workers have investigated the strontium content of shells (see especially Vinogradov, 1953; Odum, 1956a; Thompson and Chow, 1955; and Kulp et al., 1952). Lowenstam (1959) found brachiopods to be temperature sensitive in their strontium content. Pilkey and Hower (1960) found that the echinoid genus Dendraster is apparently temperature sensitive in its strontium content.

A more detailed discussion of previous work in the field of paleotemperature determination is included in the various sections concerned with specific methods.

The work of Lowenstam (1954b) on the temperature dependence of calcite and aragonite in shells indicated that the relationship is species dependent, i.e., a paleotemperature scale for one species would not necessarily be valid for any other species. The present, detailed study is of necessity limited to one or at most a few species. The selection of the particular species to be used in this study was based on the following major considerations: 1) the shell must be composed of a combination of calcite and aragonite, 2) it must live in a wide range of temperatures, 3) it must be relatively abundant and easily collected, 4) it should grow in reduced salinity situations as well as at normal salinities in order to evaluate a possible salinity effect, 5) it should be represented in the fossil record. From most of these considerations, the Pacific Coast mussel Mytilus californianus (Plate Ia, Appendix II, p. 215) is ideal. It does not, however, live in water of reduced salinity. For this reason and also in order to compare two separate but closely related species, two subspecies of M. edulis (Plate Ib and c, Appendix II, p. 215) were also studied.

The subspecies *M. edulis diegensis* lives in the southern part of the area covered in this study and *M. edulis edulis* in the northern part. Whether the northern subspecies is actually the same as *M. edulis* from Europe remains to be seen. Here it will be referred to as *M. edulis edulis* in order to distinguish it from the other subspecies. It is not the intent of this study, however, to become involved in a taxonomic discussion. These subspecies names are used to distinguish what appear to be closely related but genetically distinct groups within the genus *Mytilus* on the Pacific Coast of North America.

Both fossil and modern shells were used in this study. Modern shells came from points along the Pacific Coast of North America from Bahía Santo Tomás, Baja California, Mexico, to Neah Bay, Washington (fig. 1). When possible, collections were made at or near temperature recording stations of the U. S. Coast and Geodetic Survey and the Scripps Institute of Oceanography. The modern material was collected as live specimens from the intertidal zone. Most of the shells were collected in one month during the summer of 1958. Additional collections were made during the fall of 1959. Periodic collections were made between the spring of 1958 and the summer of 1960 at Corona del Mar, California. Fossils were collected from several localities in Baja California and California (fig. 2). They were collected between the spring and fall of 1960. The analytical work on modern and fossil shells was done between the spring of 1959 and the fall of 1960.

Facing p. 4

Localities corresponding to numbers in Fig. 1

1. Bahía Santo Tomás, Baja California
2. El Morro, Baja California
3. Halfway House, Baja California
4. La Jolla, California
5. Corona del Mar, California
6. Santa Monica, California
7. Port Hueneme, California
8. Avila Beach, California
9. San Martin, California
10. Pacific Grove, California
11. San Francisco (Fort Point), California
12. Sausalito, California
13. San Pedro, California
14. China Camp, California
15. Westport, California
16. Cape Mendocino, California
17. Trinidad, California
18. Crescent City, California
19. Ophir, Oregon
20. Bandon, Oregon
21. Umpqua, Oregon
22. Waldport, Oregon
23. Indian Beach, Oregon
24. Point Grenville, Washington
25. Hoh, Washington
26. Neah Bay, Washington
27. Port Townsend, Washington
28. Brinnon, Washington
29. Eldon, Washington
30. Potlatch, Washington
31. Twanoh Park, Washington

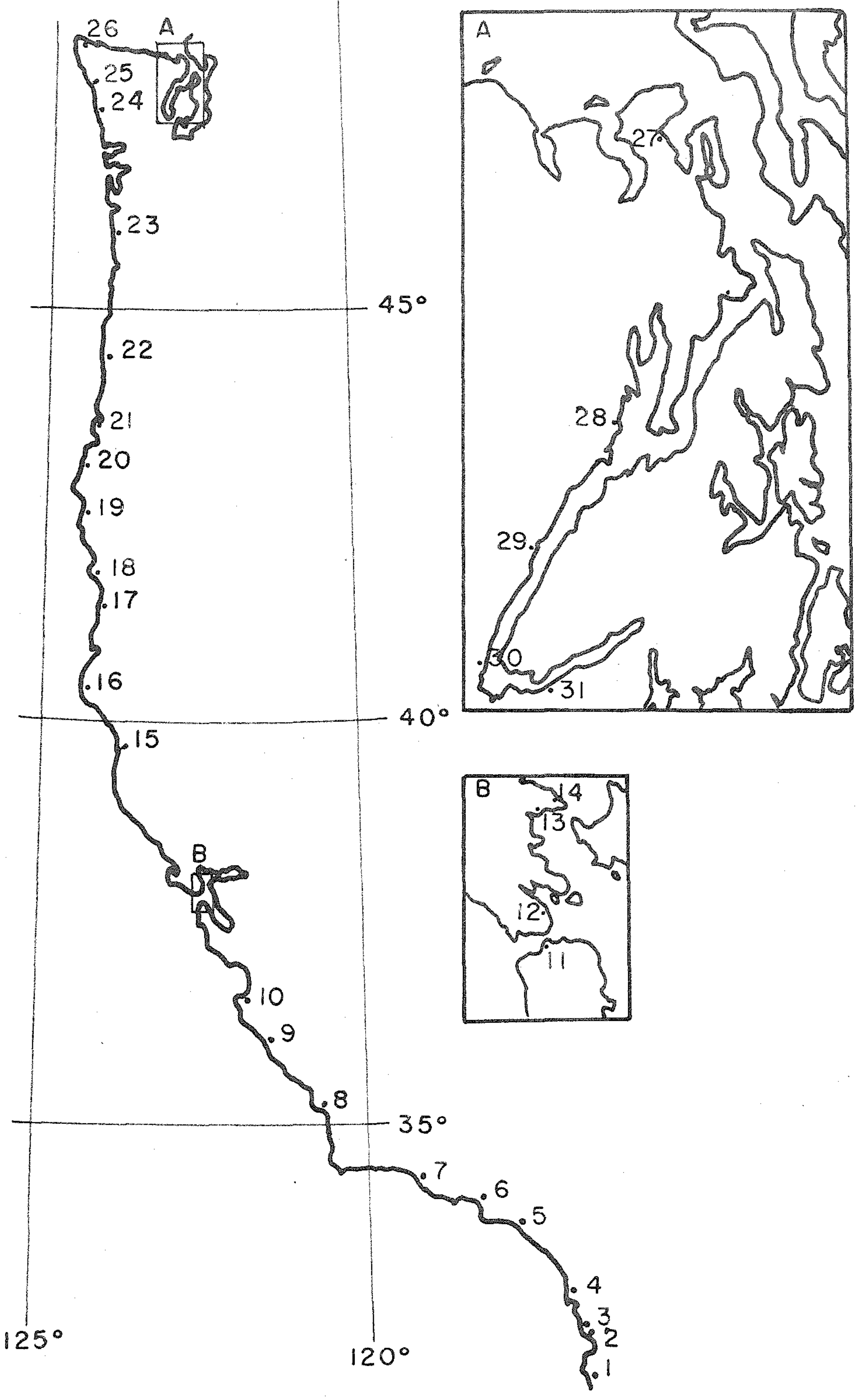

Figure 1. - Collecting localities of modern shells.

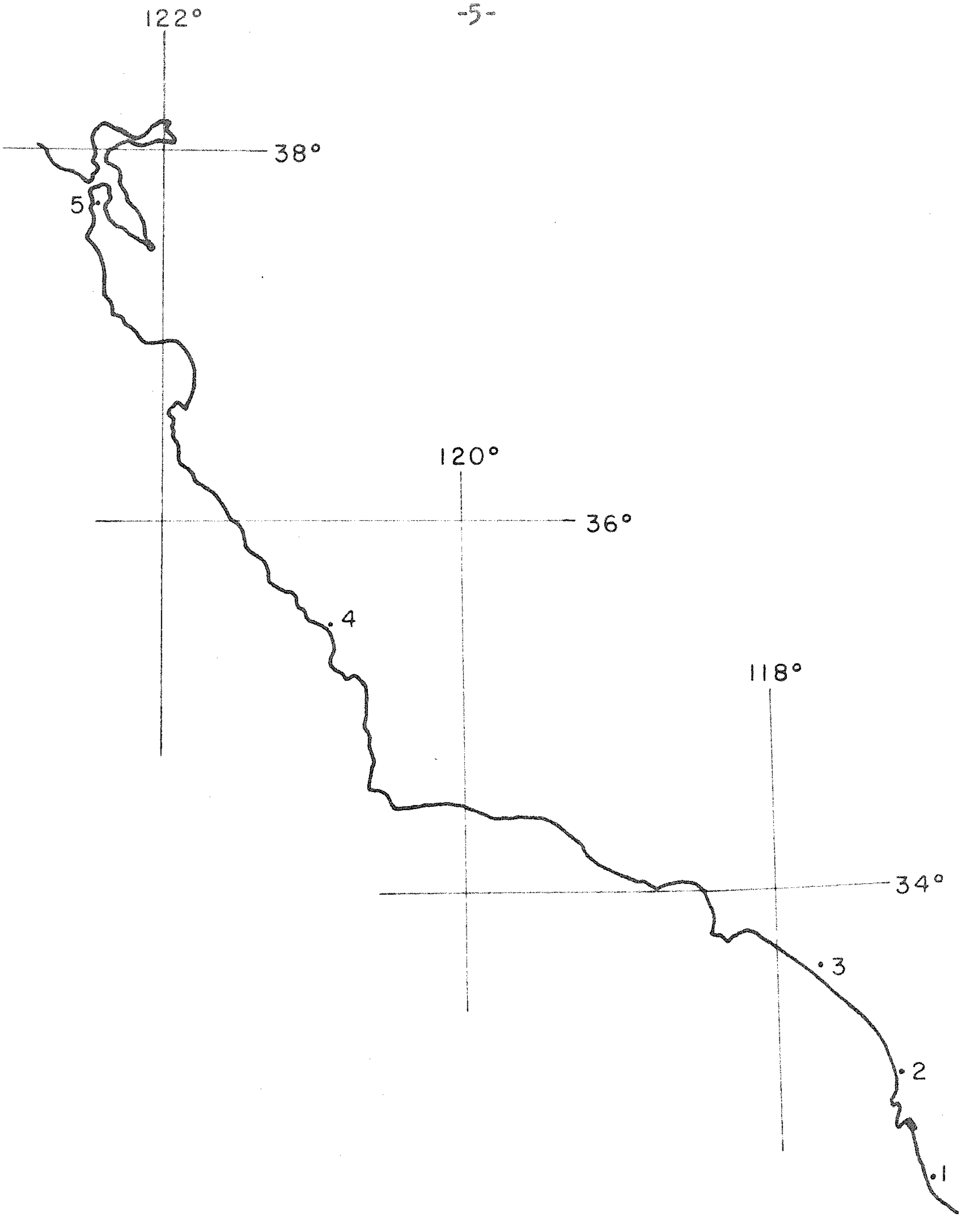

Figure 2. - Collecting localities of fossil shells

1. Rosarito Beach, Baja California
2. Torrey Pines, California
3. Newport Bay, California
4. Cayucos, California
5. San Francisco, California

MYTILUS SHELL STRUCTURE

Literature Review

A number of workers have studied the structure of Mytilus shells, in particular Ehrenbaum (1885), Schmidt (1924), Field (1922), and White (1937). These workers studied the structure of the shell of M. edulis. They described the mineralogic form and arrangement of the crystals in the outer prismatic and inner nacreous layer of this species. No special consideration was given to the beak area. The structure of the shell of M. californianus has not been previously studied. Bøggild (1930) made a survey of molluscan shell structure with many important generalizations on structural types which are pertinent to a study of the Mytilus structure. Recent work has been done on the nacreous and prismatic structure utilizing the technique of electron microscopy (Grégoire, 1957; and Tsujii et al., 1958). (For a review of the literature of pelecypod shell structure in general, see Schenck, 1934).

Methods of Shell Structure Study

Thin sections, polished sections and nitrocellulose peels were used in studying the shell structure of Mytilus. In preparing peels, the shells were cut and embedded in plaster of Paris. The surface was then ground smooth and etched for 30 seconds in a 5% solution of hydrochloric acid. When a section was not etched, observation of crystal boundaries was difficult. Small abrasive scratches also are obliterated by the etching process. After the etched portion had dried, the liquid nitrocellulose solution was poured onto the surface. Thick peels were necessary to prevent tearing. The most satisfactory procedure to insure a peel of adequate thickness was to pour as much solution onto the plaster block as surface tension would hold. After this had dried for one or two hours, an equal amount was added. The sections were allowed to dry for a minimum of 15 hours. The peel was then removed from the plaster block with the aid of a sharp knife to loosen the edges. The edges were trimmed and excess plaster adhering to the peel removed. The peel was mounted on a microscope slide under a cover glass with cellophane tape.

The nitrocellulose solution used to make these peels had the same composition as that used by Darrah (1939).

Peels have many advantages over thin sections in studying shell structure. Individual crystals only a micron in diameter can be clearly distinguished in what appears in thin sections to be a homogeneous mass. Peels can be made of curved surfaces (such as the inside of shells) and then flattened. Serial sections only a few microns apart in shells can be made. It is possible to study a polished surface at the exact plane where a peel is also available. Actual crystals of the shell often are pulled off in making a peel. This makes three dimensional study of the crystals possible. Other advantages of peels are discussed by Darrah (1939) and Romer (1959).

Polished sections of shells mounted in plaster blocks were found to be useful in this study, particularly when used in conjunction with a peel from the same surface. Pigmentation and texture of the shell layers differ significantly so that it is possible to study the relationships between layers from inspecting these surfaces. Staining techniques were also used, particularly in studying the beak area. Feigl's solution (Leitmeier and Feigl, 1934) which stains aragonite brown or black but does not affect calcite, was used to bring out detail.

Structural Units of *Mytilus* Shells

The *Mytilus* shell is composed of three and in some cases four layers. Proceeding from the outside in, these layers are: 1) periostracum, 2) outer prismatic layer, 3) nacreous layer, 4) inner prismatic layer (not found in all specimens). In addition, a blocky aragonite layer can sometimes be recognized within the nacreous layer and on the muscle scars. The beak of *Mytilus* shells contains varying amounts of calcite which cannot be included with one of the regular layers. The aragonitic ligamental ridge is also a distinct structural unit. Figure 3 shows the orientation of sections used in the following discussion of the shell layers and gives some of the terms used. Figure 4 shows the generalized arrangement of structural units in the shell of *M. californianus*. *M. edulis edulis* and *M. edulis diegensis* have the same general structure except that they lack the inner prismatic layer. Figure 4 also shows the relationship of some of the photographs used to illustrate shell structural features to the complete longitudinal section.

Periostracum

The outermost layer of the *Mytilus* shell is the periostracum. It is composed of organic material. Shells exposed to surf action

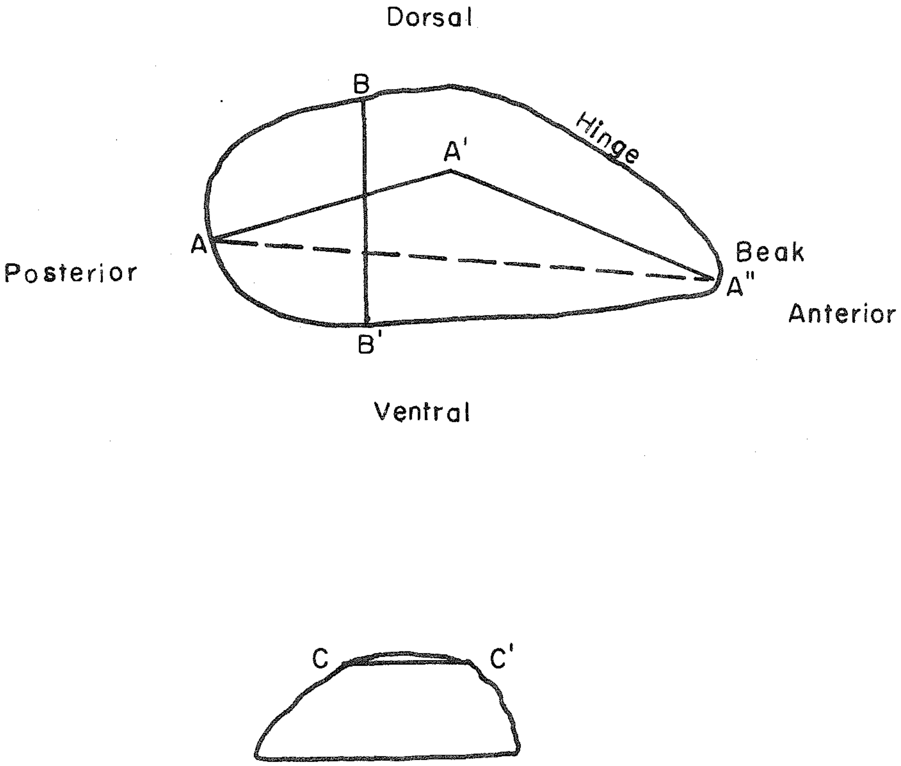

Figure 3. - Orientation of sections and terms used in describing sections. AA'A'' - longitudinal section (AA'' in small shells), BB' - transverse section (position between anterior and posterior ends of shell may vary), CC' - tangential section.

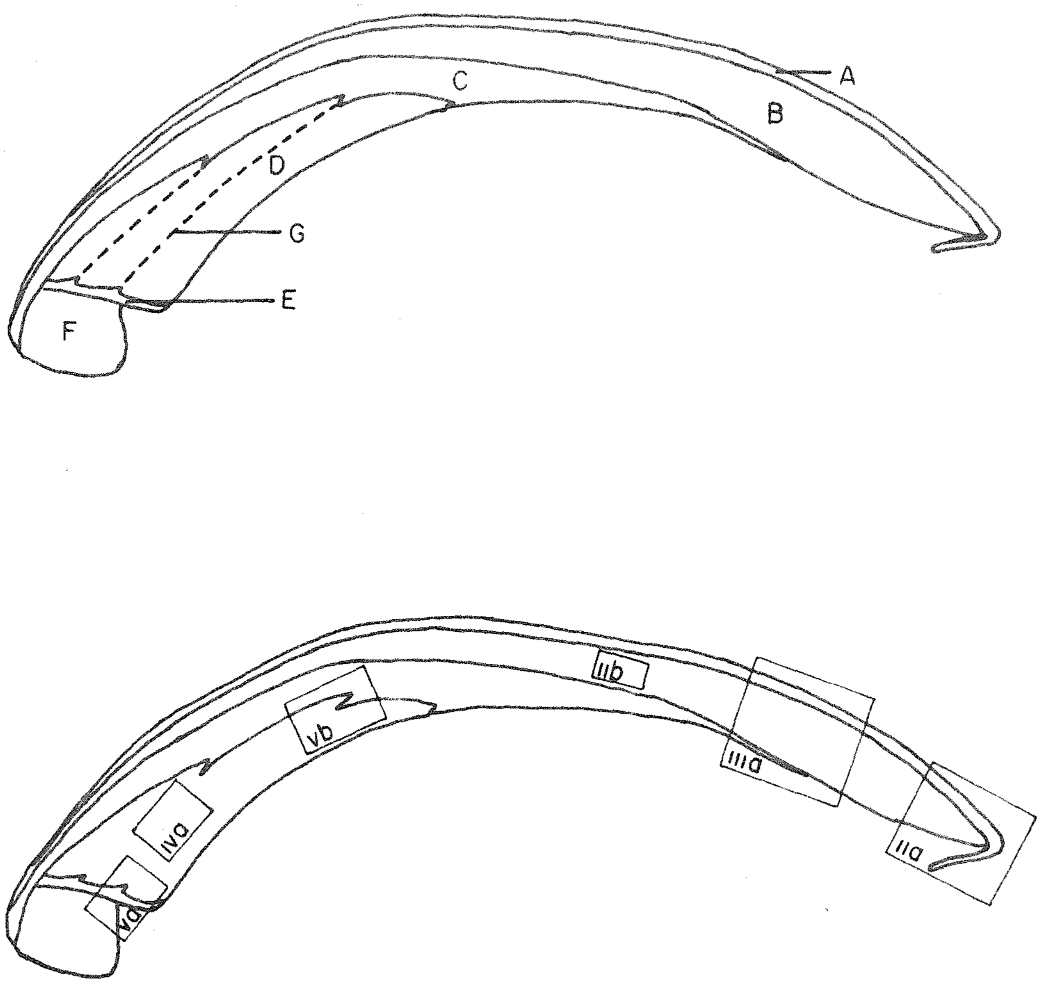

Figure 4. Diagrammatic representation of the relationship between layers in M. californianus. The lower sketch shows the position of the photographs showing shell structural features. The numbers and letters in the rectangles refer to plates in Appendix II. A - periostracum, B - outer prismatic layer, C - nacreous layer, D - inner prismatic layer, E - blocky aragonite layer, F - beak area, G - "color band" in inner prismatic layer.

soon lose their periostracum. This layer is often worn from a large portion of the shell of living specimens which are exposed to surf action due to abrasion with other shells or the substrate.

In thin section the periostracum layer has a light greenish-brown color. It may contain streaks of deep red to black pigmentation, particularly toward the outer edge. Except for these color streaks, the structure of this layer seems to be homogeneous. Previous workers (Field, 1922 and White, 1937) have noted a three layered structure of the periostracum on the basis of staining with organic dyes. Ehrenbaum (1885) recognized five layers.

The thickness of the periostracum is rather uniform within a given specimen. Its thickness increases slightly towards the posterior end of the shell. It is almost invariably worn from the beak area. The larger the shell is, the thicker the periostracum at the posterior margin. It often thickens somewhat in depressions in the shell and thins on ridges where it is more exposed to abrasion.

The structure of the periostracum of M. californianus and the two subspecies of M. edulis appears identical. This layer is much thinner, however, in individuals of the latter species than in individuals of the same size of the former.

Previous workers have interpreted the periostracum to be secreted by the cells in the outer surface of the middle fold of the mantle edge (White, 1937). The layer folds around the posterior edge of the shell (Plate IIa, Appendix II, p. 216) and in this region is not attached to the calcareous part of the shell. The free edge of the periostracum can be observed in contact with the mantle edge of living specimens. The periostracum is thus being formed only at the edge of the shell. It is thicker in the posterior region because it was formed when the individual was larger and because it has been subjected to less wear.

The ligament of Mytilus appears to be continuous with and made of the same material as the periostracum.

Outer Prismatic Layer

The outer prismatic layer of the shell is composed of elongate crystals of calcite (as determined by x-ray diffraction and staining) having a diameter of 1-3 microns and a length of up to 35 microns and probably more (Plate IIa and b, Appendix II, p. 216). It is difficult to determine the length of these long crystals as the section would have to be oriented exactly parallel to the long axis for the length of the crystal. The optic axis parallels the long axis of the crystal.

The crystals as seen in longitudinal section are inclined toward the beak at an angle of 0 to 45 degrees with a line normal to the shell surface. Occasionally small reverse angles are observed. This angle may vary considerably within an individual shell. Individual groups of crystals may have the same orientation or may diverge inward from a common point or area forming fan-shaped groups or cones in three dimensions (Plate IIIa, Appendix II, p. 217). These crystal fans commonly occur at points of apparent shell damage.

Crystals often terminate at growth lines (Plate IIa, Appendix II, p. 216), but in many cases they pass on through. It is uncertain whether these growth lines are due to crystal termination or some other textural difference. The long axes of the crystals are usually normal to growth lines but may be inclined. The growth lines curve down anteriorly from the outer surface at an angle as high as 60 degrees and gradually become sub-parallel with the surface until they reach the contact with inner layers where they disappear.

In transverse sections of the shell, the individual crystals are usually seen in oblique section (Plate IIIb, Appendix II, p. 217). Occasionally the long axes of the crystals are parallel to the plane of the section. These are usually in fan-shaped aggregates as described above, and correspond to those crystals which can be observed as nearly normal to the shell surface in longitudinal section. The above generalizations do not apply to the ends of transverse sections, where the direction of section is parallel to the direction of growth. Here the section looks much like the posterior end of longitudinal sections.

The growth lines appear much the same in transverse section as in longitudinal section. The lines curve downward from the shell surface towards the interior until becoming parallel with the surface in the center of the section. They then curve upward to the surface at the other side of the shell.

Thin sections of the outer layer show streaks of blue-violet pigmentation. In longitudinal section they seem to be parallel to the growth lines. The degree of pigmentation varies considerably between shells and even within a particular shell. In tangential section, the pigment has a streaked appearance with the streaks being parallel to the direction of growth.

The above comments on the outer prismatic layer in general apply to M. edulis edulis and M. edulis diegensis as well as M. californianus, but they differ in some respects. In longitudinal section crystal fans are not as common as in M. californianus. The crystals are more uniformly oriented with a beakward inclination of 50 to 60 degrees for the most part. Growth lines are more distinct than in M. californianus. Transverse sections show a greater difference between ends and center of the section than in M. californianus, because of the fewer fans and the greater inclination of the crystals.

The thickness of the outer layer at any point is largely a function of the size of the individual at the time when that particular segment was deposited. In general, as seen in longitudinal section, the thickness rapidly increases from the posterior end of the shell towards the beak to the point where the nacreous layer begins (pallial line). From the pallial line to the beak, the layer more or less gradually decreases in thickness. This decrease is due to the fact that the individual was progressively smaller when increments progressively nearer the beak were formed. Minor fluctuations in thickness are observed in this zone, particularly in M. californianus. They decrease in amplitude toward the beak. These fluctuations are due to shelving and undulations parallel to the growth lines as seen on the shell surface. In M. californianus, they are due in part to the broad plications of the shell. Worn portions of the shell may also contribute in some cases.

In transverse section, through the posterior part of the shell, the layer rapidly increases in thickness from both ends to the point where the nacreous layer begins and then decreases to a minimum in the center. This is due to the fact that the shell was growing outward, and the oldest part, which was formed when the animal was smallest, is in the center. The outer layer reaches a greater thickness near the dorsal edge and thickens more rapidly inward from the dorsal edge than from the ventral. Perhaps this is incipient hinge formation.

Since the thinnest part of the outer layer (where it is underlain by nacreous layer) is presumably the oldest, it is possible to trace the center of growth in successive transverse sections through a shell. In the anterior portion of the shell, this center is near the hinge indicating that there is little growth at the hinge (probably none after the hinge is established). Toward the posterior part of the shell, the center of growth progressively moves toward the center and the ventral side of the shell indicating that dorsal growth gradually increases until it surpasses ventral growth.

Nacreous Layer

The nacreous layer of the Mytilus shell is typical for the Mollusca (Bøggild, 1930), consisting of laminae composed of tabular crystals of aragonite. The nacreous layer of molluscs has been rather extensively studied previously (see Grégoire, 1957). The crystals have been shown by x-ray diffraction and staining to be aragonite. They have their optic axes parallel to their least dimension and therefore perpendicular to the surface of the lamellae. As seen in tangential section, these crystals have an average diameter of 5-6 microns and are uniform in size. They have irregular polygonal outlines. In longitudinal and transverse section they are seen as thin (1 micron or less) streaks with a maximum length of 5-6 microns. Nitrocellulose peels of the inner surface of a Mytilus shell reveal a characteristic arrangement (Plate IIIc, Appendix II, p. 217) of irregular, zigzag lines which are due to crystal borders on overlapping laminae (Field, 1922). This same structure has been found in the nacreous layer of other molluscs (Grégoire, 1957).

In longitudinal sections of M. edulis edulis and M. edulis diegensis and some M. californianus this layer can be seen to increase in thickness uniformly from the pallial line to the beak. This is what would be expected from the fact that the nacreous layer is secreted by the surface of the mantle. The more anterior parts of the layer began forming when the animal was younger and the more posterior portions as it was progressively older. Thus the anterior parts have had a considerably longer time in which to thicken. In some specimens of M. californianus, the layer increases uniformly in thickness to the point where it is covered by the inner prismatic layer. From this point the layer somewhat irregularly decreases in thickness toward the beak. The explanation for this decrease is the same as for the outer prismatic layer, i.e., the smaller animal secretes a thinner shell.

In transverse section, the nacreous layer gradually thickens from inside the dorsal and ventral margins to a maximum near the center. This maximum corresponds with slight variation to the minimum in the outer prismatic layer thickness, i.e., the oldest part of the section.

Inner Prismatic Layer

This layer is found only in M. californianus but is quite common in that species. It is composed of calcite crystals as determined by x-ray diffraction and staining. These crystals are similar to those of the outer prismatic layer although they tend to be somewhat larger (3-6 microns in diameter). The crystals are up to 40-50 microns in length and probably often longer. The length of such narrow prisms is difficult to measure since they pass out of the section unless exactly parallel to it. Impressions of the inner surfaces of shells having this layer (Plate IVb, Appendix II, p. 218) show a mosaic of polygons 3-6 microns in diameter with some ½ micron of intervening space. As the above measurements indicate, crystal size in this layer is more variable than in the other two. More complex structure appears in this layer.

The fan arrangement of crystals described above for the outer prismatic layer is the usual arrangement in the inner prismatic layer (Plate IVa, Appendix II, p. 218). The angle of divergence of crystals in a fan is usually larger in this layer than in the outer prismatic layer. Divergences from 0° to 90° are found in this layer. Divergences of 0° to 45° are more common in the outer prismatic layer. These crystal fans (actually cones in three dimensions) usually extend from top to bottom of the layer unless interrupted by streaks of nacreous structure within the inner prismatic layer. New fan systems begin below these streaks. In those areas where there are no obvious fans, the crystals usually are reclined toward the beak as in the outer prismatic layer. The symmetry axes of the crystal fans are perpendicular to the layer surface to slightly reclined toward the beak.

Growth lines or zones of a different type occur in the inner prismatic layer. These are zones of smaller (and perhaps differently oriented) crystals parallel to the surface of the layer (Plate IVb, Appendix II, p. 218). In nitrocellulose peels this gives a different texture which is expressed as zones of yellowish-white in a background of gray. In regular thin sections they appear as brownish streaks in the generally clear layer. The zones may be more or less continuously traced from the beak to a juncture with the nacreous layer. Streaks of nacreous structure sometimes appear within these zones.

The inner prismatic layer begins at varying relative positions between the beak and the posterior edge of the shell. All transitions seem to exist from shells having extensive inner prismatic layers extending half the length of the shell or occasionally even more to shells having no inner layer (Plates VII and VIII, Appendix II, p. 221). Some shells have a beak area composed largely of aragonite. In others, the beak is composed of calcite. This calcite material may extend outward from the beak, as a wedge (or wedges) within the nacreous layer. In shells with progressively better developed inner layers, this material forms a wedge to the inside of the nacreous layer and then extends progressively further forward. Thus a completely uniform transition exists between the normal three-layered structure and the four-layered structures, all within the same species.

In longitudinal section, the inner prismatic layer appears as a thin wedge and increases very rapidly in thickness toward the beak. If the section passes through the depression of the anterior adductor muscle scar, there is a sharp decrease followed by another increase in the layer thickness. When this layer is well developed, it constitutes practically all of the beak area, particularly in shells which are worn in this area.

In transverse sections of the anterior portion of the shells, the inner prismatic layer begins a short distance inside the ventral edge of the shell and increases rapidly toward the hinge on the dorsal side. There is no decrease in thickness on this side since the thickened hinge area is composed largely of this layer.

No true inner prismatic layer is found in *M. edulis edulis* or *M. edulis diegensis*. Varying amounts of calcite do, however, occur in the beak area. In some northern forms this beak calcite extends forward for a distance equal to the width of the beak (Plate VIb, Appendix II, p. 220). The southern California forms have a much more limited amount of calcite in the anteriormost part of the beak (Plate VIa, Appendix II, p. 220). A small "pseudo-inner prismatic layer" is often present in the hinge area,where the nacreous layer wedges out within the outer prismatic layer.

The inner prismatic layer must be deposited by the mantle surface just as is the nacreous layer. The same mantle cells must change from aragonite to calcite precipitation. This has rather interesting physiologic implications.

An aragonitic layer which differs from the nacreous layer by its irregular, equidimensional crystals is often found on the muscle scars and within the nacreous layer. This is probably the durchsichtige substanz of Ehrenbaum (1885). The crystals of this blocky aragonite layer (Plate Va, Appendix II, p. 219) are relatively coarse (25-60 microns). A very thin zone of this structure can occasionally be observed between the outer prismatic and nacreous layers of both species. This appears to be the usual form of calcium carbonate secreted under the muscles of these species.

Relationships between Layers

Figure 4 is a diagrammatic representation of the generalized relationship between layers in a specimen of M. californianus.

The periostracum covers the outer surface of the shell and is in contact with the outer prismatic layer. No apparent intertonguing occurs between these layers.

Only in rare cases does intertonguing occur between the nacreous and outer prismatic layer. No intertonguing would be expected if deposition of the outer layer occurs only outside of the pallial line and this line never regresses during the life of the individual.

Contact near the dorsal margin may occur between the inner and outer prismatic layers in those individuals having an inner prismatic layer. Since these two layers are quite similar, their contact is difficult to define. The layers are in contact only where the nacreous layer wedges out between them.

The relationship of the nacreous and the inner prismatic layer is the most complicated. Lenses of inner prismatic structure occasionally occur within the nacreous layer. Tongues of the nacreous layer may project anteriorly and occasionally posteriorly into the inner prismatic layer (Plate Vb, Appendix II, p. 219). The "color bands" of finer crystal structure within the inner layer described above are continuous with these nacreous tongues. Sometimes these projections of nacreous structure do not appear to be connected with the main body of the nacreous layer. These streaks are usually associated with the fine grained zones of the inner prismatic layer.

Small projections of the blocky aragonite layer in the posterior muscle socket of <u>M. californianus</u> into the inner prismatic layer can sometimes be observed (Plate Va, Appendix II, p. 219). These projections extend into the fine grained zones of the inner layer and thus are also associated with the anteriorly projecting tongues of the nacreous layer.

The lenses of inner prismatic layer within the nacreous layer are particularly common in worn shells. Points of excessive wear apparently are strengthened by deposition of calcite on the interior of the shell. Subsequently, the normal nacreous layer is deposited over these areas.

The anteriorly projected tongues of nacreous structure are interpreted as representing summer deposition. Increased deposition of aragonite relative to calcite in <u>Mytilus</u> is favored by higher temperatures (see below). In the summer, the limits of aragonite deposition would extend further toward the anterior portion of the shell, i.e., would cover a larger portion of the inner surface. With the advent of colder temperatures, the boundary between calcite and aragonite deposition would move posteriorly once again, enclosing a tongue of aragonitic nacreous layer within the inner layer. If this interpretation is correct, one should be able to determine the approximate age of the individual by counting the number of anteriorly extending aragonite tongues. This can apparently be done in many cases. Weymouth (1923) indicated that he could determine the age of the Pismo clam (Tivela stultorum) from its shell structure. Coe (1947) indicates that this cannot be done reliably for that species.

Formation of posteriorly projecting tongues of nacreous layer into the inner prismatic layer is more difficult to visualize. A zone of aragonite deposition must have existed for a time within the limits of calcite deposition. Perhaps this occurred when the limit of calcite deposition was moving rapidly posteriorly with the onset of cold temperatures. This "island" of aragonite deposition then moved toward the posterior with time and gradually decreased in size until it disappeared, forming a posteriorly projecting tongue. If this interpretation is correct, the posteriorly projecting tongues should represent fall or winter deposition. These posteriorly projecting tongues are almost always associated with anteriorly projecting tongues which are interpreted as representing summer deposition.

The explanation of the formation of the projections of the blocky aragonite layer is the same as for the anterior nacreous layer projections.

If these interpretations are correct, there are three possible methods of determining the age of specimens of M. californianus: 1) counting projections of nacreous structure, 2) counting "color bands",

3) counting projections of the blocky aragonite layer. The three methods were used in determining the ages of several specimens of *M. californianus*. Each method gave the same age for a particular individual.

SHELL MINERALOGY

Literature Review

That shells may be composed of either calcite or aragonite or of a combination of the two minerals was first recognized by Brewster (1836, from Vinogradov, 1953). Sorby (1879) confirmed this observation and noted the variable position of layers containing the two minerals in shells of different species. Cornish and Kendall (1888) observed that some shells contain both polymorphs of calcium carbonate. Various papers concerned with shell structure mention the mineralogic nature of the layers in shells of different species of organisms (see Schenck, 1934 and Bøggild, 1930). For example in his study of shell structure, Schmidt (1924) includes observations on mineralogy. Bøggild (1930) made an extensive survey of the distribution of calcite and aragonite in the invertebrates with special emphasis on the molluscs. Bøggild made the first observation of an ecological control of mineralogic composition when he noted that, with only one exception, all fresh water molluscs consist of aragonite. Lowenstam (1954b and c) noted a temperature effect on shell mineralogy. He noted three manifestations of this effect: 1) the great increase in abundance of species and individuals in the tropics of groups characterized by aragonitic shells, 2) the restriction of some aragonite precipitating groups to tropical and subtropical waters, 3) an increased percentage of aragonite with increase in temperature in groups containing both minerals. Mytilus was noted to be in the third group. In the present study an attempt has been made to determine quantitatively the relationship between temperature and relative amounts of calcite and aragonite within a species.

Sample Preparation

Samples were prepared in the same manner as by Lowenstam (1954b). For larger specimens (approximately 30 mm. or more in length), only one valve was used. For specimens less than approximately 20 mm. in length, both valves of two or more individuals were used when appropriate material was available. Commonly the shells of Mytilus are worn in the beak area. Only unworn or insignificantly worn shells were used in this study. The shells were first mechanically cleaned under a binocular microscope of encrusting organisms and adhering sediment. Next the shells were placed in a solution of commercial Clorox to remove the organic material. The Clorox oxidized the periostracum and adhering soft parts but removed only a portion of the protein matrix and pigmentation from the shell. After the sample had remained in the Clorox for from one to five days, the solution was filtered and the sample washed with distilled water. After drying, the sample was ground in an agate mortar until all of it passed through a 200-mesh screen. Very large shells were quartered after they had been reduced to coarse fragments. Large shells were ground in portions to prevent excessive grinding on already fine material which could conceivably cause some conversion of aragonite to calcite. The ground portions were thoroughly mixed.

Method of Analysis

Percentages of aragonite were determined by x-ray diffraction.

A North American Phillips x-ray diffraction unit, a goniometer spectrometer equipped with Geiger counter, a Brown recorder, and an automatic timing and recording unit were used. Nickel filtered copper radiation at 35 kv. and 20 ma. was used. Some samples were run by chart as by Lowenstam (1954b). Most samples were run by counting over the strongest calcite peak (3.03Å) and the strongest aragonite peak (3.40Å).

In order to minimize the effect of preferred orientation, samples were packed by brushing the powder through a 100-mesh screen onto an aluminum disk which was covered with a thin film of petroleum jelly. Crystal fragments should thus fall randomly onto the disk and stick in the petroleum jelly in the orientation in which they fall. The disk was placed in a rotating sample holder to further reduce the effect of preferred orientation.

For those samples run by chart, a goniometer speed of one degree per minute and a chart speed of one half inch per minute was used. Peak heights at 29.4° 2θ (calcite) and 26.2° 2θ (aragonite) were measured and background subtracted. When the aragonite value is multiplied by the factor 3.76, the peak heights are directly proportional to the amounts of the minerals in the sample. The actual percent aragonite was taken from a graph based on a series of known standard samples. A minimum of three runs with three separate packings was made on each sample. The error of this method was at least 10%.

Most samples were analyzed by step scanning over the peaks. In this technique the time required to take 6400 counts at each point was determined at 0.01 degree 2θ intervals over the peaks with an automatic timer and recorder. The shortest peak times as well as background times determined by linear interpolation from readings at 32.00° and 24.00° 2θ were converted to counts per second and background subtracted. The value for the aragonite peak was multiplied by the factor 3.76. The percent aragonite was then determined from these corrected values. A final small correction was made to take into account the deviation of the theoretical and empirical curves.

In order to determine the precision of this technique of analysis, one sample was run eight times on eight different days and with eight different sample packings. The mean value for the percent aragonite obtained in these runs was 30.2% with a standard deviation of 0.6%. This is a precision of 2% and is adequate for this study. Samples used in this study at the extremes of the range in percent aragonite were also run three and four times and gave similar precisions. For the sake of simplicity in plotting graphs, all samples analyzed by this technique were considered to have an uncertainty of plus or minus 1% aragonite. Most samples were run only one time although some were run twice. Those samples showing an uncertainty in graphs of greater than 1% aragonite were run by chart.

Percent Aragonite in Seasonal Collections of *Mytilus*

Since young specimens of *Mytilus* are continually being spawned (Whedon, 1936; Coe and Fox, 1942; and Young, 1942 and 1946), small specimens can be collected throughout the year. Small individuals of *M. edulis diegensis* ranging in length from 6-32 mm. were collected every three to six weeks from the pier of the Kerckhoff Marine

Biological Station in Corona del Mar, California. Small specimens of M. californianus ranging in length from 11-29 mm. were collected from rocks on the open coast approximately a mile south of the Marine Station.

The specimens were always taken from approximately the same spot in order to minimize any microenvironmental effect. All were from intertidally exposed positions. The samples were composed of from one to four individuals.

Figure 5 shows the percent aragonite in specimens of M. californianus of varying sizes. The smallest individuals (11-14 mm. in length, probably 2-2½ months old*) show no regular seasonal variation. This indicates that these specimens have mineralogy which is independent of temperature.

The next group of specimens of M. californianus (17-22 mm., probably 3-4 months old) does show a probable minor cyclic variation. This curve could be due in part at least to chance. One would expect the lowest proportion of aragonite in shells collected from mid- to late winter, but the March value is the highest of the series. The highest value would be expected in mid- to late summer. The variation in the percentages in the 17-22 mm. series is only slightly greater than in the apparently temperature insensitive 11-14 mm. shells. Even if the 17-22 mm. individuals are beginning to show a temperature effect in

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* The probable ages shown here are based on the work of Coe and Fox (1942) and Coe (1945) for specimens from La Jolla. As the conditions under which the specimens used in this study grew were different than those in La Jolla, these age estimates are uncertain. They are likely to be somewhat too low.

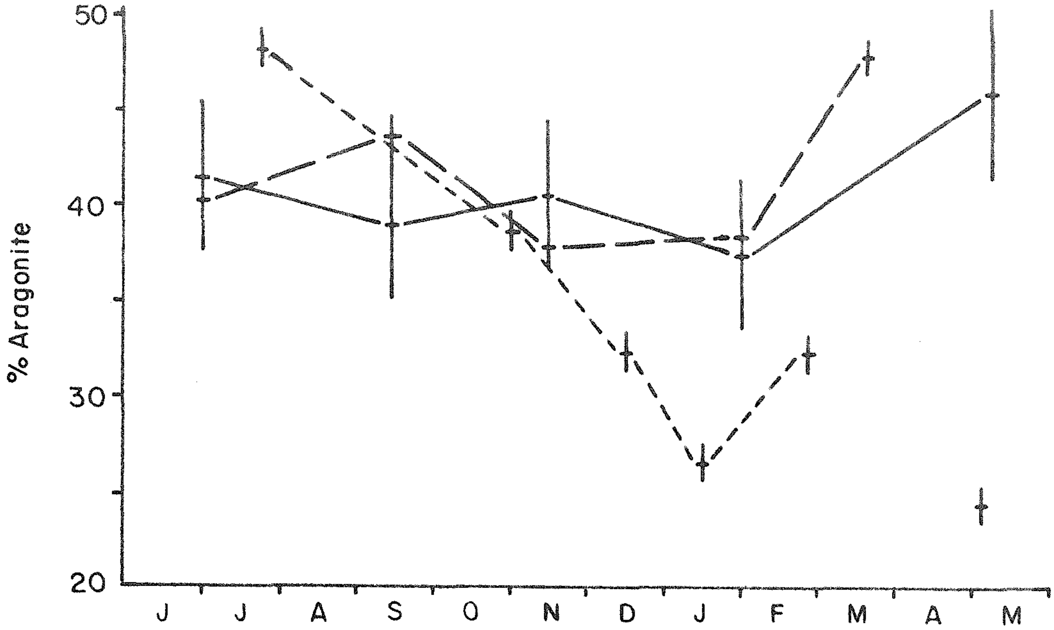

Figure 5. - Seasonal variation in the percent aragonite in specimens of varying sizes of M. californianus. The solid line connects points for specimens 11-14 mm. in length, the long dashed line specimens of 17-22 mm., and the short dashed line specimens of 25-29 mm.

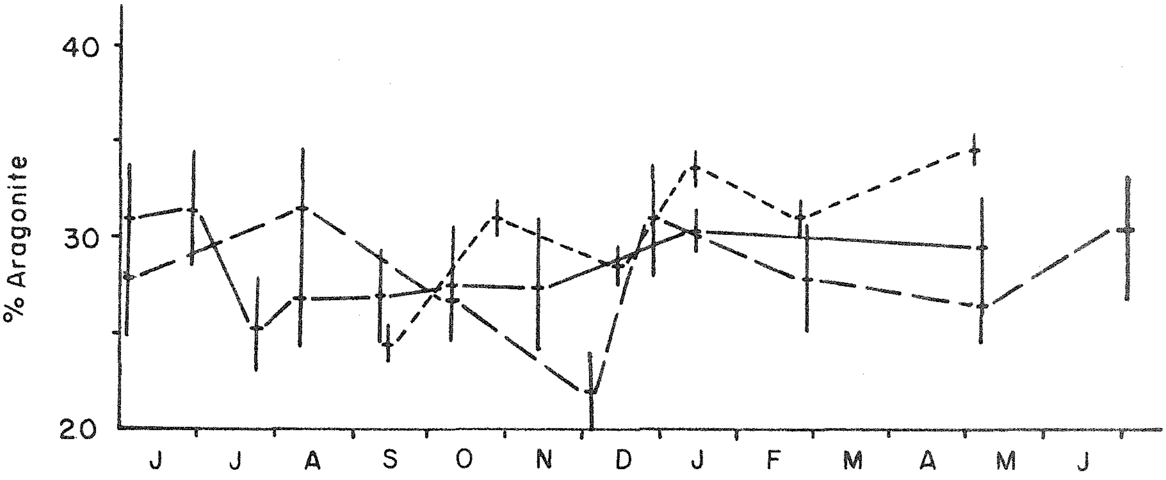

Figure 6. - Seasonal variation in the percent aragonite in specimens of varying sizes of M. edulis diegensis. The solid line connects points for specimens 6-10 mm. in length, the long dashed line specimens of 13-17 mm., and the short dashed line specimens of 28-32 mm.

their mineralogy, the larger portion of their shell was not affected by temperature during its formation. This tends to mask the effect of the temperature sensitive portion.

The largest individuals (25-29 mm., probably 4-5 months old) are clearly temperature sensitive. The highest value is for late July (no August or September samples were analyzed) and the lowest for mid-January. The range of values is larger than in the smaller individuals and is outside of the range of normal individual variation. One point (May) is off the expected curve. Why such a low value should occur at this time of year is not known.

One would expect that if other groups of still larger individuals were analyzed, the variation would reach a maximum and then decrease. After a certain size, the shell laid down in any one season would be a relatively small part of the total shell.

These results thus indicate that small specimens of M. californianus are not sensitive to temperature in the relative amounts of calcite and aragonite that they secrete. After reaching a certain size (15-20 mm.), they become temperature sensitive. All larger individuals then contain a portion of their shells which may be called temperature insensitive in the sense that its mineralogic composition does not reflect the temperature at which it grew. The remainder of the shell is apparently temperature sensitive.

The presence of a temperature insensitive portion has rather interesting physiologic implications. It would seem to suggest that a profound change occurs in the animal at this stage of life, perhaps even comparable to the change from the larval stage.

The samples of M. edulis diegensis give different results (fig. 6). The percentage of aragonite in the smallest individuals (6-10 mm., probably 1-1½ months old) do not fluctuate with the seasons. Their values are rather constant around 29 ± 3% which is a variation only a little greater than the precision of the technique of analysis. Somewhat larger individuals (13-17 mm., probably 1½-2 months old) vary considerably more in their mineralogy but do not vary seasonally.

Still larger specimens (28-32 mm., probably 2-3 months old) show no seasonal trend. They vary less in percent aragonite than do the specimens in the 13-17 mm. group.

From the results of these three groups, it appears that specimens of M. edulis diegensis, at least through the size of approximately 30 mm., are not temperature sensitive in their shell mineralogy.

These results differ considerably from those of Lowenstam (1954c) for M. edulis from Ocean City, Maryland. Shells collected from a wooden stake in the summer at this locality showed that the smaller individuals definitely had a higher proportion of aragonite than the larger ones. Since the smaller individuals grew mainly in the summer and the larger ones more in the winter, a definite temperature sensitivity of shell mineralogy is indicated. This differing response may be a subspecific difference. It lends support to Coe's (1946) contention that M. edulis diegensis is a valid subspecies.

Model Growth Series

If the relative amounts of calcite and aragonite in the shells of Mytilus are temperature dependent, a series of specimens of increasing size collected at one place and time should show a cyclical variation in percent aragonite. Some shells will contain a relatively larger amount of material deposited in one season than another.

Although the many variables in a biological system make rigorous mathematical treatment difficult, a mathematical model will help to illustrate the nature and magnitude of this variation. For purposes of this consideration, it is assumed that at a particular locality, the sea water temperature varies as a sine function of season:

$$\text{Temperature} = M + K \sin t$$

where M is the mean temperature, K is the maximum deviation in temperature from the mean, and t is time (in seasons with $\pi/2$ radian to the season). It is further assumed that the rate of increase in shell weight for the particular hypothetical species under consideration is constant. The mean temperature of deposition of the shell (actually the mean life temperature) at any time can be determined by dividing the integral of the temperature function by the length of growth time:

$$\frac{\int_a^b M + K \sin t}{b-a} = M + K\left(\frac{-\cos b + \cos a}{b-a}\right) = T$$

where a is the time of the start of growth, b is the time of completion of growth of any particular fraction of the shell, T is the mean temperature of shell deposition and the other symbols are as above. For any particular specimen, a is constant. In fig. 7, the variation of T with b has been plotted for four specimens starting growth in the middle of

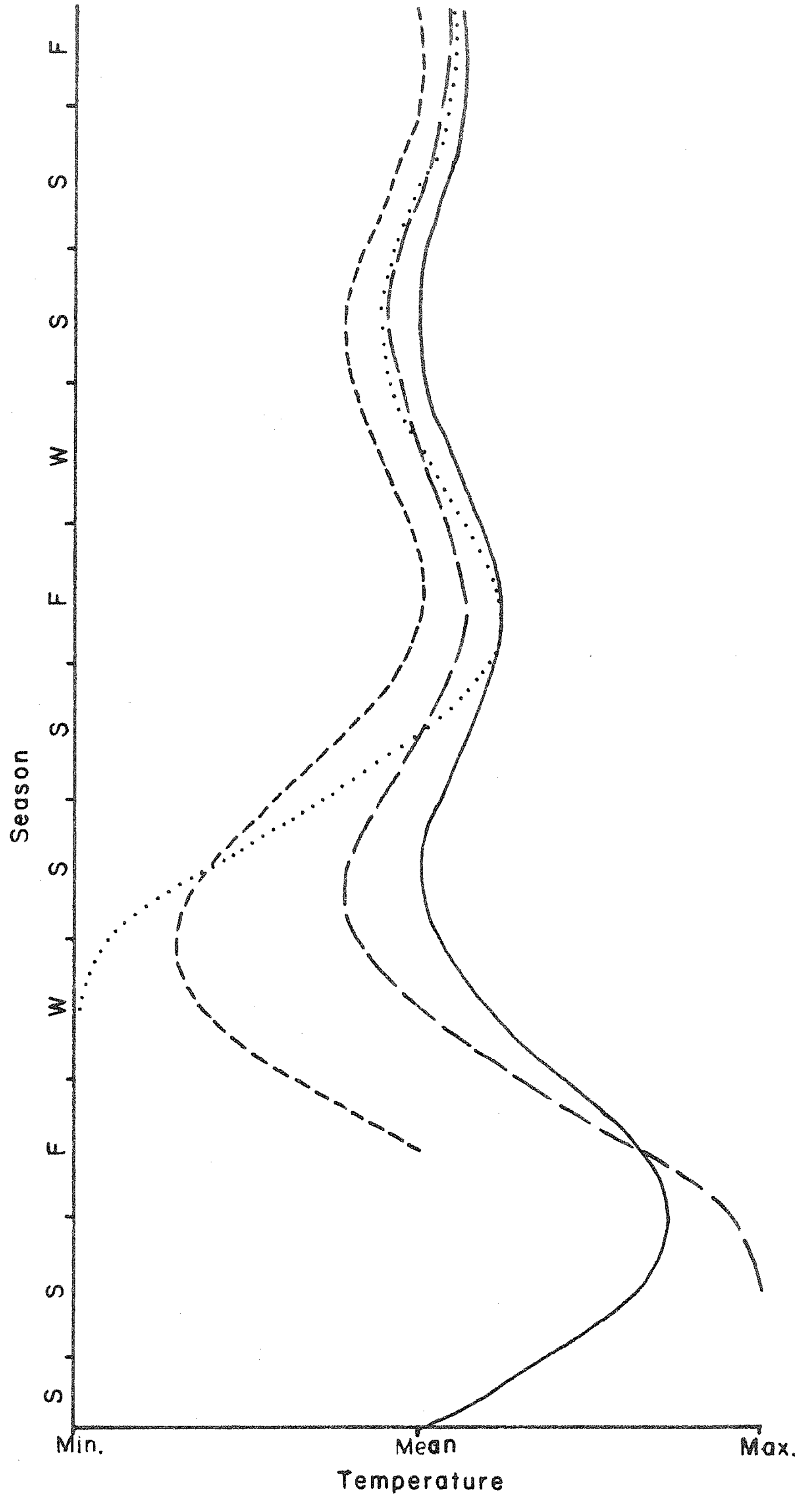

Figure 7. - Variation in mean temperature of shell deposition with season. The four lines represent individuals starting growth in the middle of each of the four seasons.

each of the four seasons.

Several significant facts concerning seasonal variation in the mean temperature of shell deposition can be noted from this graph. For example, a specimen which begins growth in mid-spring will show a maximum temperature at the end of the summer and will never show a temperature lower than the mean annual temperature. Conversely, a specimen starting growth in mid-fall shows a minimum temperature at the end of winter and never shows a temperature higher than the mean annual temperature. After an initial period of extreme temperatures, individuals starting growth in mid-summer and mid-winter fluctuate about the mean. The range of variation in a specimen decreases with age. The older the specimen, the less the extreme values differ from the mean annual temperature. Larger individuals show maximum temperatures in the fall and minimum temperatures in the spring. As the individual increases in age, this maximum occurs nearer mid-fall and the minimum nearer mid-spring. From a consideration of these factors, it appears that summer and winter collections of the largest possible individuals would give the most representative sample of shell material showing the mean annual temperature of a given locality. Spring and fall would seem more appropriate since the temperature is then nearest the mean annual temperature. Maximum variation from the mean annual temperature of the temperature of shell deposition for individuals of a particular age can be determined. Specimens between one and two years of age differ by as much as 11% of the total range in temperatures from the mean annual temperature. Those between two and three years differ by up to 6% of the range. Individuals with an age of exactly an integral number of years will always give the exact mean annual temperature.

If the rate of increase in weight is constant as has been assumed in this model, specimen weight would correspond to age and can be used as the ordinate of a similar graph (fig. 8). For this graph, it is assumed that the growth rate is x grams per year. Individuals of varying weights were assumed to have been collected at the beginning of spring. The mean temperature of deposition corresponding to individuals of various weights is taken from fig. 7 and plotted on the graph in fig. 8. This yields a curve much like what has been called a growth series in this study and that of Lowenstam (1954b).

Certain pertinent observations about growth series curves in general can be made from this model study. As in the seasonal variation curves for individuals discussed above, this curve shows a seasonal fluctuation of gradually decreasing amplitude. The distance between maxima and between minima (with the exception of the first minimum) is approximately x grams or one year's growth. The curve fluctuates around, but largely below, the mean annual temperature. This is because collecting was assumed to be in early spring when all individuals were approaching their lowest mean temperatures.

Before applying the results of this model study to actual cases, the assumptions used in the model study must be evaluated. Sea water temperature cannot be considered strictly a sine function of season. However, recorded seasonal temperature variation at various points along the Pacific Coast shows that, at least in a general way, temperatures do follow a sine function pattern (U. S. Coast and Geodetic

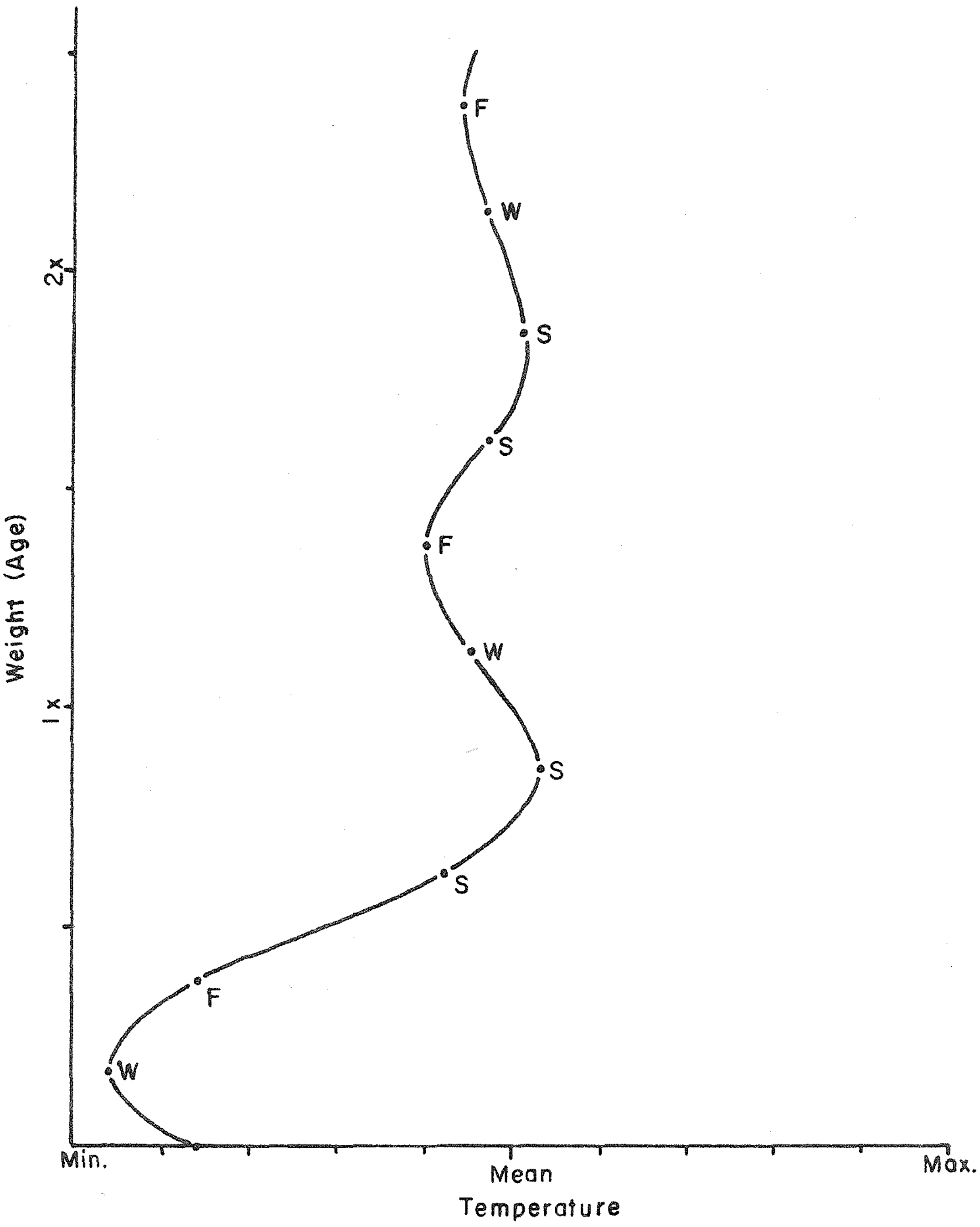

Figure 8. - Model growth series. See text for detailed explanation.

Survey, 1956). Highest temperatures are usually displaced towards the fall and lowest temperatures towards the spring. The seasons as used in the above discussion are defined strictly on the basis of temperature and do not necessarily correspond to seasons determined by relative position of earth and sun. The assumption of a constant rate of shell weight increase is only approximately correct for Mytilus. Coe and Fox (1942 and 1944, and Fox and Coe, 1943) made an extensive study of the rate of increase in both length and weight in M. californianus. Their plot of weight against age shows a slightly sigmoidal curve which indicates that rate of increase is relatively lower at the beginning and end of the life span than in between. Growth rate is lower during the first two months and reasonably constant thereafter except for seasonal fluctuations. Growth rate in M. californianus at La Jolla is somewhat faster in summer than in winter. Growth rate is retarded during exceptionally warm periods. The deviation from the assumed growth pattern would result in some inaccuracy of the early portion of the growth curves in fig. 7 and some shifting of the whole curve toward higher temperatures. The general form of the curves should not be altered.

In the model case above, mean temperature of shell deposition was used as the abscissa. Actually, any property which is a linear function of the temperature of shell deposition can be used (any monotonic function should give the same generalized form of the curves). If the relative amount of calcite and aragonite is such a function, a plot of percent aragonite vs. shell weight should give the same general form. A factor other than shell weight or age can be the ordinate. Any property which is proportional to age can be used. Shell length is such a property. The rate of length increase decreases exponentially with age of the individual in _Mytilus_, however, so that cycles will have a gradually decreasing wave length with length of the individual. Figure 9 shows a semi-logarithmic plot of length vs. age based on the data of Coe and Fox (1942) for _M. californianus_ from La Jolla.

Growth Series in _M. californianus_

Figure 10 shows a plot of shell length vs. percent aragonite for a series of specimens of _M. californianus_ from Corona del Mar. As was noted above, the early stages of _M. californianus_ are apparently temperature insensitive. This adds an additional complication to the model case discussed above. A true cycle does not begin until the individual reaches a size of 15-20 mm. Most of the points lie close to the cycle indicated. Two points are significantly off the curve. The proposed reason for this deviation and a corrected graph is presented below. The first minimum on the graph is at 55 mm. From the model study above, it would appear that 55 mm. individuals started temperature sensitive growth in the fall. At that time the individual must have already been 15-20 mm. long. This would indicate 35-40 mm. of growth since the preceding fall. Since the collection was made in early fall (temperature fall) 55 mm. individuals should have grown 35-40 mm. in a little less than a year. This growth rate is considerably less than that found by Coe and Fox (1942) for _M. californianus_ at La Jolla. However, the La Jolla specimens were continually submerged

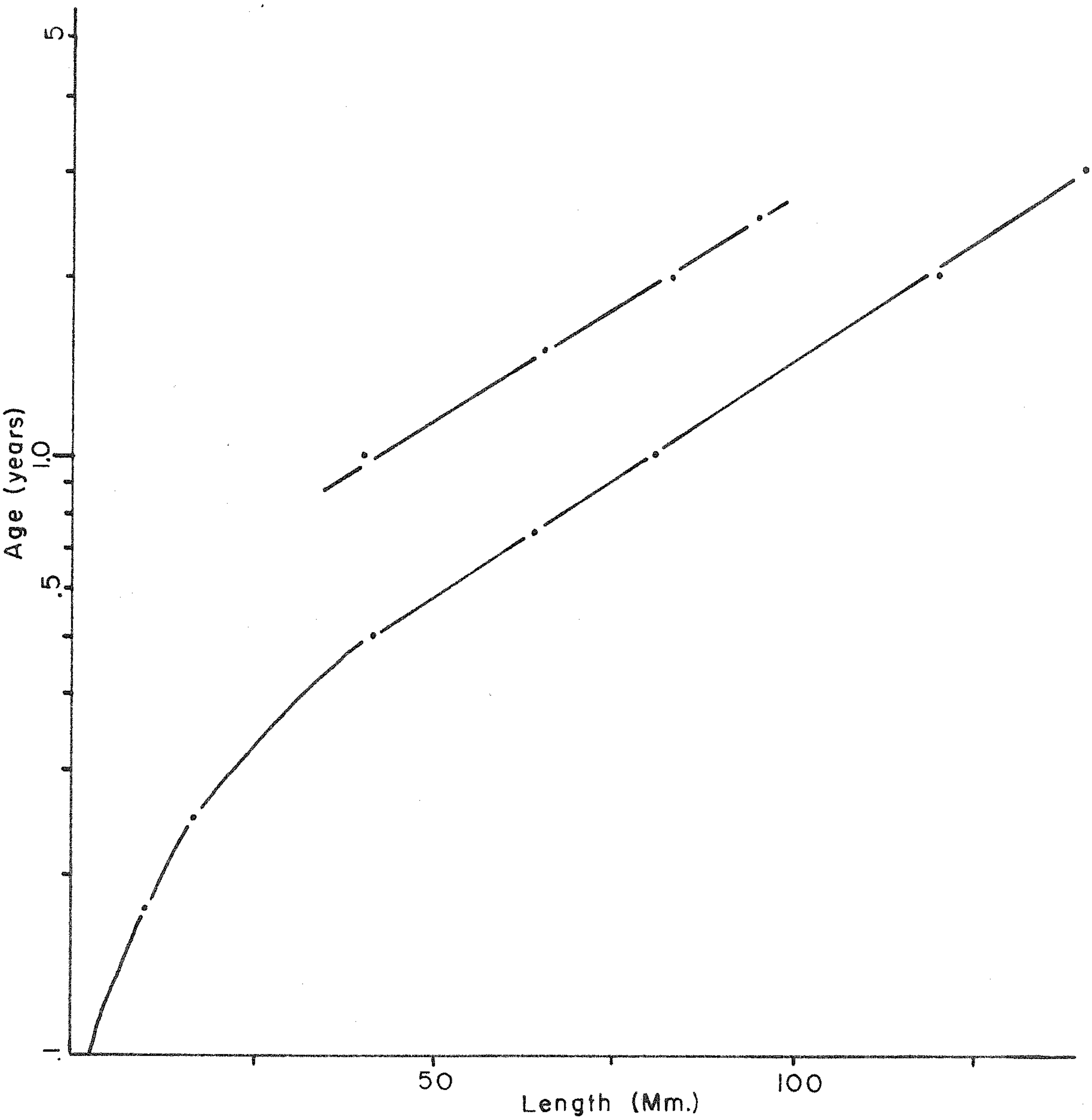

Figure 9. - Rate of increase in length in M. californianus. The lower line is for specimens from La Jolla (Coe and Fox, 1942). The top line is based on the growth series from Corona del Mar.

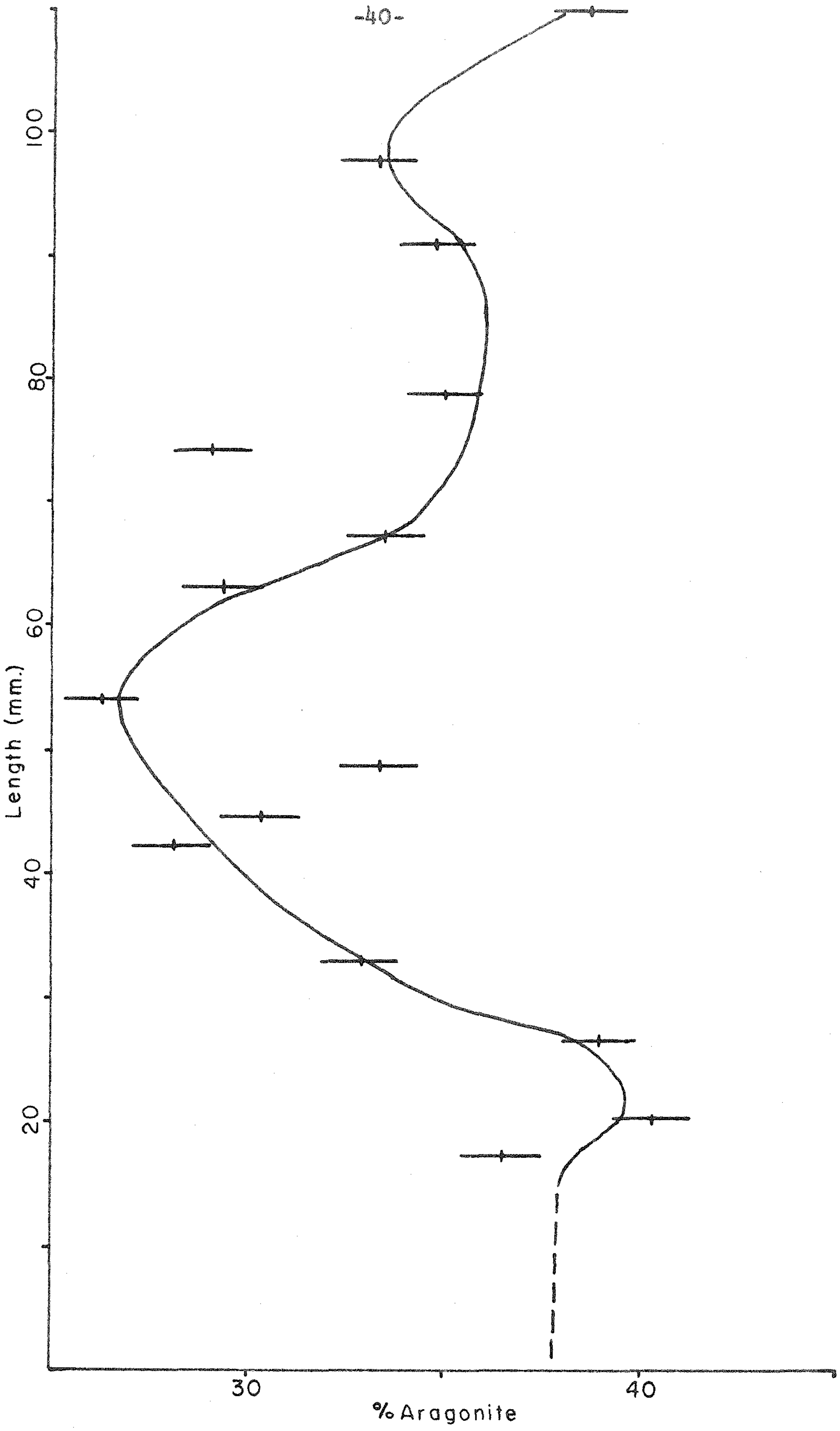

Figure 10. - Growth series of M. californianus from Corona del Mar.

and grew at a locality with a 0.5°C higher mean annual temperature than the Corona del Mar specimens. The first certain maximum in the curve at about 80 mm. represents individuals which became temperature sensitive in the spring a little less than $1\frac{1}{2}$ years before the collection was made. The second minimum at 97 mm. represents individuals a little more than 2 years old. The distance between the two minima gives a measure of the growth rate for the second year of life for the individuals of 40 mm. The largest specimen would appear to be between $2\frac{1}{2}$-3 years old. According to the model study, the value for the percent aragonite in this specimen is too high to be explained solely in terms of temperature. Figure 9 shows that the growth rate determined from this series is exponential, and the curve has approximately the same slope as the one for the La Jolla specimen.

The above growth series leaves little doubt that the relative amounts of calcite and aragonite are affected by some seasonally varying factor, the most obvious of which is temperature.

If the percent aragonite in this growth series is temperature dependent, temperatures determined by oxygen isotope analysis of the samples used for percent aragonite determinations should have the same order relationship as the aragonite percentages. Oxygen isotopic determinations of temperatures were made on three samples from this growth series. The oxygen isotope temperatures were determined from the relationship:

$$T = 16.5 - 4.3\,(\delta - A) + 0.14\,(\delta - A)^2$$

where $$\delta = \left(\frac{O^{18}/O^{16}\ \text{sample} - O^{18}/O^{16}\ \text{standard}}{O^{18}/O^{16}\ \text{standard}} \right) 1000$$

and A is the δO^{18} value for the water in which the specimens grew (Epstein et al., 1953). An uncertainty of 1°C is estimated for these temperatures. They are reported to the nearest ½°C. The mass spectrograph was not operating at peak efficiency when these samples were analyzed. The uncertainty of 1°C assigned to the temperatures may be too low. The relationship of oxygen isotope temperature to percent aragonite was:

38.8% aragonite - 19.5°C ± 1.0
33.7% aragonite - 19.0°C ± 1.0
26.8% aragonite - 19.0°C ± 1.0

All the temperatures appear to be too high for this locality which has a mean annual temperature of 16.4°C. The first two samples give the expected order but the second and third have the same value. Thus these data neither contradict nor prove the hypothesis of temperature control of mineralogy.

That isotopic temperatures are higher than the recorded mean annual temperature is not surprising. Epstein and Lowenstam (1953) showed that in Bermuda, many shells, particularly pelecypods, give temperatures which are higher than the mean annual temperature. This is apparently because some species grow only during the warmest part of the year or at least grow fastest then. Coe and Fox (1942) showed that M. californianus does grow all year but has a faster growth rate in the summer (with the exception of unusually warm periods).

Care must be taken in the interpretation of growth curves such as the above because of the many uncertainties involved. For example, it is assumed that length is proportional to age; however, growth rates can vary considerably between individuals. It is also assumed that the rate of increase in weight is the same for all individuals, and that weight increase approaches linearity. Neither of these assumptions is completely correct. The presence of a temperature insensitive portion of the shell probably presents the biggest problem. It is uncertain at precisely what size M. californianus becomes temperature sensitive and whether or not the change is abrupt or gradual. All specimens may not change at the same time. All these uncontrolled variables may interact to confuse the apparently straightforward consequences derived in the model study above.

Growth Series in M. edulis diegensis from Corona del Mar

As a class project, a paleoecology class at the California Institute of Technology made a series of analyses of a group of specimens of M. edulis diegensis of increasing size. The specimens came from a float in Newport Bay, California (they were thus continuously submerged). Figure 11 shows the results of that study. The large spread in the results is due to the use of the graphic technique of analysis. The ordinate of this graph is weight and not length.

A possible cycle can be drawn through the points. The collection was made in the fall. If no temperature insensitive portion of the shell is postulated, the first minimum at approximately 0.2 grams should represent shells starting growth during the preceding fall. This rate is much lower than that obtained by Coe (1945) for M. edulis diegensis from La Jolla. The second minimum at 2.0 grams would represent two years of growth which again is much lower than would be

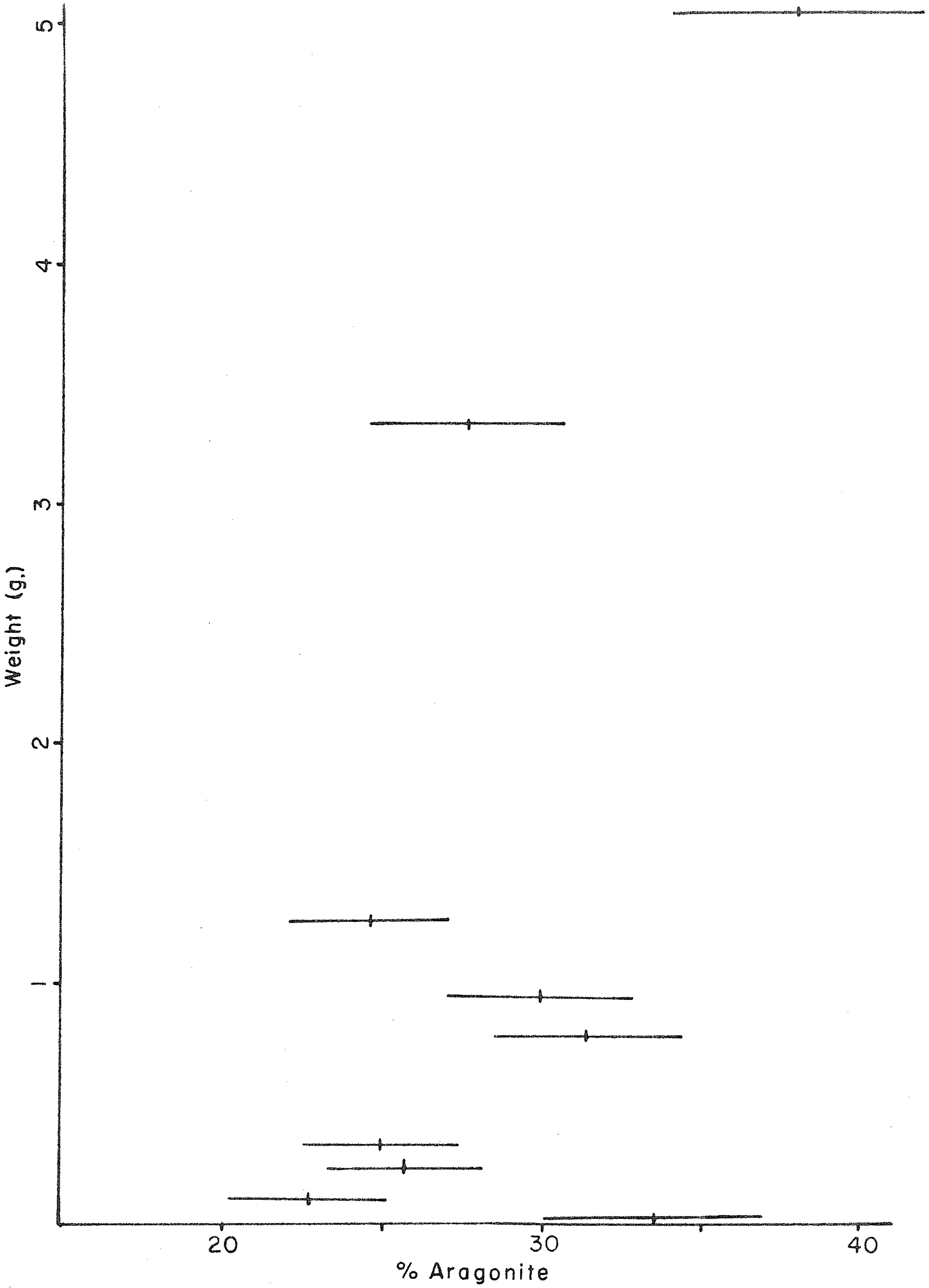

Figure 11. - Growth series of M. edulis diegensis from Corona del Mar. These analyses were done as a class project in a paleoecology class at the California Institute of Technology.

expected from Coe's data. The first minimum probably represents about 20 mm. of growth and the second an additional 25 mm. Thus, a faster growth rate for the second than the first year would be indicated. This is contrary to the usual growth pattern shown in fig. 9. Perhaps a more reasonable interpretation of these data is that some factor other than temperature causes the scatter of values.

Growth Series in *M. edulis diegensis* from Avila Beach

Another series of determinations was made for *M. edulis diegensis* from Avila Beach, California (fig. 12). These specimens were collected in the fall from one large boulder, low in the intertidal zone. In contrast to the Newport Bay series described above, these specimens come from an open coast location. The variation in the proportion of aragonite in these specimens is large. A possible seasonal cycle can be drawn through this group of points. The over-all trend of this series seems to be an increase in percent aragonite with size, and the possible cycle is secondary. If the minima represent individuals starting growth in the fall, reasonable growth rates may be interpreted. A growth rate of 40 mm. for the first year is about what would be expected. The mean annual temperature is 3.8°C lower at Avila Beach than at La Jolla where growth of continuously submerged specimens averaged 76 mm. for the first year (Coe, 1945). An increase of 30 mm. in the second year fits the pattern of length increase shown in fig. 9. This gives a growth rate similar to that for *M. californianus* from Corona del Mar as determined by the growth series. More samples would help to delineate the seasonal cycles. The dominant trend is

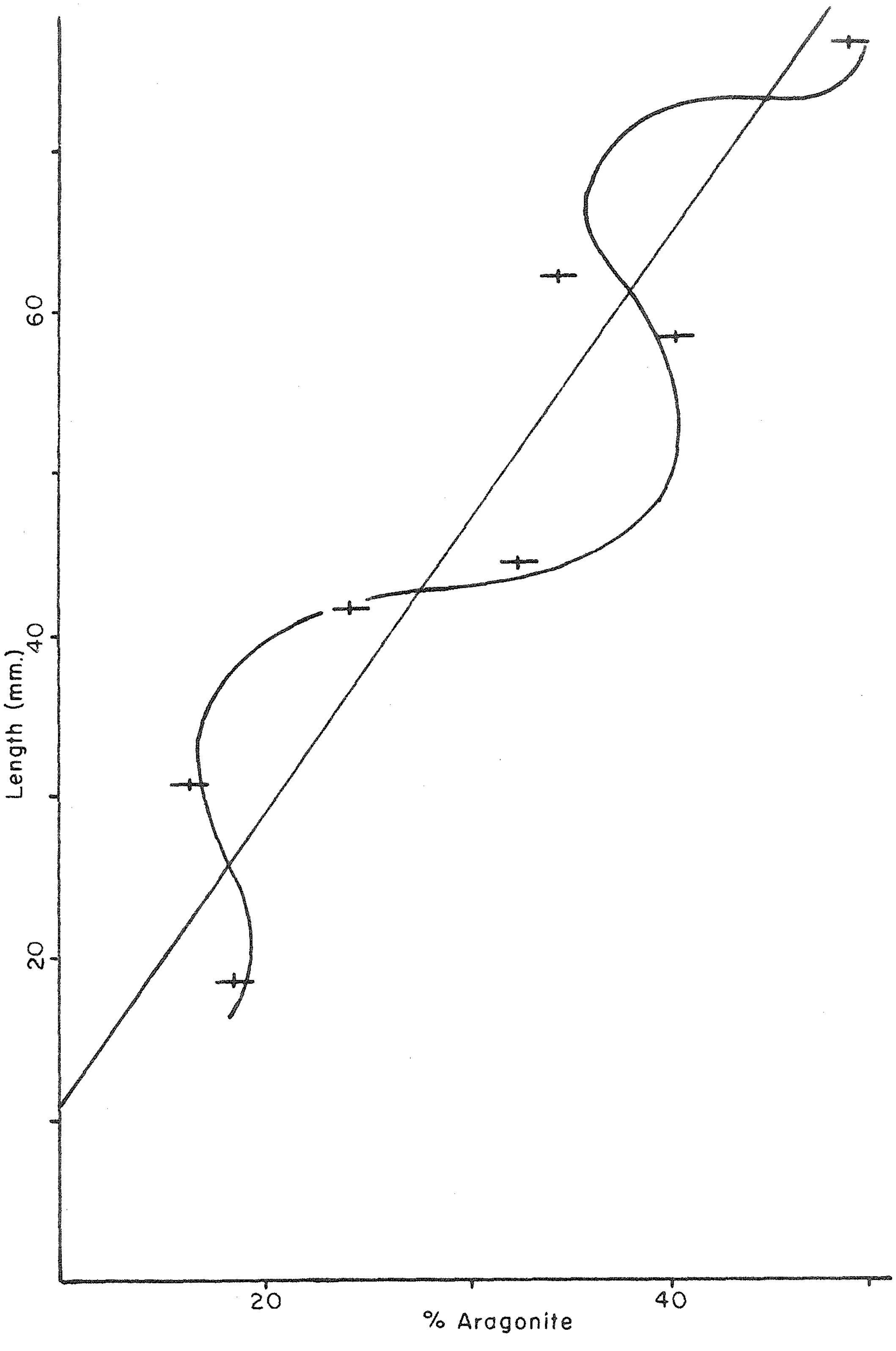

Figure 12. - Growth series of M. edulis diegensis from Avila Beach.

a general increase in percent aragonite with size. The coefficient of correlation for the relationship between length and percent aragonite is 0.94. Figure 11 does not clearly show such a trend although it is suggestive. Lowenstam's (1954b) two growth series of M. edulis from Woods Hole, Massachusetts, show a definite trend towards increase in proportion of aragonite with increased size; although his values show a much greater fluctuation in mineralogy with temperature. This is due in part to the fact that the temperature range at Woods Hole is much greater than at Avila Beach.

None of the values for Avila Beach lies more than approximately five percentage units off the least squares line. The total difference in percent aragonite between 25 and 80 mm. specimens (apparently due to the size difference) is 30%. The largest difference due to the other factors would appear to be 5%. Thus the size effect is apparently the most important factor in determining the relative amount of calcite and aragonite in M. edulis diegensis at this location.

Geographic Variation of Percent Aragonite in Small Specimens of M. californianus

The percent aragonite in small (less than 20 mm.) specimens of M. californianus (fig. 13) appears to vary irregularly around a value of approximately 30% aragonite. The magnitude of the variation is significant. The variation between individuals at any one locality is much less than that between stations. The Corona del Mar samples vary only within a range of 8% while the total range of variation of all samples is 20%. Individual variation was further reduced by combining three

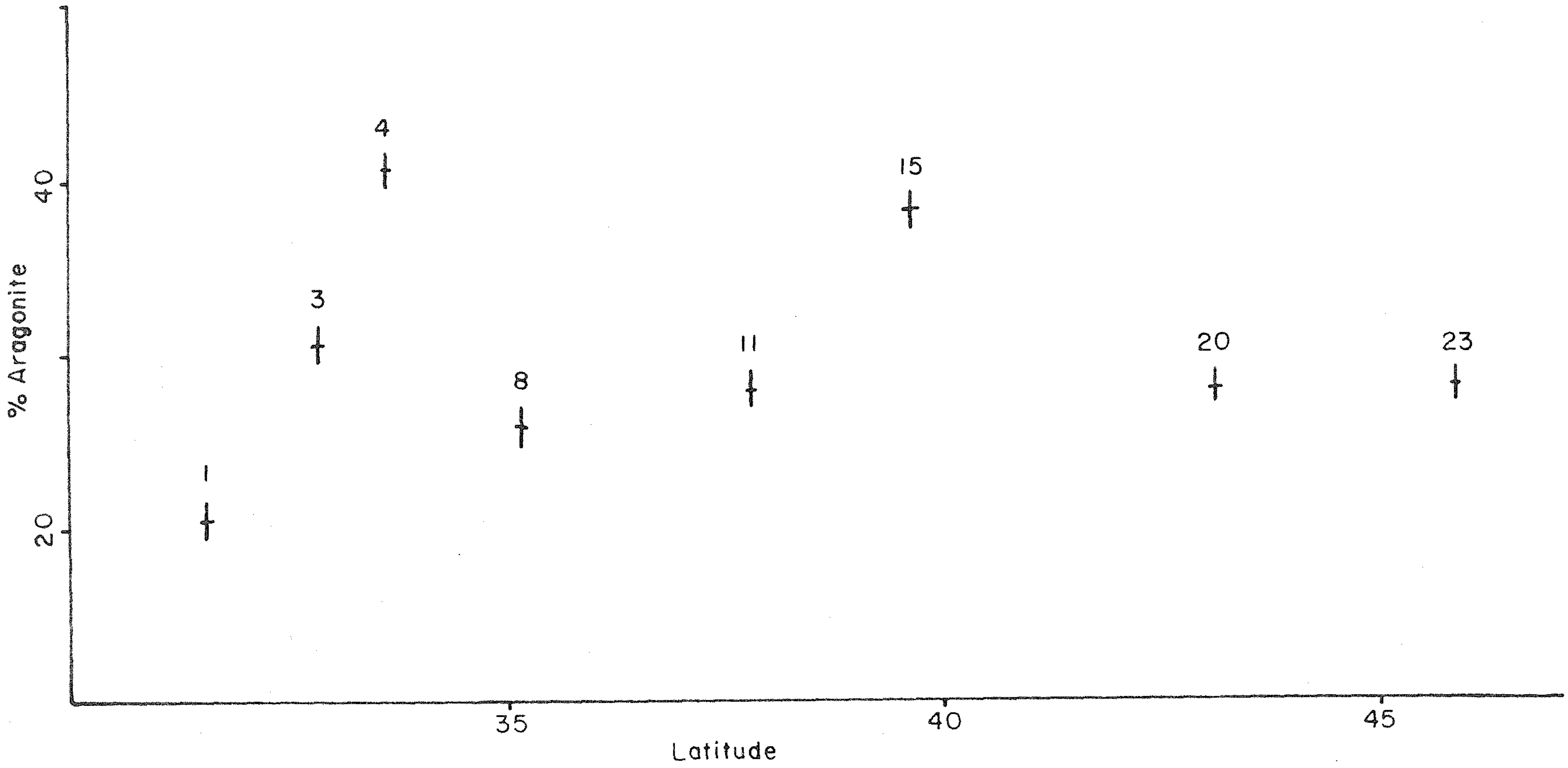

Figure 13. - Geographic variation in shell mineralogy in small specimens of M. californianus. The numbers above the points are the station numbers taken from fig. 1.

or four individuals into each sample for analysis. The percent aragonite may vary between localities due to ecological factors which have not been measured in this study. It is perhaps genetically controlled. At any rate, the lack of regular variation of percent aragonite in the shells of small specimens of *M. californianus* with latitude indicates that their mineralogy is independent of temperature. This agrees with the data for specimens collected seasonally from a single location.

Geographic Variation in Percent Aragonite in Small Specimens of *M. edulis edulis* and *M. edulis diegensis*

The percent aragonite in the two subspecies of *M. edulis* varies with latitude in a much more regular manner (fig. 14). With the exception of one point, the values of the percent aragonite for *M. edulis diegensis* decreases rather regularly with increase in latitude. This indicates that the proportion of aragonite in small shells is temperature dependent. This contradicts the apparent lack of variation with season in small individuals from Corona del Mar.

North of San Francisco, a sharp discontinuity exists. The six points north of San Francisco show an irregular decrease with latitude. This division of points into two distinct groups clearly indicates two genetically separate groups.

This distribution agrees reasonably well with the distribution of *M. edulis edulis* and *M. edulis diegensis* suggested by Coe (1946). Prior to the early 1940's only a few specimens of *M. edulis diegensis* were found south of San Francisco. They were assumed to be the same

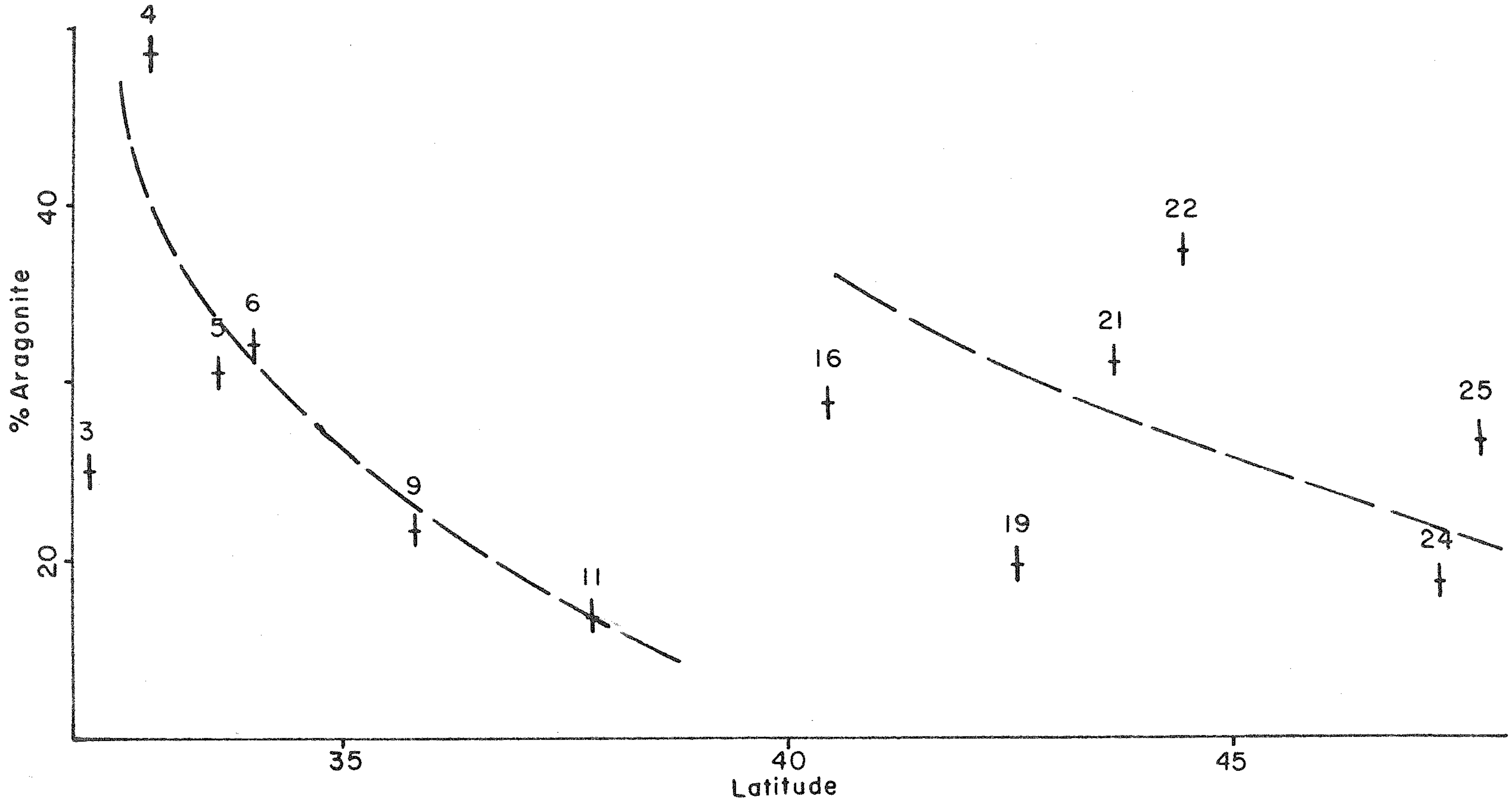

Figure 14. - Geographic variation in shell mineralogy in small specimens of _M. edulis edulis_ and _M. edulis diegensis_. The numbers above the points are the station numbers taken from fig. 1.

as M. edulis found farther north. In the early 1940's, M. edulis diegensis increased enormously in abundance along the southern California Coast. Coe states that this resurgence was probably due to the development of a genetically different strain which was able to rapidly expand in the more southerly area. It may have been a different subspecies accidentally introduced at that time from some other part of the world. M. edulis diegensis differs somewhat morphologically from M. edulis edulis*. For instance, M. edulis diegensis is usually broader, has a more poorly developed anterior adductor muscle, and usually has fewer teeth than M. edulis edulis. M. edulis is such a variable species that differentiation of ecological and genetic differences is difficult. On morphological grounds some doubt remains as to whether or not M. edulis diegensis is a true subspecies.

Lowenstam (1954b) has analyzed specimens of Littorina saxatilis obligata from a single tide pool in Greenland. They were morphologically identical but fell into two distinct groups with respect to percent aragonite. One group was 100% aragonite while the other group had a variable proportion (between 12 and 48%) which appears to vary with season.

A study of shell mineralogy would thus seem to be a useful taxonomic tool for differentiating morphologically identical or

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* The northern subspecies may in fact be different from M. edulis from Europe. It has been called M. trossulus (Gould, 1850) and Coe (1946) suggested M. edulis trossulus. Some authors (Schenck, 1945) have recognized both M. edulis (probably from bays) and M. trossulus (from the open coast) in the Pacific northwest area. The taxonomy remains to be clarified.

similar groups. Since variation in shell mineralogy is reflected in variation in shell structure, mineralogic variation is reflected morphologically.

Geographic Variation of Percent Aragonite in Larger Specimens of *M. edulis edulis* and *M. edulis diegensis*

Figure 15 shows the variation in the percent aragonite in larger specimens of both subspecies of *M. edulis*. The large gap in the middle of the graph is due to the lack of samples of larger specimens in this region. This is because most collecting was done at open coast locations. Both subspecies of *M. edulis* are common on the open coast at the extremes of the range; however, large specimens could not be found between Avila Beach and Point Grenville. Apparently larvae are present in the water, probably coming from nearby bays. Small specimens are thus sometimes able to develop for a short time but apparently are not able to compete successfully in this environment for long. What makes them adaptable in some places and not in others is not known. The southern specimens are in the size range of 37-47 mm. The specimen from Avila Beach which falls within this range is circled on the graph. The Avila Beach samples are the same ones used in the growth series discussed above. The northern specimens are smaller, 29-33 mm. in length. The three northern and the La Jolla specimens were collected in the summer. The remainder of the specimens were collected in the fall.

The general decrease in percent aragonite with increase in latitude may have little significance. The fact that the northern

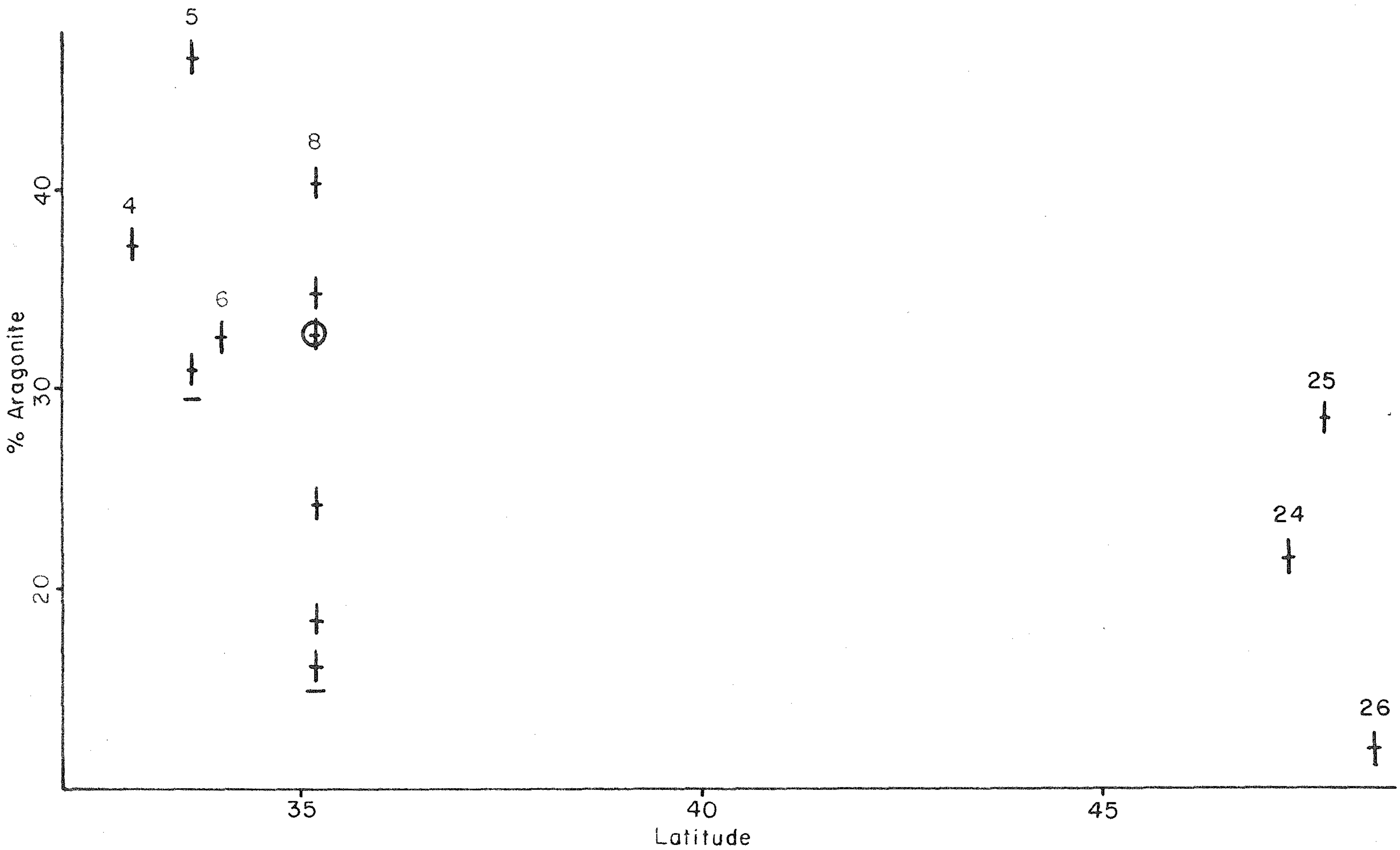

Figure 15. - Geographic variation in shell mineralogy in larger specimens of *M. edulis edulis* and *M. edulis diegensis*. The numbers above the points are the station numbers taken from fig. 1. See text for explanation of special symbols.

specimens have a lower percent aragonite may be a subspecies difference. The difference may be due to the discrepancy in size of the individuals. The points in fig. 15 for the specimens from Avila Beach and Corona del Mar which fall within the size range of the northern specimens have been underscored. If only these points are included, no decreasing trend is obtained. Thus geographic variation gives no conclusive evidence that the percent aragonite in M. edulis is temperature dependent. These results agree with those of lack of seasonal variation in small specimens from Corona del Mar and the low seasonal variation in the growth series from Avila Beach. However, it disagrees with the results based on small specimens collected from various localities.

Geographic Variation in Percent Aragonite in Larger Specimens of M. californianus

Larger specimens of M. californianus from several localities along the Pacific Coast of North America were analyzed. Series of gradually increasing size were always used.

No distinct growth curve can be seen in the series from northern stations (figs. 16, 17 and 18). The rate of growth is so slow that several seasonal cycles are represented in the largest specimens present in the series. With seasonal cycles compressed, irregularities in growth rate between individuals may completely obliterate the regular cycles on a percent aragonite vs. length graph which would show up on a percent aragonite vs. age graph. A much larger number of samples would be necessary to show the several seasonal cycles probably

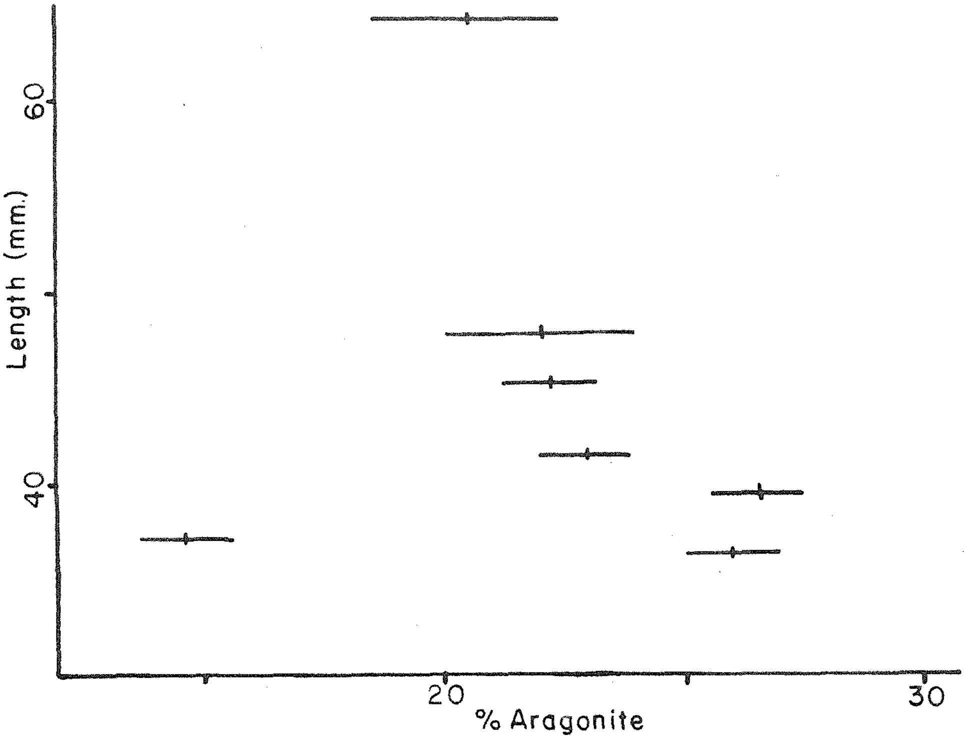

Figure 16. - Growth series of M. californianus from Hoh.

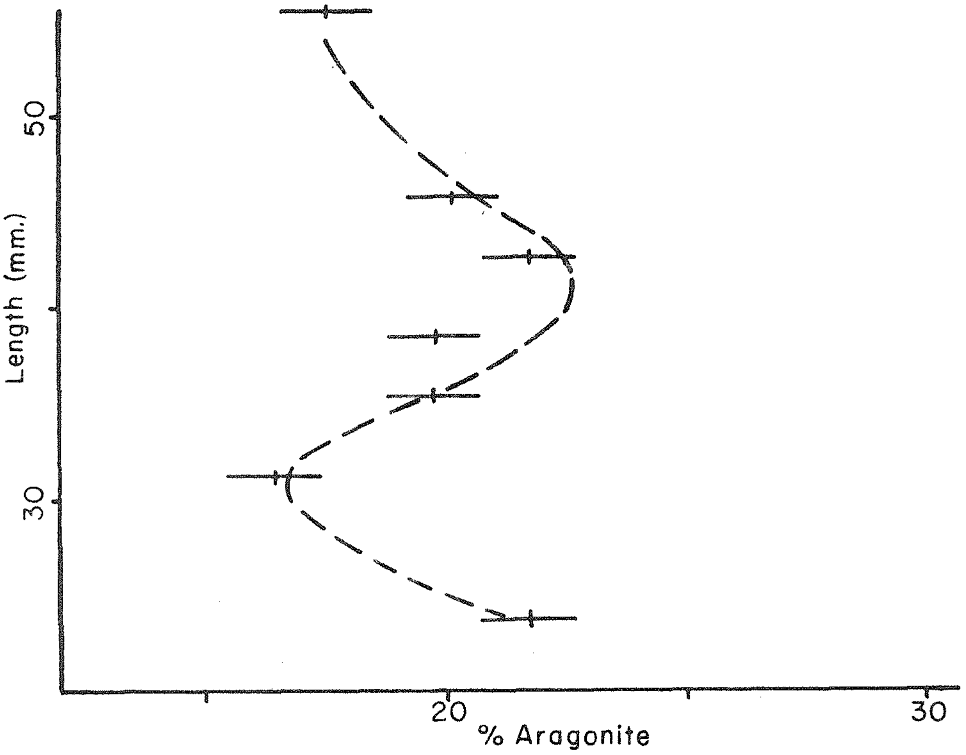

Figure 17. - Growth series of M. californianus from Waldport.

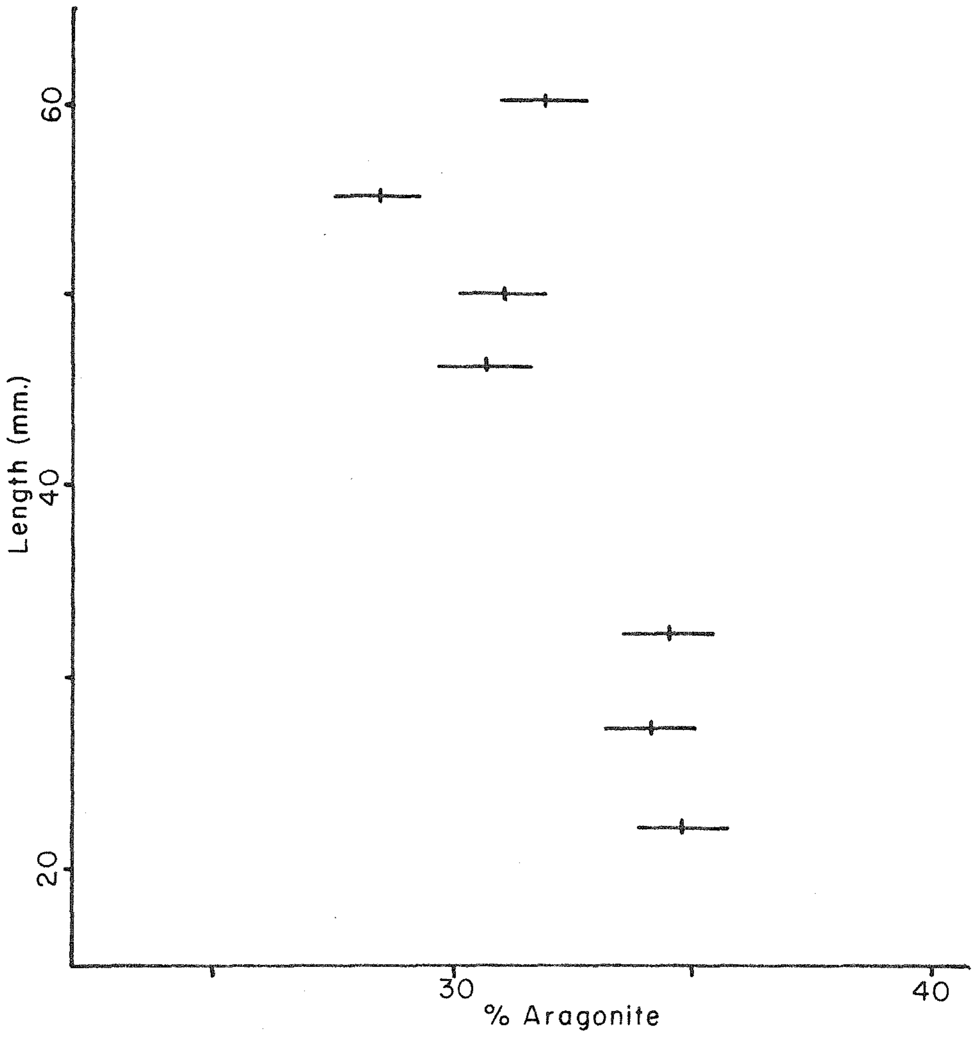

Figure 18. - Growth series of M. *californianus* from Westport.

represented. In some cases the range in percent aragonite is not large so that uncertainties in analysis tend to obscure the seasonal variations.

The meaning of what appears to be a seasonal cycle in the Avila Beach series (fig. 19) is uncertain. If the apparent cycle is taken at face value, it would suggest that the 55 mm. minimum represents individuals becoming temperature sensitive during the preceding fall. The maximum at 25 mm. would represent individuals becoming temperature sensitive shortly before collecting time in the spring or early summer. This would suggest a growth rate of the order of 55 mm. in the first year which is unduly large for intertidally exposed individuals growing at these temperatures. In fact, a study of the shell structure indicates that the largest specimen is 2½-3 years old. The reason for the difficulty is probably the lack of a sufficient number of samples to delineate the true cycles. The growth rate at this station is probably too slow for a clear seasonal cycle to be indicated.

The low value of the percent aragonite in the shells from La Jolla is unexpected (fig. 20). This series of samples outlines a seasonal growth cycle representing a little over one year. The largest individual became temperature sensitive during the preceding summer or the spring preceding that. Consequently it has a higher percent aragonite than the somewhat smaller individuals which became temperature sensitive in the fall. The percent aragonite rises again in those individuals first responding to temperature in the preceding spring. The drop in the curve is explained by the temperature insensitive portion of the shell. Although these smaller individuals started

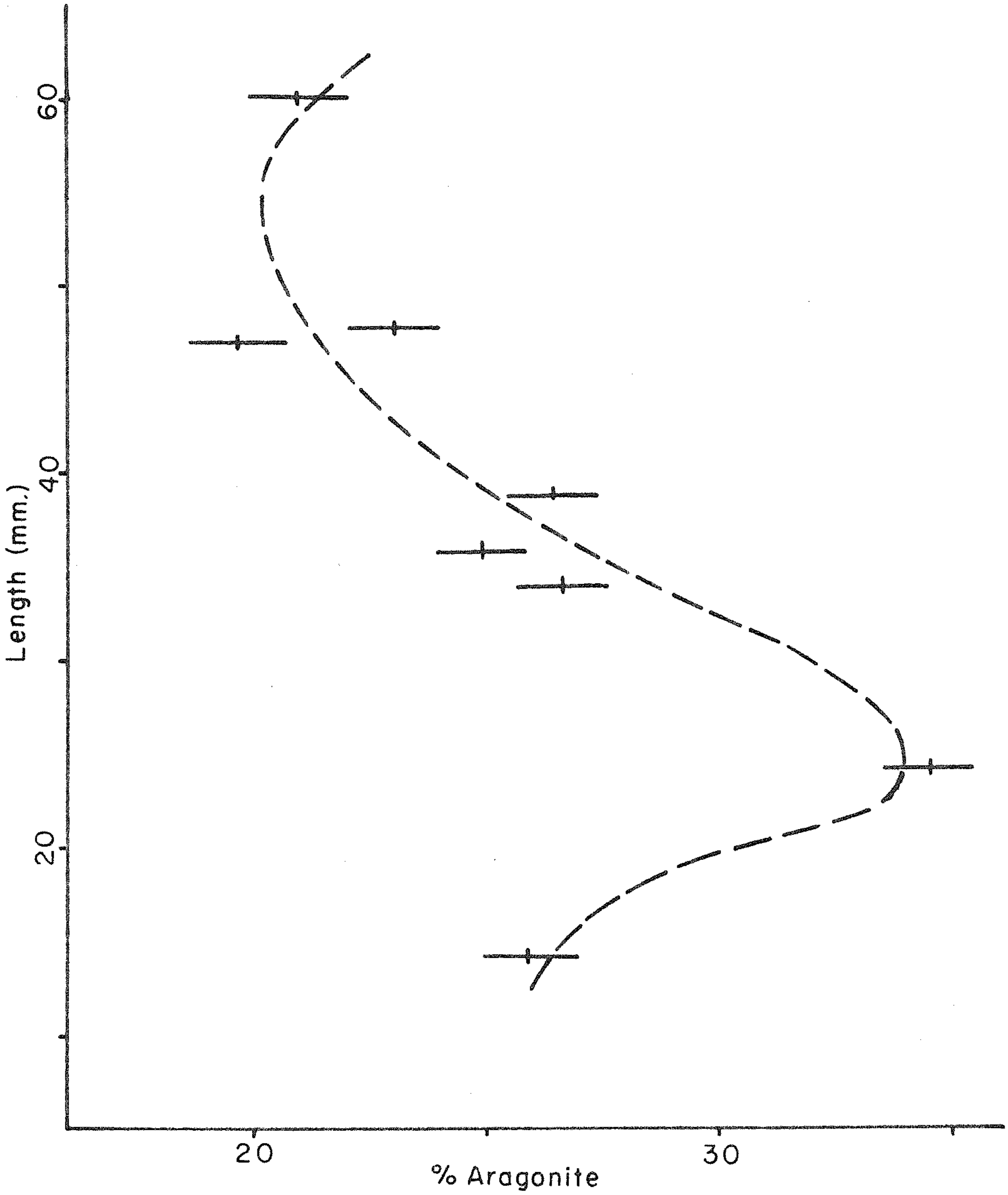

Figure 19. - Growth series of M. californianus from Avila Beach.

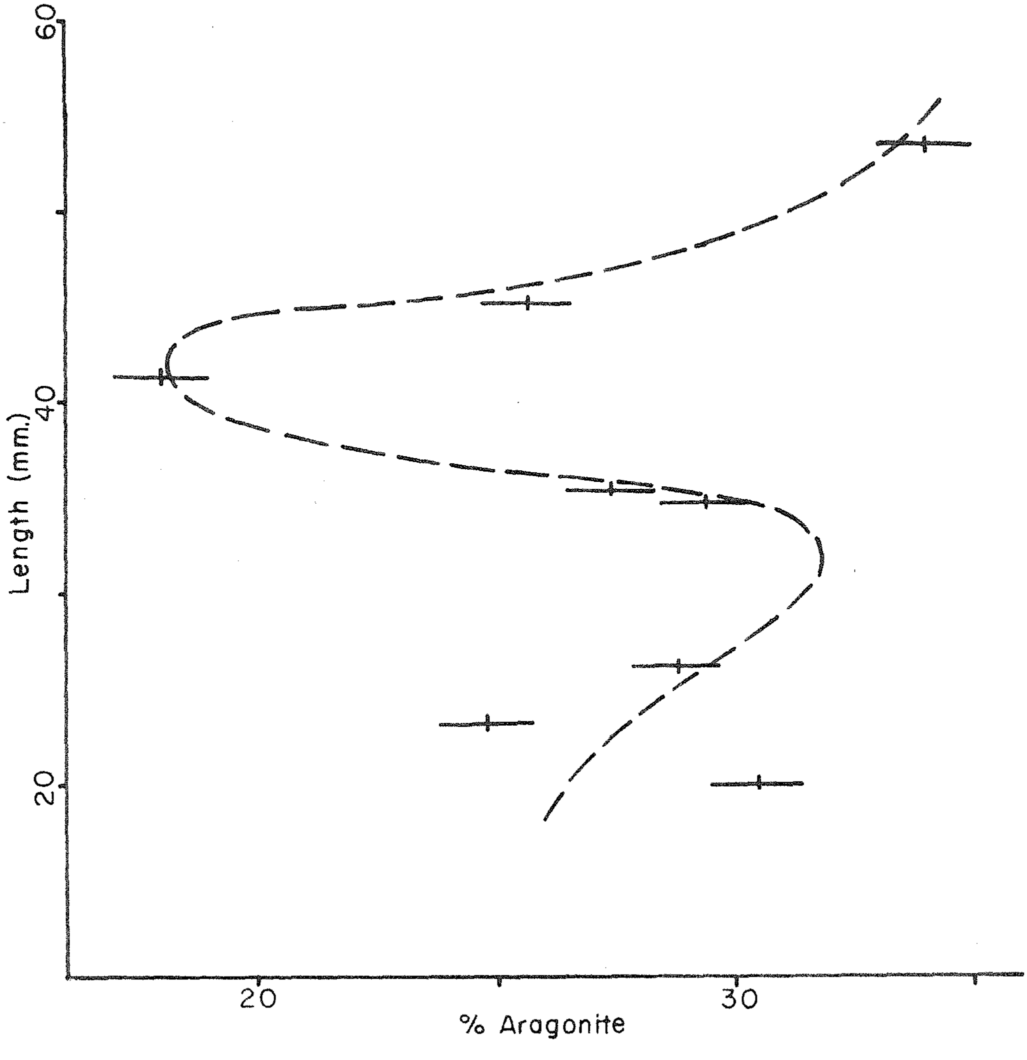

Figure 20. - Growth series of M. californianus from La Jolla.

growth in late spring or early summer their valves are composed largely of material which does not reflect growth temperature. If the above interpretation is correct, the largest individual should be slightly more than one year old. This would give a growth rate of approximately 50 mm. for the first year. This would be a reasonable rate for intertidally exposed individuals.

The La Jolla sample is thus considerably skewed toward the winter deposition direction. The largest specimen which has the highest percent aragonite would probably be the most representative sample of the mean temperature of deposition at La Jolla. Even it is probably somewhat too low because of the temperature insensitive portion. This sample is inadequate for determining mean temperature of deposition at this station. Several seasons of growth are necessary to average the seasonal fluctuations. For this reason northern stations where *M. californianus* grows much slower and are older are more easily sampled. On the other hand, a larger number of samples are necessary to outline seasonal growth cycles than at the southern stations.

Lowenstam (1954b) analyzed a larger number of samples over a greater size range from La Jolla than has been done in this study. The mean of his values is 42% aragonite and 2 years of growth are represented. His collection was made in the winter. For this reason the temperature insensitive portion cannot be observed. This sample gives a much better representation of the mean temperature of deposition at La Jolla. This value should be essentially correct since the collection was made in the winter.

The percent aragonite in different shells at a single locality varies more at southern than northern stations. This may be due in part to a lower limit effect, i.e., below a certain temperature, M. californianus may secrete a constant percent aragonite no matter how low the temperature may become. The slower growth rate at the northern stations (Fox and Coe, 1943) would also tend to make the percent aragonite more uniform. As seen from the model study, the older the individuals are, the less the variation between them.

In addition to the series of samples run from individual stations, single large individuals were run from a few stations. Large shells from Pacific Grove, Santa Monica and Corona del Mar were run. An additional specimen from Avila Beach was included. As indicated by the model study and the series of analyses above, a single, large individual gives a reasonable measure of shell material deposited at the mean annual temperature of the station.

Figure 21 shows a plot of all individual values, mean values for stations and single large individuals against the latitude of the station. The scatter in this graph is large. Some factor or factors other than temperature would appear to be responsible for such an irregular pattern. Nevertheless, a general trend toward lower percent aragonite with higher latitude is apparent.

Variation with Temperature of Percent Aragonite in M. californianus

Figure 22 is a plot of percent aragonite in M. californianus vs. mean annual temperature of the collecting station. Values for the mean annual temperature of stations were taken from Special Publication

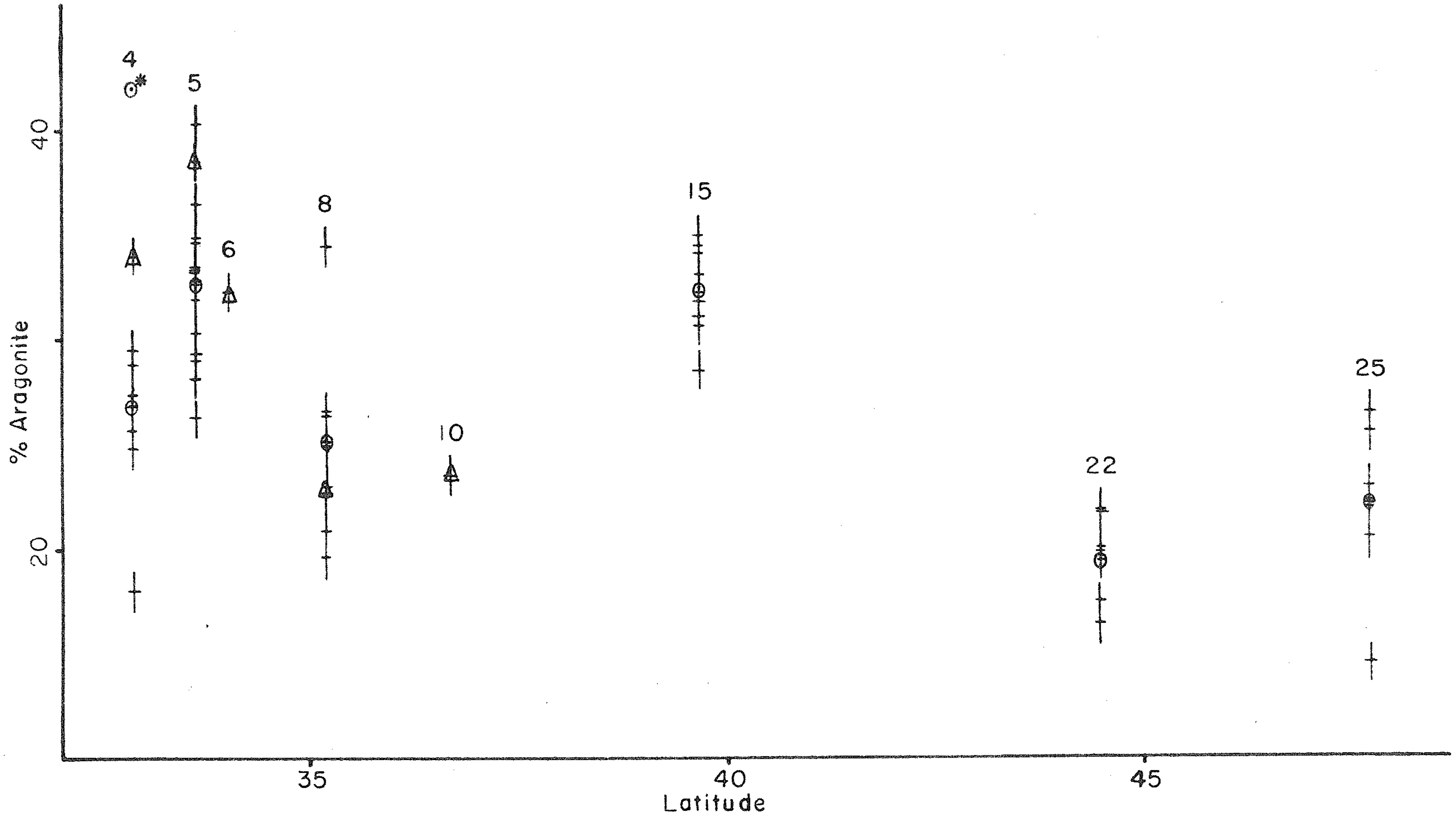

Figure 21. - Geographic variation in shell mineralogy in large specimens of *M. californianus*. The numbers above the points are the station numbers taken from fig. 1. The circled points are station means. Points enclosed in triangles represent single large individuals. The point with an asterisk is the mean value for La Jolla from Lowenstam (1954 b).

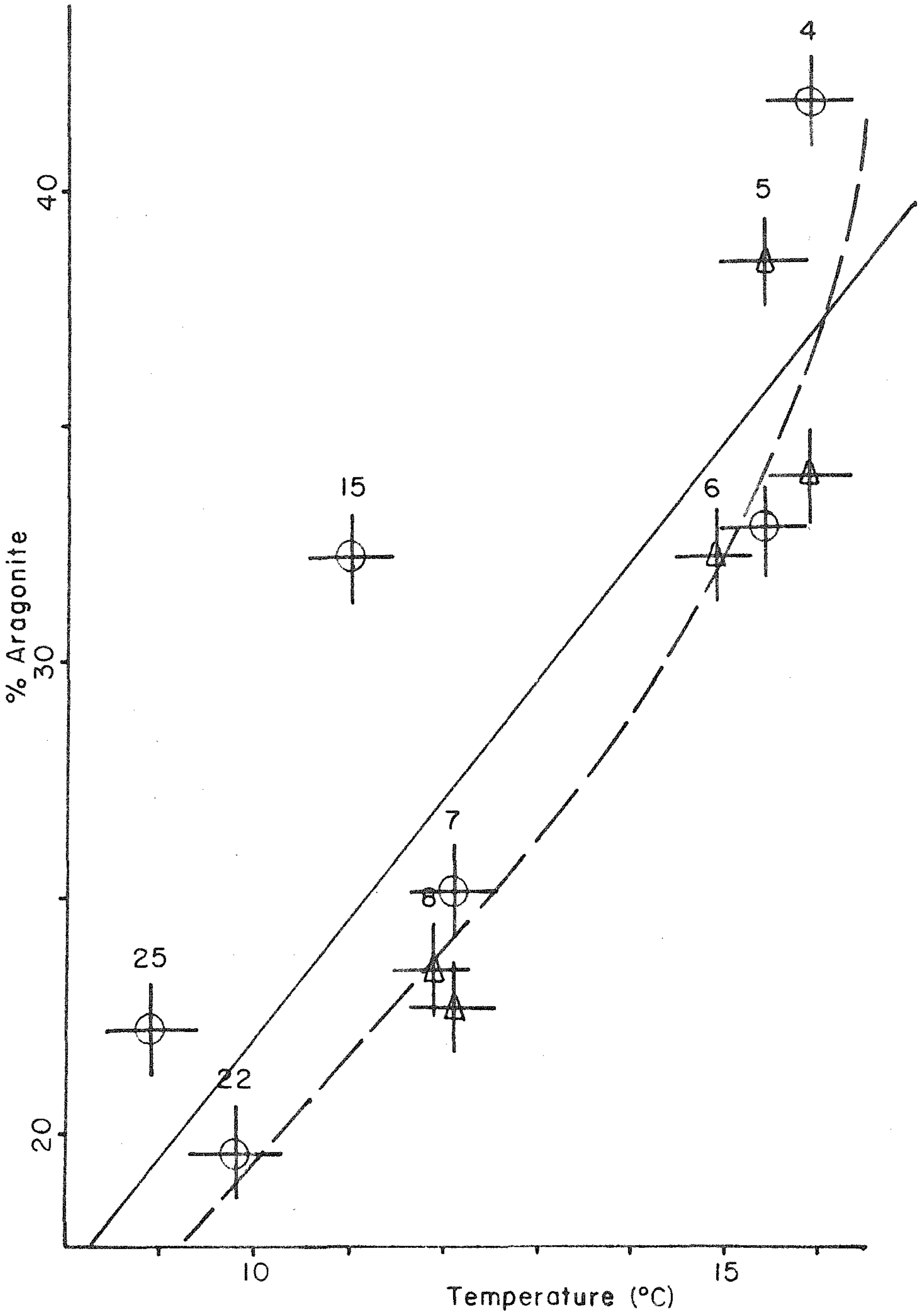

Figure 22. - Variation of the shell mineralogy of <u>M</u>. <u>californianus</u> with temperature. See text for a detailed description of this figure. The numbers above the points are the station numbers taken from fig. 1. The points enclosed in triangles represent single large individuals, and the circled points represent station means.

No. 280 of the U. S. Coast and Geodetic Survey (1956). These means cover varying numbers of years, all of them at least 10 years. For stations which were not at a temperature recording station, the mean annual temperature was estimated by interpolation from recording stations. It should be noted that the mean annual temperature as determined by readings over a number of years may vary appreciably from the temperature of any one year. Therefore, the temperatures which existed during the periods of growth of the specimens used in this study are not necessarily the same as the mean annual temperature. Temperatures during 1957-58 were as much as a degree centigrade higher than the mean annual temperature at some stations. In this graph, only the values for largest specimens of M. californianus from a station and station means are used. The station mean for La Jolla was not used for reasons discussed above. The mean of Lowenstam's (1954b) data for La Jolla was used.

This plot gives a correlation coefficient of 0.89 and a least squares line of:

$$\% \text{ aragonite} = 2.55 \text{ temperature } (^{\circ}\text{C}) - 6.1.$$

With the exception of two points (Hoh and Westport) the points lie nearly on an exponential trend as is indicated by the dashed line. When plotted on a semi-logarithmic scale (fig. 23) these points lie close to a straight line.

These results indicate that the relative proportion of calcite and aragonite in large specimens of M. californianus is definitely related to temperature, but that other complicating factors are involved. This relationship might be useful in the determination of

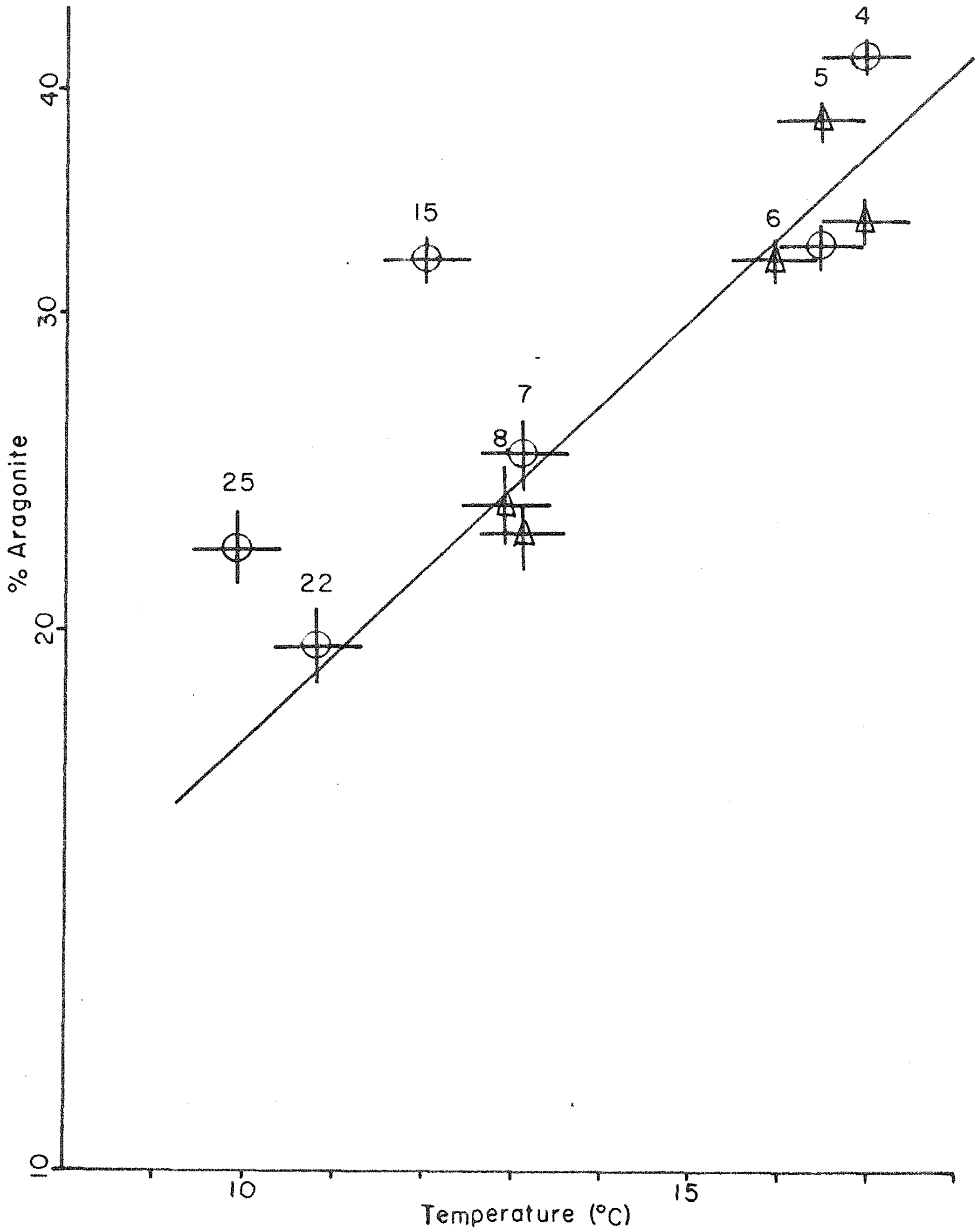

Figure 23. - Semi-logarithmic plot of the variation of the shell mineralogy of M. californianus with temperature. This figure contains the same data as fig. 22. The symbols are as in fig. 22. The equation of the line is:

$$\log \% \text{ aragonite} = 0.52 \text{ (temperature } {}^{\circ}\text{C}) + 0.47.$$

paleotemperatures. However, two factors limit the usefulness of this technique: 1) the general scatter on the curve, 2) some localities do not fit the usual pattern (Westport, for example). This technique could be useful in suggesting a generalized temperature particularly when accompanied by a study of shell structure. It would probably be most useful as a check for comparison against paleotemperatures determined by other techniques to determine if at least generalized agreement exists.

Variation of Percent Aragonite in M. californianus with Oxygen Isotope Temperature

Temperatures were determined from analysis of oxygen isotopic composition for a number of samples and plotted against the percent aragonite of those samples in fig. 24. The mass spectrograph was not functioning at peak efficiency when these analyses were made. This may in part explain the somewhat high results for the temperatures. Temperatures somewhat higher than the actual mean annual temperatures of the stations are expected because the growth rate in M. californianus is higher in summer than winter (Coe and Fox, 1942). Another reason for some uncertainty in the results is the correction for the isotopic composition of the water. A water sample collected at one time during the year may not be representative of the isotopic composition throughout the year. The only result which seems completely unreasonable is the one from Hoh. It is unlikely that the temperature here ever reaches 16.5°C. Some of the points do appear to lie on an exponential trend as in fig. 22, but three of the points are significantly off the curve.

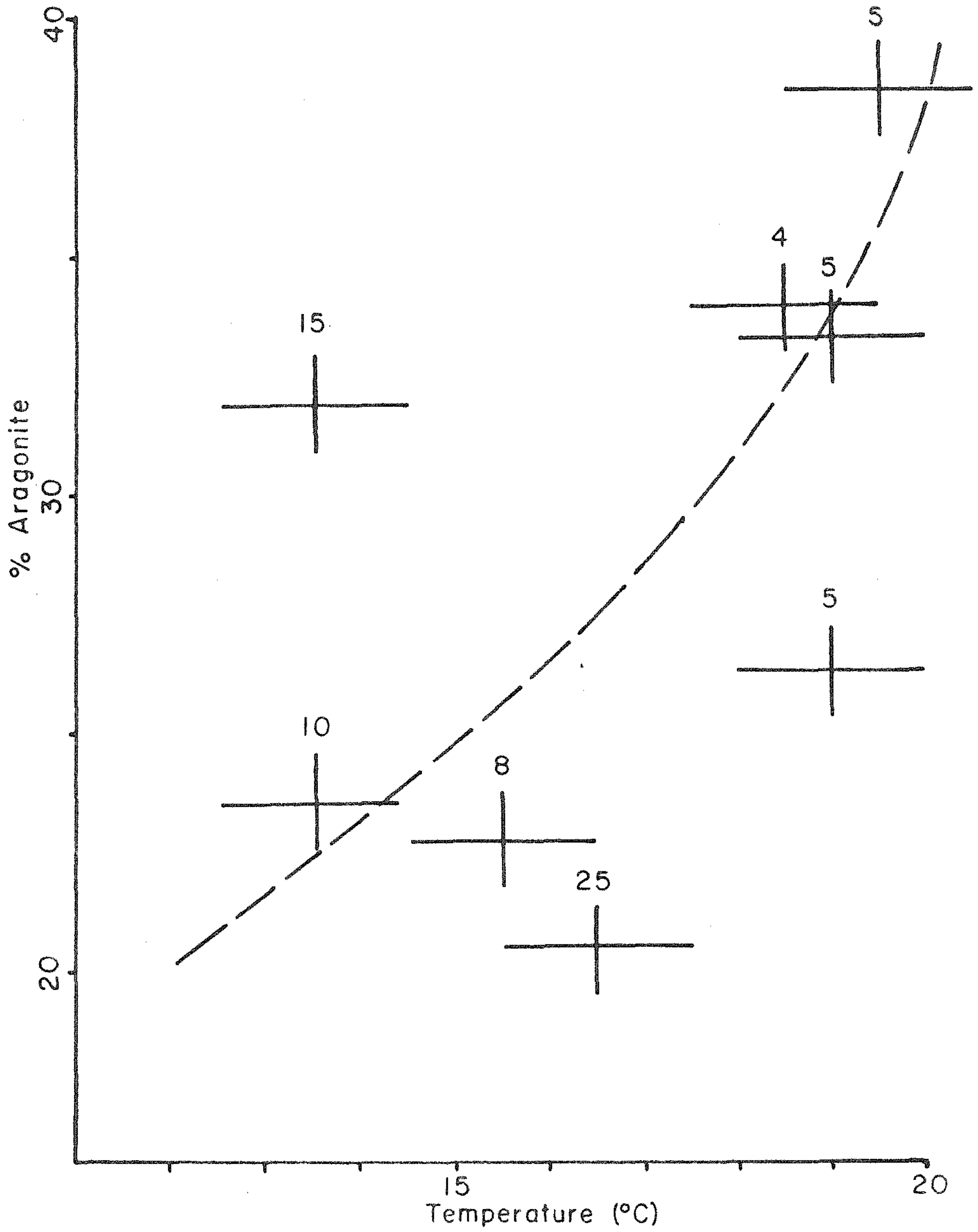

Figure 24. - Variation of the shell mineralogy in *M. californianus* with temperature as determined by oxygen isotope analysis. The numbers above the points are the station numbers taken from fig. 1.

The best method for resolving these difficulties would be to grow specimens at controlled constant temperatures from larvae to the adult stage. As is described below, an attempt was made to grow specimens from very small individuals (2-4 mm.), but the rate of growth with the available facilities was so slow as to make this impractical. There is also danger in extrapolating laboratory results to the natural situation, particularly when the laboratory set-up is unnatural.

Relationship between Shell Thickness and Mineralogy at Corona del Mar

The term thickness as used in this section refers to the actual gauge of the shell wall and not to maximum distance from the outer surface of one valve to the outer surface of the other as is the usual paleontologic meaning. The main problem in investigating the relationship of shell thickness and percent aragonite is objectively measuring shell thickness. One possible method would be to measure the thickness of the shell at the same relative point in all shells and to form a ratio between this measure and shell length. This method would, however, represent the thickness at only one point and might not be representative of the whole shell.

Shell thickness for a given sized shell should be directly proportional to shell weight. Fox and Coe (1943) showed that a plot of the log of weight vs. the log of length of shells of *M. californianus* from La Jolla gives a straight line. They further showed that thick shelled individuals collected from rocks in the intertidally exposed zone fell to one side of the line, and thin shelled individuals collected from below the low tide zone off the pier fell to the opposite side of the line. If weight and length of shells from a particular locality are plotted on logarithmic paper, the points scatter along a linear trend (fig. 25). A line can be drawn along this trend and the variation of points from this line used as a measure of shell thickness. For each shell, a calculated weight can be determined from the line. The percent deviation of the actual weight from calculated weight can then be used as the thickness measure. The actual percents have no particular significance in themselves since they are based on an arbitrarily drawn line, but the relative differences at any given station are significant. One line could be used for comparison at all stations, but the slopes of the natural trends vary between stations.

Figure 25 shows a plot of length vs. weight for the specimens used in the growth series from Corona del Mar. The lines obtained by Fox and Coe (1943) are included for comparison. It should be noted that their lines are based on both valves while the data in this paper are based on only one valve. Figure 26 shows a plot of the percent deviation of actual from calculated weight vs. percent aragonite. Although the scatter on this graph is large, a distinct trend of increased percent aragonite with increased thickness is indicated. The coefficient of correlation is 0.45 and the equation of the least squares line is:

$$\% \text{ aragonite} = 0.11 \times \% \text{ deviation} + 34.$$

The large scatter in the graph is due to the effect of other factors, most notably temperature. The points above the line

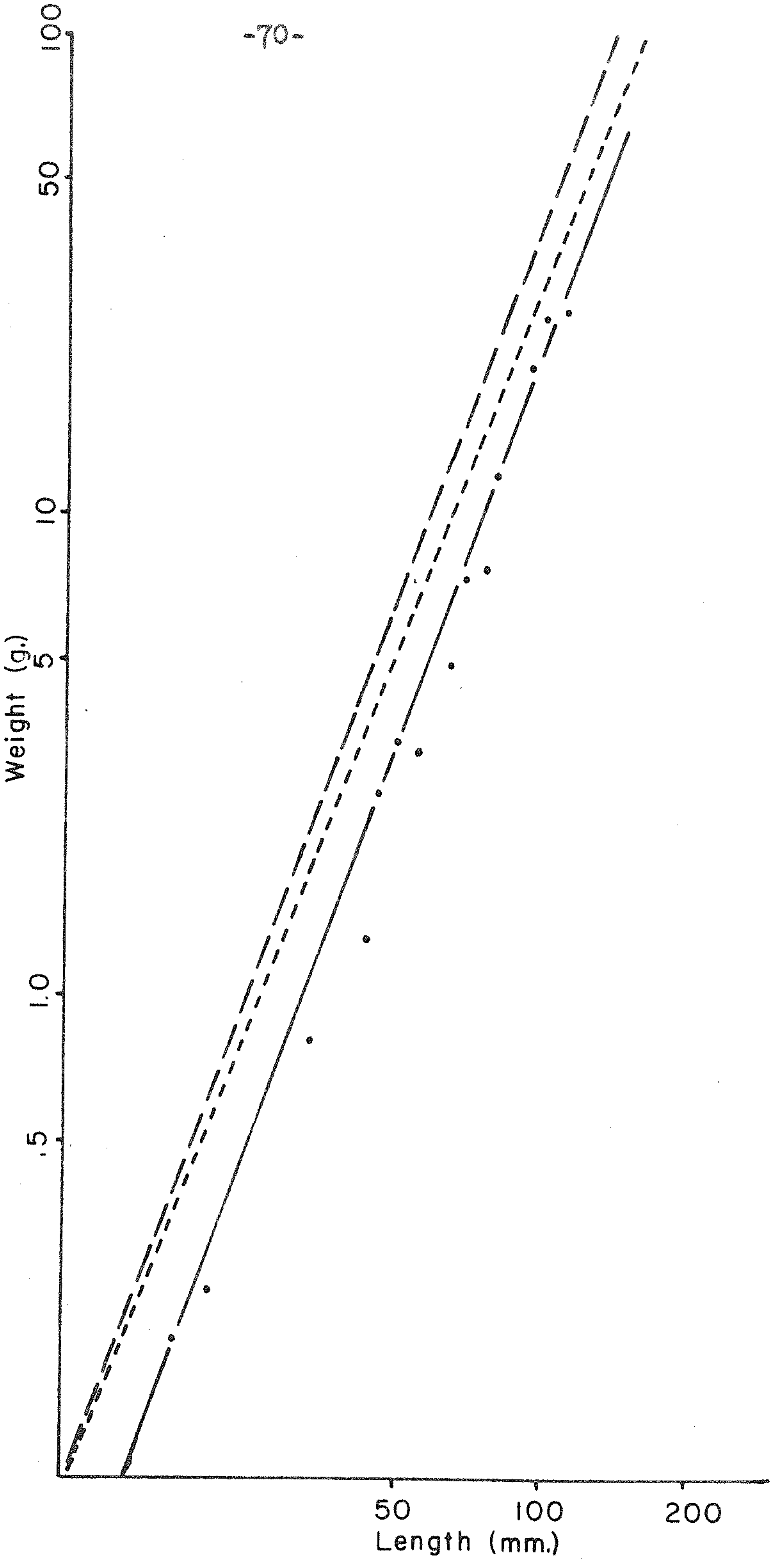

Figure 25. - Log weight vs. log length of M. californianus from Corona del Mar. The long dashed line is from the data of Fox and Coe (1943) for specimens from pier and rocks at La Jolla. The short dashed line is for specimens from the pier only. The points for the Corona del Mar specimens are based on single valves. Fox and Coe's data are for both valves.

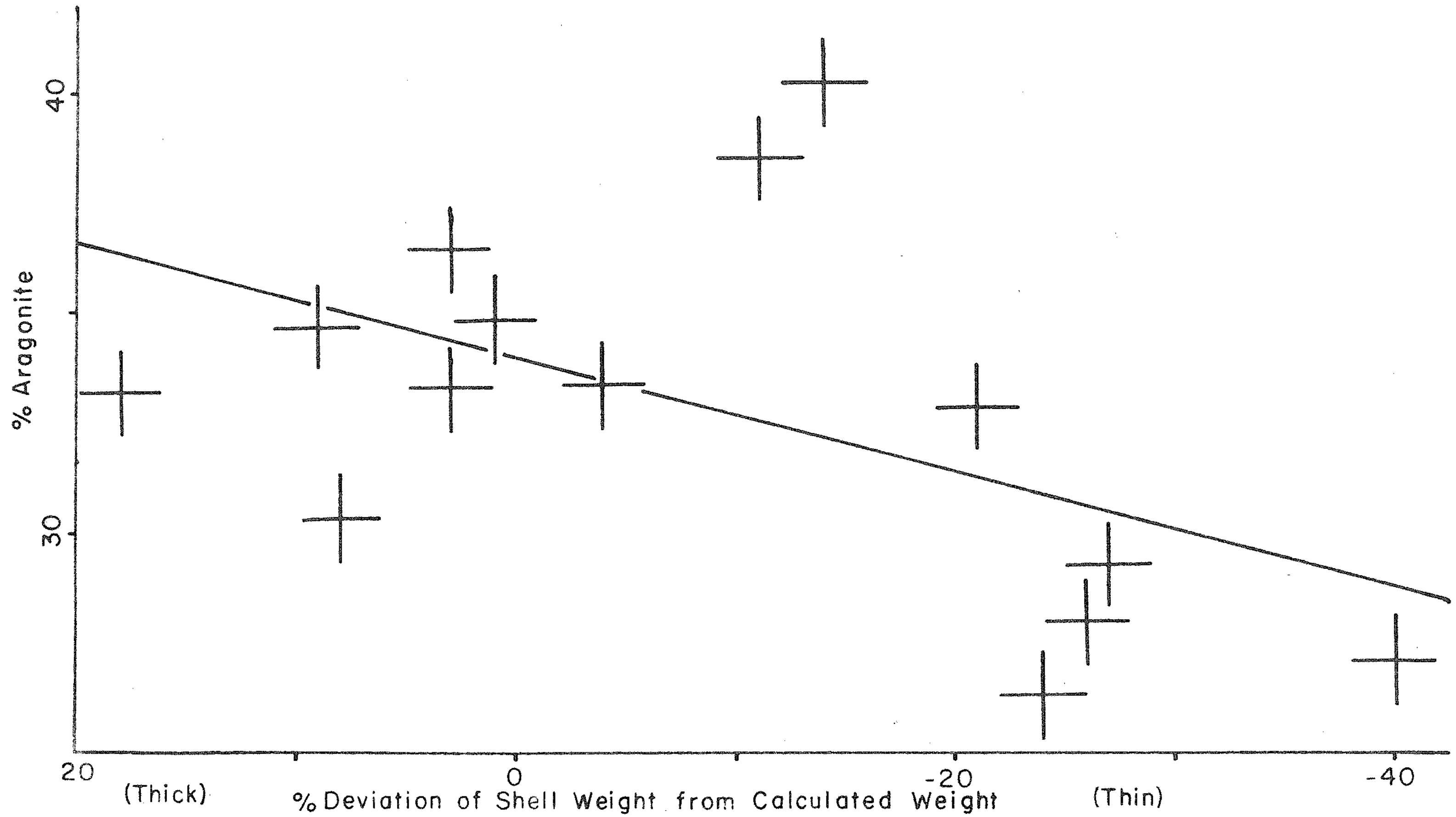

Figure 26. - Effect of shell thickness on shell mineralogy in M. *californianus* from Corona del Mar. See text for a detailed explanation.

represent shells with a relatively higher temperature of deposition than the points below the line. All points lying on or near the line should represent shells with the same mean temperature of deposition.

As a check of this hypothesis, shell length and deviation in percentage units from the line in fig. 26 were plotted. If the hypothesis is correct, this should yield seasonal cycles which have less scatter than in the uncorrected plot of length vs. percent aragonite. Figure 27 is a graph of this type. While the points still scatter, no point lies far off the cycle. The two points which are far off the curve in fig. 10 fall closer to the curve in fig. 27. Some of this scatter is probably due to the lack of sufficient data to clearly define the thickness-mineralogy relationship. A line of slightly greater slope would further reduce the scatter in fig. 27.

Relationship between Shell Thickness and Mineralogy at other Locations

Figure 28 is a plot of percent deviation of weight from calculated weight vs. percent aragonite for Lowenstam's (1954b) specimens from La Jolla. These also form a distinct trend of increase in aragonite with increased thickness. The coefficient of correlation is 0.57 and the least squares line is:

$$\% \text{ aragonite} = 0.40 \times \% \text{ deviation of weights} + 46.$$

These are the only two locations where the data are sufficient to have much meaning. More data would be preferable at even these locations since the scatter of points is great.

Least squares lines and coefficients of correlation were calculated for the other locations where several analyses were available:

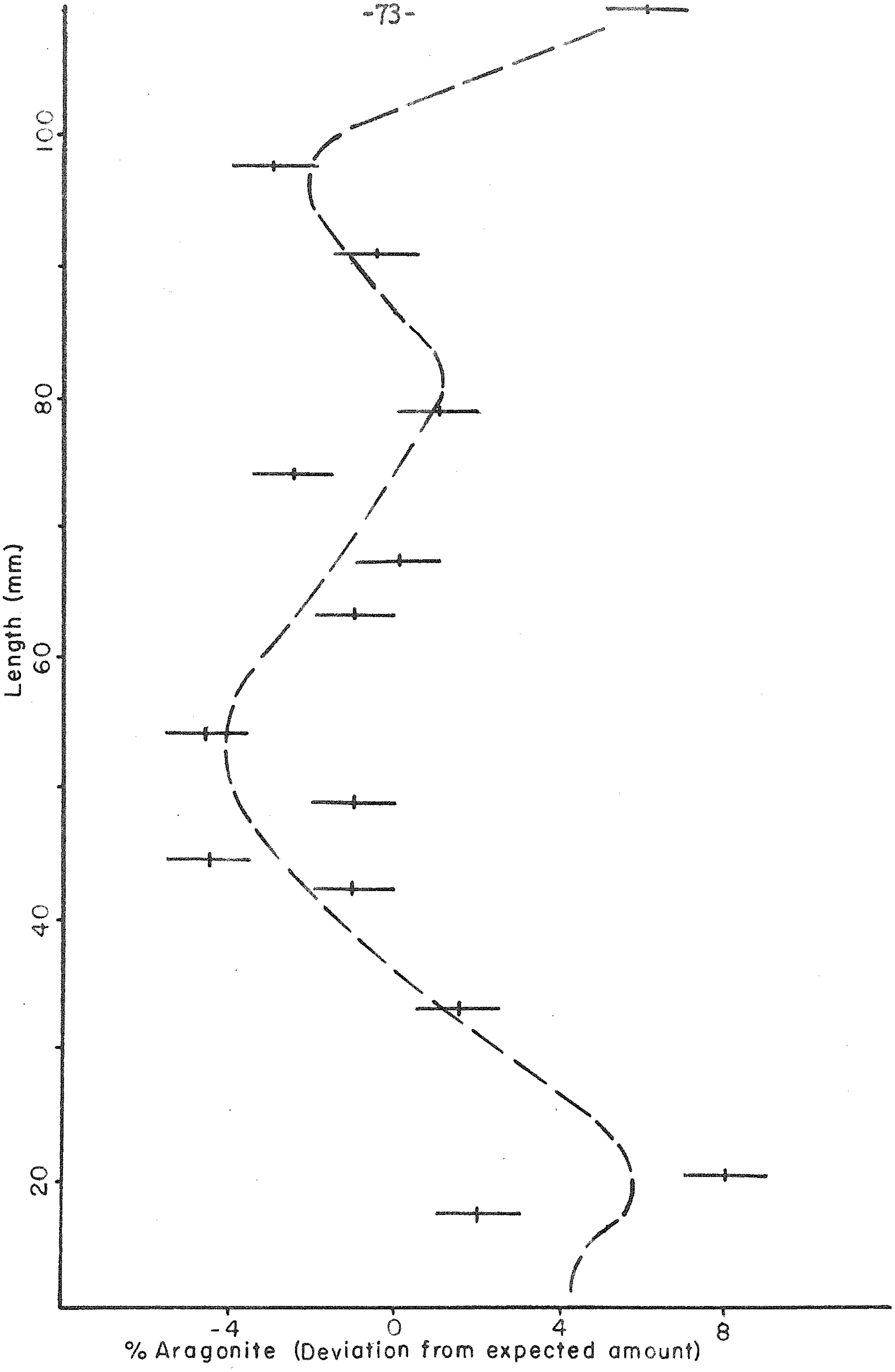

Figure 27. - Growth series of M. californianus from Corona del Mar with correction for effect of shell thickness. See text for a detailed explanation.

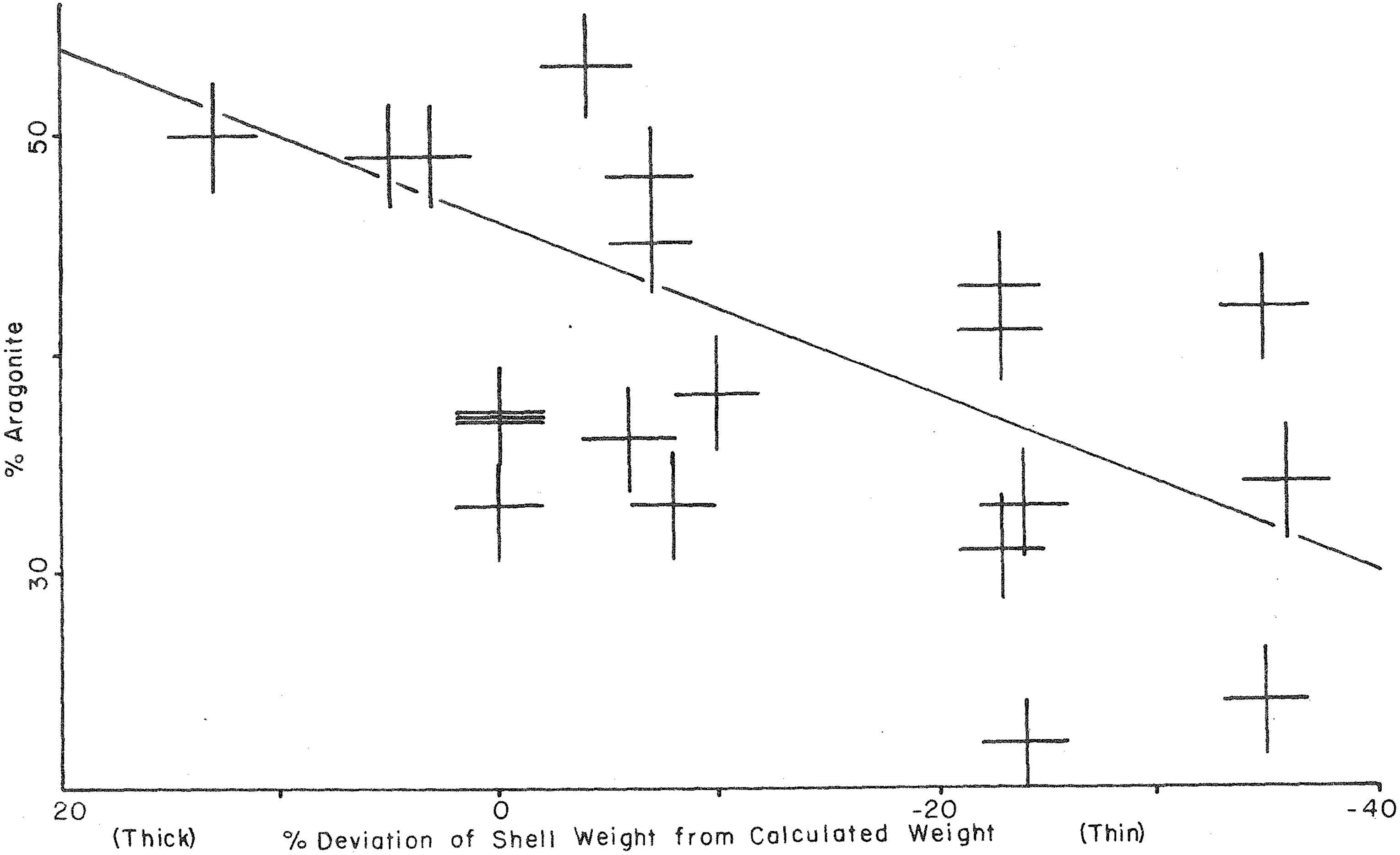

Figure 28. - Effect of shell thickness on shell mineralogy in <u>M</u>. <u>californianus</u> from La Jolla. This figure is based on the data of Lowenstam (1954 b).

Location	Correlation Coefficient	Slope of Least Squares Line	No. of Samples
Avila Beach	0.85	0.38	7
Westport	0.14	0.02	7
Waldport	0.36	0.04	7
Hoh	0.74	0.22	7

A test for the relationship of shell thickness and percent aragonite in M. edulis diegensis from Avila Beach gave a correlation coefficient of 0.00 and a slope of 0.00 for the least squares line. Thickness thus appears to have no relationship to percent aragonite in M. edulis diegensis, at least from this location. The sample size (seven) is too small to allow a conclusive statement.

The coefficients of correlation at Westport and Waldport are low, and the slopes of the least squares lines near zero. A correlation between thickness and percent aragonite appears to exist at Hoh and Avila Beach. The coefficients are relatively high as are the slopes of the least squares line. Differences between stations probably are due to the inadequate samples and perhaps in part to the placing of the lines on the log length vs. log weight graphs. With so few samples available, it is difficult to place this line. A positive correlation between thickness and percent aragonite in northern shells is unexpected. In these shells with an inner prismatic layer, thickening could result from thickening of the calcitic inner prismatic layer as well as thickening of the aragonitic nacreous layer.

A possible source of error results from the method of measuring thickness. If two shells were exactly alike in all respects except that one was entirely aragonite and one entirely calcite, the aragonite shell would be 8.5% heavier than the calcite one due to the difference in density of the two minerals. Determining shell thickness on the basis of weight would thus make the aragonite shell appear thicker than the calcite shell. The actual differences in weight observed are much greater than 8.5%, and the range of variation in mineralogy is less than half the pure calcite-pure aragonite case cited above. Therefore difference in density of the minerals has a very minor effect in the relationship between percent aragonite and shell thickness.

Percent aragonite may not vary as a result of increased thickness, but shells which happen to have more aragonite for some reason may be thickened as a result. This study does not exclude this possibility.

This study did not determine what factors cause some shells to be thicker than others. Other workers have noted (Fox and Coe, 1943) that shells of _M._ _californianus_ subjected to relatively greater water turbulence have relatively thicker shells. For example, intertidally exposed individuals have thicker shells than continuously submerged ones. This relationship was also noted in collecting for this study. Since all specimens used were collected from the intertidal zone on the open coast, the degree of turbulence should have been reasonably constant except as it might be affected by microenvironmental factors. Fox and Coe (1943) also suggest that growth rate may be a factor in determining shell thickness, slow growing shells being thicker than fast growing ones. This is not always the case. Some northern shells which have a slower growth rate than southern ones are no thicker than the southern shells. Other factors must affect shell thickness. A certain amount of variation would be expected due to random genetic variation.

Variation of Shell Mineralogy with Salinity in M. edulis edulis

Salinity values for this section were determined by the silver nitrate titration method. Two or three runs were made of each sample and the mean determined. Analytical errors and other variables such as possible small evaporation due to storage in polyethylene bottles for several months probably make the results no more accurate than the nearest two tenths of a per mil.

Samples of M. edulis edulis were collected at various points in the Juan de Fuca Strait and Hood Canal regions of Washington. The salinity at collecting time at these stations varied from 32.48°/oo at Neah Bay to 18.60°/oo at Potlatch. The difference in mean annual salinity is probably much greater. The collecting was done in early August when salinity was probably considerably higher than usual at the locations in the Hood Canal. At Seattle, where records of variation in salinity are kept by the U. S. Coast and Geodetic Survey (1954), the mean August salinity is higher than the yearly mean. Mean annual temperature should be near the same for all stations since they are from the same latitude and are protected from rapid exchange with the open ocean. No records are available to prove this, however. Collecting time temperatures were influenced by the time of the day when collecting was done (due to solar heating of low turbulence water). The specimens analyzed in this series were 28-32 mm. in length. Figure 29 shows the variation in percent aragonite with salinity at collecting time.

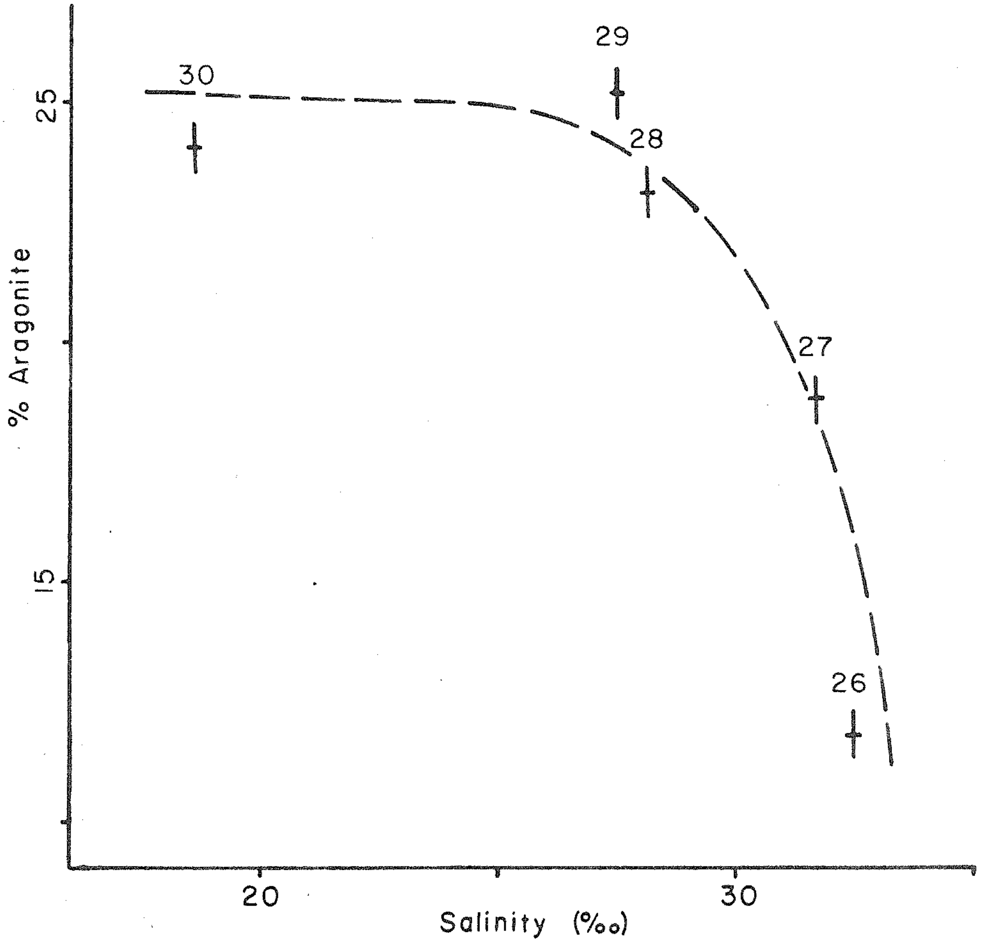

Figure 29. - Variation of salinity at collecting time and shell mineralogy of M. edulis edulis from the Washington area. The numbers above the points are station numbers taken from fig. 1.

Such a sharp rise in percent aragonite with the drop from near normal salinity is unexpected. It should be noted that an open coast, normal salinity sample from Hoh has a much higher percent aragonite than the Neah Bay sample although it is only 50 miles farther south. This may be due to water turbulence. The open coast specimens have thicker shells which is evidently the result of thickening of the nacreous layer. The possibility exists that the open coast and bay forms are different subspecies.

On the basis of analysis of European specimens from the Baltic Sea, Lowenstam (1954b) suggested that shell mineralogy might be affected by salinity. Bøggild (1930) noted that all fresh water molluscs, with one exception, have aragonitic shells.

Variation of Shell Mineralogy with Salinity in _M._ _edulis_ _diegensis_

Figure 30 shows variation of percent aragonite with salinity at collecting time for a series of samples of _M._ _edulis_ _diegensis_ from the San Francisco area. Salinities at collecting time may not be representative of the mean annual salinity. The San Francisco samples were collected in late July. The mean annual salinity is thus probably lower than the salinities shown on these graphs. Mean annual temperature should be approximately the same at all localities, although perhaps cooler at the Fort Point and Sausalito stations which are in more direct communication with the open ocean. The other two stations are farther back in San Pablo Bay and are subject to greater extremes in temperatures, particularly higher summer temperatures. Specimen size range was 15-38 mm. The San Pedro sample was composed

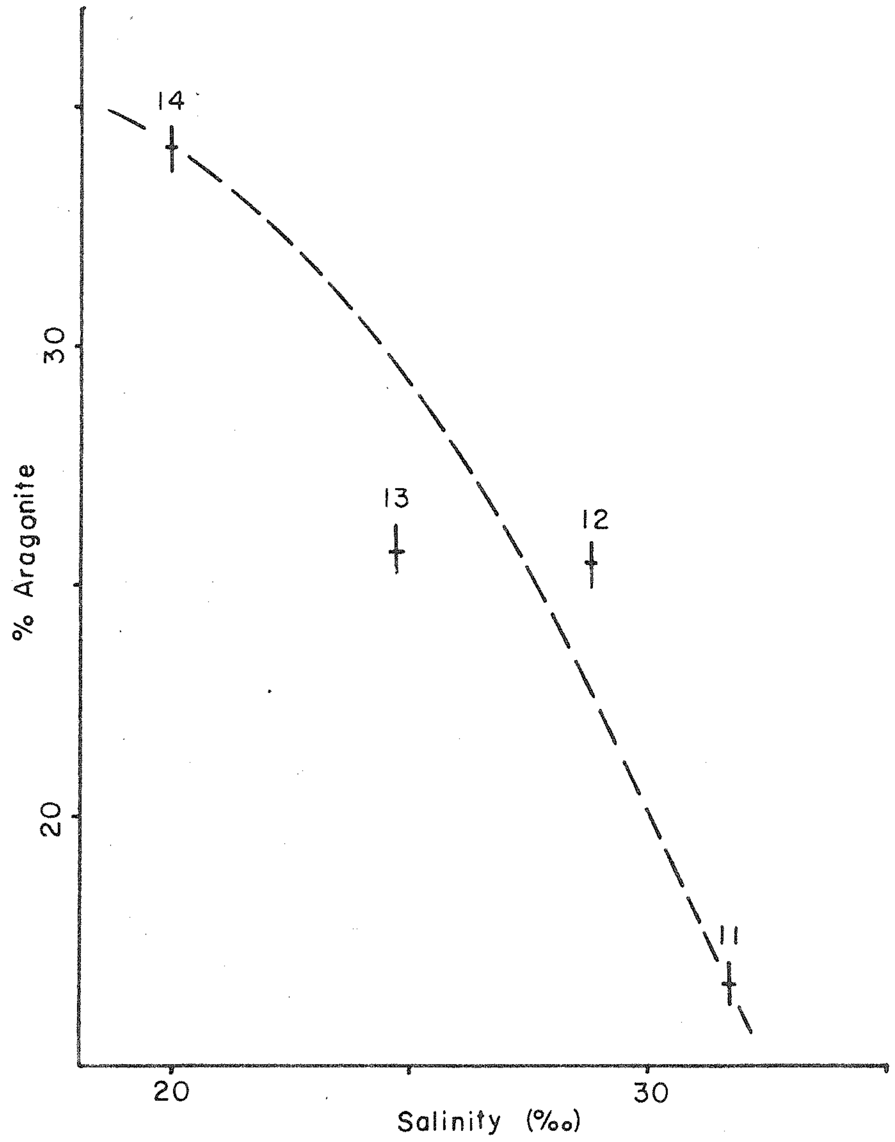

Figure 30. - Variation of salinity at collecting time and the shell mineralogy of M. edulis diegensis from the San Francisco area. The numbers above the points are station numbers taken from fig. 1.

of dead shells. No live specimens could be found at that location at the collecting time.

A trend of increase in the percent aragonite with decrease in salinity was noted. The San Francisco samples do not show the rapid rise and subsequent leveling off of the curve as shown in the Washington series. The reason for this is unknown but may be a subspecies difference.

The effect of salinity on the mineralogy of M. californianus is not certain. M. californianus is a relatively stenohyaline form, seldom found in habitats of more than slightly reduced salinity. This relationship may be more apparent than real since the true limiting factor on the distribution of M. californianus may be water turbulence (Young, 1941). Environments of reduced salinity, at least on the Pacific Coast of the United States, usually have low turbulence. One open coast collecting locality, Crescent City, California, had a distinctly reduced salinity (30.48°/oo) at collecting time. M. californianus collected from this locality had 42.9% aragonite in longitudinal thin section (see below). This is substantially higher than would be expected from a specimen growing in water of normal salinity at a locality with the mean annual temperature of 11.5°C.

Variation of Shell Mineralogy between Microenvironments

The shell mineralogy of small specimens of Mytilus from differing microenvironments at one general location was investigated. Specimens of M. edulis diegensis collected from high on a piling at Corona del Mar had shells containing 27.5% aragonite. Specimens collected from

2½ feet lower on the piling where they were under water for longer periods of time had shells containing 28.6% aragonite, an insignificant difference. M. californianus specimens were collected from a tide pool which was not in open communication with the ocean at low tide. Shells of these specimens contained 32.0% aragonite as compared to the 48.0% aragonite of specimens from the open coast at the same location. These were large enough to be past the temperature insensitive stage. The results are not what might be expected. Tide pool temperatures may be significantly warmer during sunny days than the open ocean. Other unknown factors must be involved here.

Unknown Factors Affecting Shell Mineralogy in Mytilus

The various factors discussed above account for a large part of the variation in the mineralogy of the Mytilus shell, but do not seem to be the only factors involved. In the two subspecies of M. edulis, most of the variation in shell mineralogy can be explained as temperature, size, or salinity effects. The major unexplained observation in this species is the lack of seasonal variation among small individuals from one locality, while geographic variation does occur. In addition, some of the variation between stations in larger individuals of the northern subspecies do not seem to be explainable in terms of the above factors.

In most cases variation in the relative proportions of calcite and aragonite in M. californianus can be explained as resulting from the effect of temperature and shell thickness. This may explain most of the variation at any given location. Other factors must be involved, however, as indicated by the anomalous results obtained from individuals from Westport and Hoh.

Mytilus Specimens Grown in Aquariums

In the early stages of this study, it was thought that growing specimens of *Mytilus* from a very small size to a considerably larger size in temperature controlled aquariums would demonstrate the effect of temperature on shell mineralogy. It was later realized that this would not be possible due to the temperature insensitive nature of young specimens of *M. californianus* and the apparent temperature insensitivity of small specimens of *M. edulis diegensis* from a given locality. Growing specimens in aquariums would be meaningful if they could be grown from a very small to at least a moderately large size. Growth rate was much too slow in the set-up used for this study to make this practical.

In order to facilitate feeding and thus to increase the growth rate of the experimental specimens, they were placed in one liter beakers sitting in temperature controlled aquariums. The water in the beaker was aerated. Using the beakers allowed the food to be concentrated and more quickly and completely filtered out by the individuals. A small number of calcareous oolites was added to the beakers to keep the water saturated with calcium carbonate. The water was changed at intervals of two to three days. The specimens were fed two or three times a day with approximately 20 ml. of a concentrated suspension of diatoms. The diatom *Nitzschia* was used in some of the earlier experiments but *Dunaliella* was used in later ones because it is easier to maintain and grows more rapidly. Various other foods such as fine fish food, flour, and milk were tried but without success.

The results shown below are x-ray analyses of individuals of M. edulis diegensis which had at least doubled in weight in the temperature controlled aquariums. These individuals were all very small, in most cases less than 5 mm. long at the beginning and less than 10 mm. at the end of their growth in the aquariums.

Temperature($^{\circ}$C)	% Aragonite
12.3	23.3
15.1	26.7
18.3	28.1
21.0	25.5
24.2	28.8

The slight general increase in percent aragonite with temperature in these samples may be considered as evidence of a positive correlation of these two variables. However, the variation between samples is no greater than the normal variation between individuals collected at any one time from a given location. The very generalized trend observed may be purely fortuitious.

The amount of new growth in the aquariums of the calcite layer can be easily observed in thin section. It is possible to make a reasonable estimate of the increase in thickness of the aragonite layer from an observation of the thin section. An estimate of the relative amounts of calcite and aragonite in the new growth as seen in longitudinal thin section can thus be made. The results of such observations on specimens of M. edulis diegensis from 16.4 to 23.0 mm.

in length are as follows:

Temperature (°C)	% Aragonite in New Shell in Longitudinal Section
12.3	26
15.1	24
18.3	27
19.9	19
21.0	29

No general trend is evident. These estimates have a very low precision, probably no better than 20%.

Miscellaneous Observations on Specimens Grown in Aquariums

Certain other observations were made on the specimens grown in the aquariums. These do not necessarily have any bearing on the relationship of shell mineralogy to temperature but have interesting ecological implications.

Both species grew at temperatures as low as 10°C. Too many uncertainties exist to make a quantitative measure of the growth rate. Qualitatively, a general increase in growth rate of both species was apparent to a maximum at 15 and 18°C. The rate decreased at 21°C, particularly in M. californianus. The rate appears to remain high in M. edulis diegensis. At 24°C, growth apparently stopped in M. californianus; and all specimens died after about one month. M. edulis diegensis survived at this temperature and even showed substantial growth. M. edulis diegensis survived for over a month at 26°C. Death at that time may have been from lack of food rather than high temperature. In general, growth rate was much higher in M. edulis diegensis.

This may be due to the lack of turbulence which M. californianus seems to require in natural situations.

Specimens were also grown at varying salinities. Both species survived in substantial numbers at salinities as low as approximately 12°/oo. Most specimens did not grow as rapidly at these reduced salinities as did those in water of normal salinity. The specimens survived an immediate transition from normal to greatly reduced salinities apparently with no ill effects. M. californianus had a somewhat higher fatality rate, but nevertheless, several specimens lived even at the low salinities. This would suggest that perhaps factors other than salinity may be involved in restricting M. californianus from environments characterized by low salinity. Fox (1936) conducted experiments which showed that M. californianus could survive for considerable lengths of time at salinities between 17 and 45°/oo.

The general morphology of both species often changes during growth in the aquariums. The shell deposited in the aquariums was usually thinner than the earlier part of the shell. Gibbous shells usually begin to grow thinner. Broad shells became narrower. A very distinctive shelf or growth line usually developed at the division between old and new shell. This suggests that the great morphologic variability in these species is not controlled genetically but is an individual response to a variable environment.

The relative distance between the pallial line and the posterior margin of the shell varies slightly with temperature. Shells grown at lower temperatures have a relatively broader zone between pallial line and edge than those grown at higher temperatures. This difference is subtle and difficult to measure, however. As the pallial line marks the boundary between nacreous and outer prismatic layers, this correlates with the relationship of increased aragonite with temperatures although this relationship was not noted in the aquarium specimens.

SHELL STRUCTURE VARIATION

Determining Percent Aragonite in Thin Section

Since calcite and aragonite in the shells of *Mytilus* are segregated into discrete structural units, variation in the mineralogy of the shells should be reflected in the shell structure. In fact, one possible method of measuring the variation in mineralogy is by estimating the variation in volume of the structural units. A method of measuring variation in the mineralogy, although not necessarily the exact magnitude of the variation, is to measure the relative amount of calcite and aragonite in sections of constant orientation. In this study, the percentage of aragonite in longitudinal sections (fig. 3) was determined for several specimens of *M. californianus*.

The percent aragonite in section was determined by measuring traverses across the section at regular intervals (usually of one or two mm.). The total distance measured across each structural unit was determined for each unit. The percent aragonite was determined by dividing the traverse distance across the aragonitic unit by the total traverse distance. This is essentially the same as the line integral technique used in petrography. All determinations included traverses of at least 1000 units and large shells contained many more.

In order to check the precision of this technique for determining the percent aragonite in a longitudinal section, nine determinations were made on the same section. These determinations were made on separate days to minimize the effect of memory of the section. The traverses on this section measured a total of approximately 2500 units. The mean of these determinations was 36.7% aragonite with a standard deviation of 0.8%. Variation in orientation between sections of different shells produced a larger error than this.

An attempt was made to determine the effect of variation in orientation of the longitudinal section. A shell was sectioned transversely at intervals of approximately 2 mm. Traverses were made across each section at 2 mm. intervals. By taking one traverse from each transverse section at a position with constant relationship to the center of the section,the equivalent of measurements from longitudinal sections could be made. Variation in the proportion of aragonite for variously centered sections could then be studied. Figure 31 shows how percent aragonite varies with centering of the section. It can be seen that the maximum proportion of aragonite is exposed in sections from 1 to 2 mm. to the dorsal side of a perfectly centered section. The percent aragonite falls off rapidly from both sides of this maximum. The orientation of the section thus has a significant effect on the percent aragonite observed in a longitudinal section. Most sections in this study were probably within 1 or 2 mm. of being centered. Many polished sections were reground until they gave a maximum value for the percent aragonite. This maximum value was then used. Except in some obviously badly centered sections, regrinding usually did not change the percent aragonite by more than 3 or 4%.

In many cases, percent aragonite in longitudinal section of one valve of <u>M. californianus</u> was determined and the mineralogy of the opposite valve of the same individual was determined by x-ray diffraction. Figure 32 shows a plot of percent aragonite in longitudinal

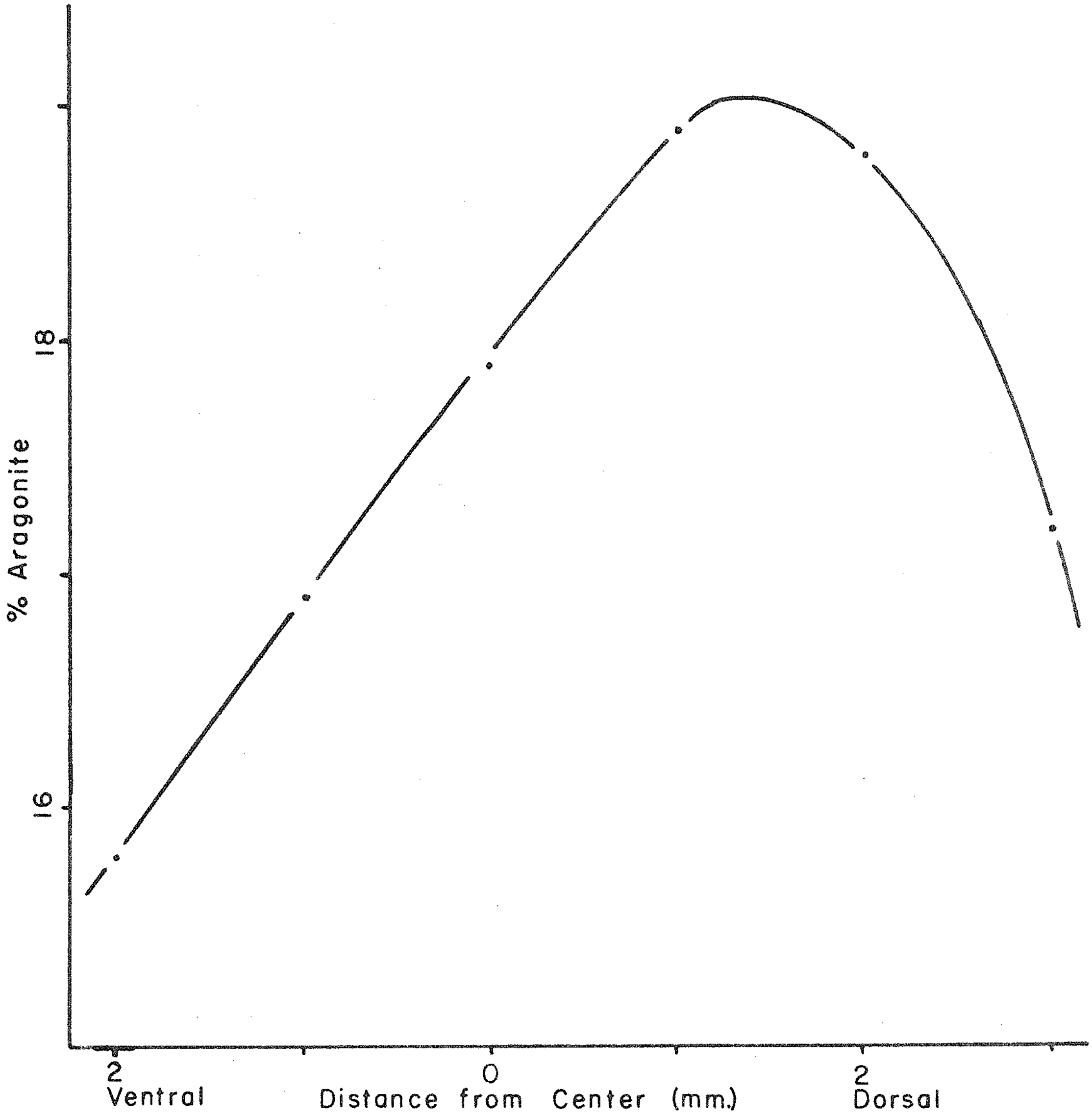

Figure 31. - Effect of orientation of the section on the percent aragonite in longitudinal section. See text for detailed explanation.

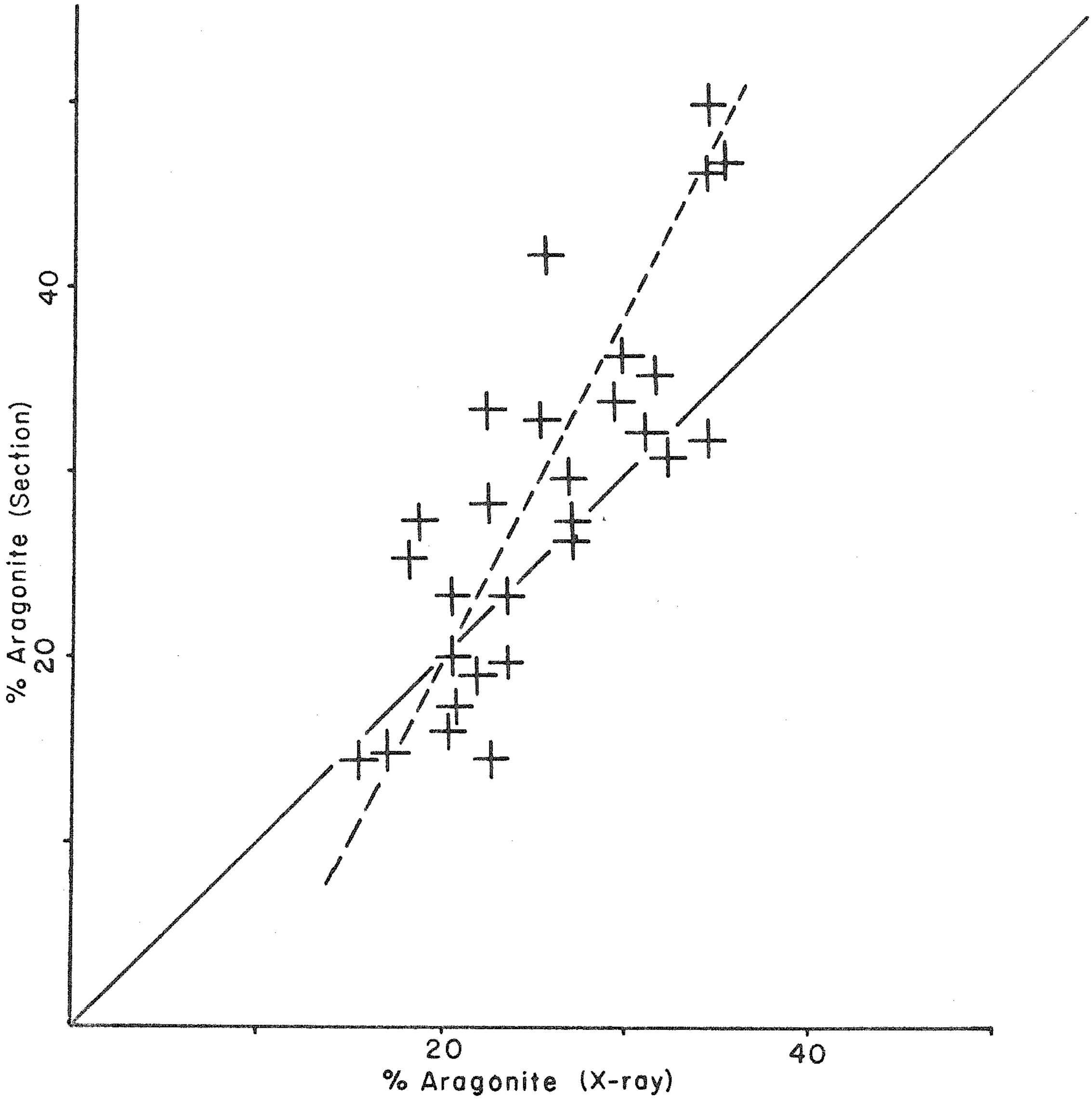

Figure 32. - Comparison of x-ray determined percent aragonite with percent aragonite in longitudinal section of the opposite valves of the same individual.

section vs. percent aragonite in the opposite complete valve as determined by x-ray diffraction. The large scatter noted in this graph can be attributed to such factors as variation in the orientation of the sections, variation between individuals in the distribution of structural units, small differences in the mineralogy of opposite valves, and the uncertainty of the determinations. A definite trend exists for the percent aragonite in longitudinal sections to increase more rapidly than x-ray determined percent aragonite in the complete valve. This is probably largely due to the change in mineralogy of the beak area. Being very thick but narrower than the rest of the shell, the beak area contributes more to the total area of a section than it does to the total volume of the shell. Specimens having a low percentage of aragonite usually have beaks composed largely of calcite and specimens having a higher percentage of aragonite have largely aragonitic beaks.

Variation with Latitude of Percent Aragonite in Section

Figure 33 shows how the percent aragonite in longitudinal section varies with latitude of the collecting locality. The percent aragonite shows a definite increase with decreasing latitude but with a great deal of scatter. With a few exceptions, shells greater than 45 mm. in length were used. The three triangles represent worn shells. The low values for these shells are apparently due to thickening of the inner prismatic layer to patch the damaged area. The linear trend is clear for points north of Westport. The range of values from individual stations is lower in the north. This is due in part to the

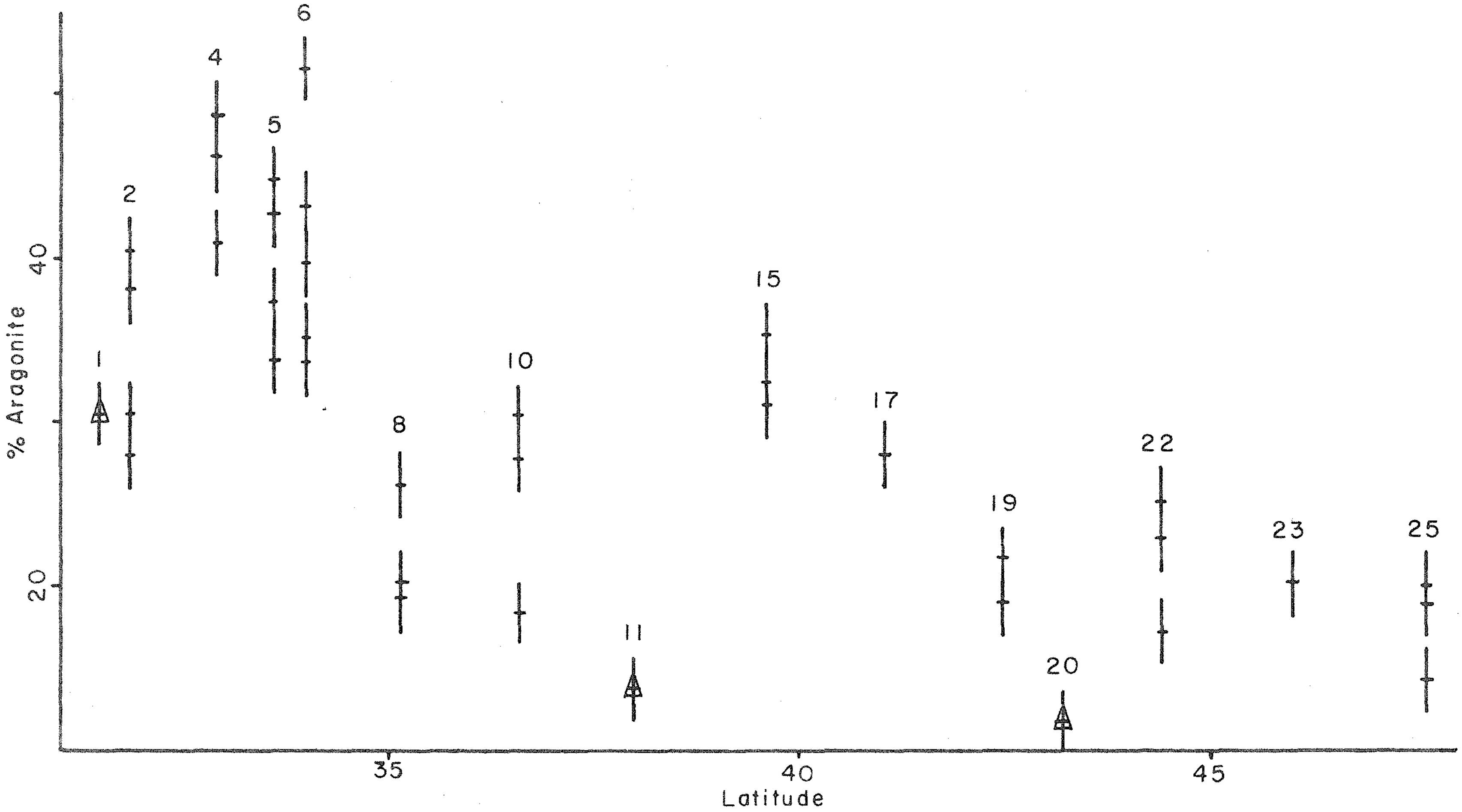

Figure 33. - Variation with latitude of percent aragonite in longitudinal section. The points enclosed in triangles represent worn specimens. The numbers above the points are station numbers taken from fig. 1.

fact that the northern shells are from older individuals and less subject to seasonal fluctuations in temperature. It may be in part due to the lower seasonal range of temperature at the northern stations. The x-ray determinations of percent aragonite from southern stations discussed above also have a wider range than those from northern stations.

The variation of percent aragonite in longitudinal section with mean annual temperature of the collecting locality is shown in fig. 34. As in the case of fig. 22, data for the temperatures is taken from Special Publication No. 280 of the U. S. Coast and Geodetic Survey (1956) where possible and interpolated from the data in this publication where not available directly. Only the mean and extreme values used in fig. 33 are included in this graph. An uncertainty of 0.5°C is allowed for each station as in fig. 22. The trend of increasing percent aragonite with increasing temperature is seen in this graph. The trend is not exponential in this case as it is in the plot of x-ray determined percent aragonite vs. temperature. The stations north of Westport form a clearer linear trend than all stations together.

From a study of longitudinal sections of _M. californianus_ from various localities along the Pacific Coast, it is evident that a definite correlation between latitude or temperature and shell structure exists. This variation is only partially expressed in the determination of percent aragonite in section. For example, although the Avila Beach specimens have the same relative amounts of aragonite in section as do specimens from as far north as Oregon, the structure of the shells is distinctly different. The inner prismatic layer of

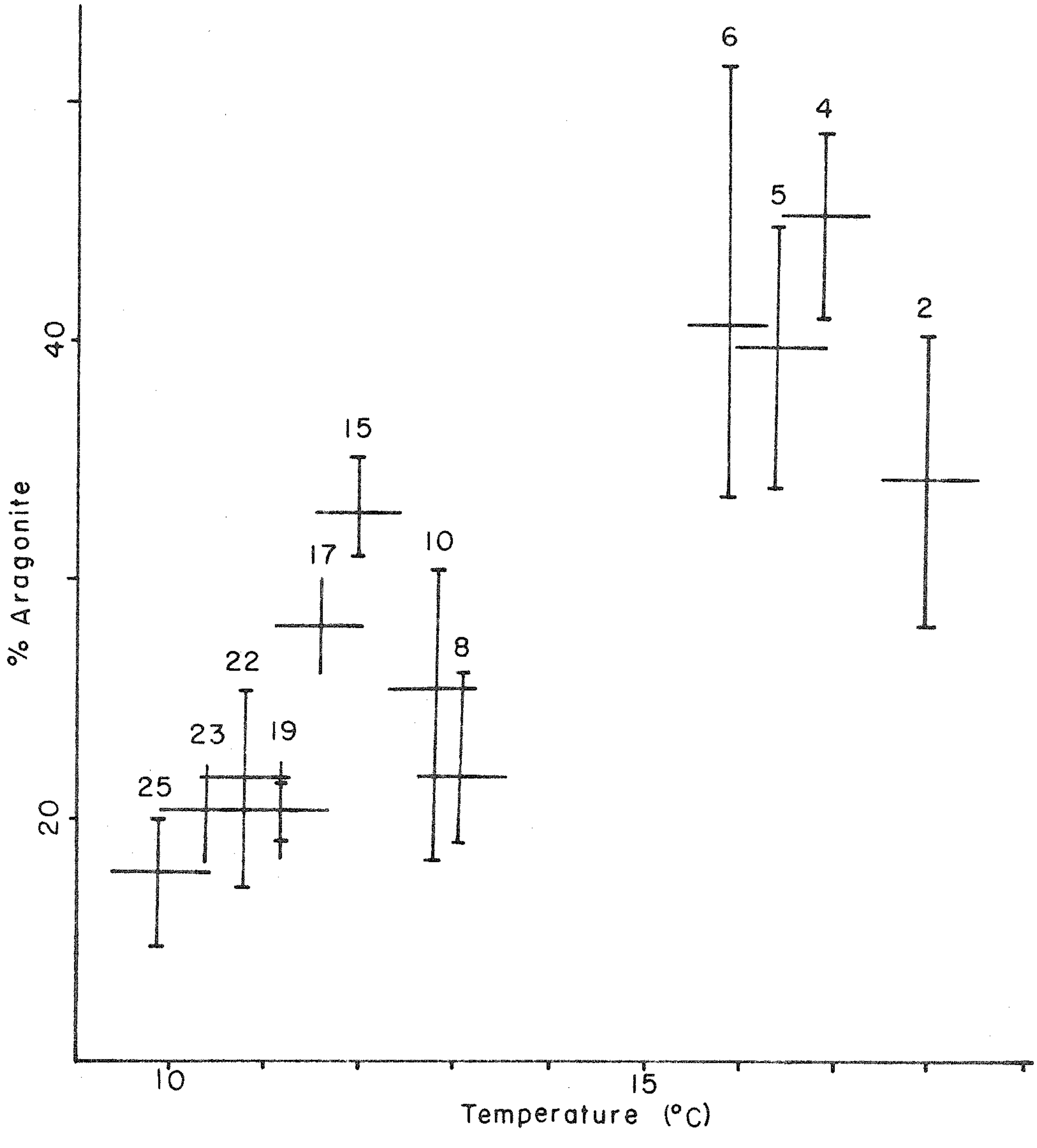

Figure 34. - Variation in percent aragonite in longitudinal section with mean annual temperature of the collecting locality. The top and bottom horizontal bars represent the extreme values for the station. The middle bar is the station mean. The numbers above the points are station numbers taken from fig. 1.

the Avila Beach specimens is much less developed. It is in some cases discontinuous and is often broken by wedges of the nacreous structure continuous with the nacreous layer. Some of the southern shells which have only slightly more aragonite than northern ones actually have little inner prismatic layer. Distinguishing the approximate mean annual temperature of the collecting locality by examining the extent of development of the inner prismatic layer in a qualitative manner is possible. It is in fact possible to make a generalized approximation of the temperature of deposition by observing the inner prismatic layer visible on the inner surface of the shell (Plate VIc, Appendix II, p. 220). In making these interpretations, using only unworn or very slightly worn shells is important. A worn southern shell which has been "patched" by the addition of an inner prismatic layer may resemble a specimen collected far to the north.

Structural Types

Before the quantitative relationship between shell structure and temperature can be determined, a quantitative method of measuring shell structure must be devised. In this study, a completely arbitrary system of designation has been developed. It is not presented as a unique method of numerical notation of structure but as one possible method.

Structure type numbers have been assigned to certain ranges of variation in shell structure, particularly as affected by the degree of development of the inner prismatic layer. A higher structure type number denotes a better developed inner prismatic layer. Plates VII and VIII (Appendix II, pp. 221 and 222) give a diagrammatic representation of each structure type and show actual photographs of longitudinal sections of shells with the various types of structure. An effort was made to make the boundary between structure types sharp. However, in some cases, distinguishing the precise boundary may be difficult.

For purposes of structure type determination, the beak is defined as that area of a longitudinal section anterior to a straight line which is a projection of the posterior side of the muscle scar or socket (fig. 4). If the section is not properly centered, the anterior muscle scar may not be visible and the position of the line bounding the beak must be inferred. Percentages used in the descriptions are areal percentages. The table below gives a description of the structural types.

<u>Type</u>	
0	No inner prismatic layer or calcite is present in the beak except in the outer prismatic layer (beak area calcite may be continuous with the outer prismatic layer outside the plane of the section, but beak area calcite is not here considered as part of the outer prismatic layer). No examples of this type have yet been found.
1	No inner prismatic layer occurs outside the beak proper. The beak contains some but less than 50% calcite.
2	No inner prismatic layer occurs outside the beak area, but the beak contains more than 50% calcite.
3	Small patches of inner prismatic layer occur outside the beak

Type

area, but the area of calcite outside the beak is less than 50% of the total calcite area in the beak. In structural types of 3 or higher, the beak is usually completely calcite, but small patches of aragonite, usually forming less than 10% of the beak area, often occur.

4 A distinct wedge of inner prismatic layer occurs outside the beak area but has a maximum posterior extent equal to less than the maximum width of the beak.

5 The inner prismatic layer extends to the posterior from more than one to less than three times the maximum width of the beak. The inner prismatic layer in structure types 5 through 7 in a few cases is not continuous.

6 The inner prismatic layer extends to the posterior more than three but less than six times the maximum width of the beak.

7 A fully developed inner prismatic layer occurs (extending posteriorly more than six times the maximum width of the beak), but the layer may be discontinuous or incised for more than half its length by tongues of aragonite.

8 A fully developed inner prismatic layer occurs. The nacreous layer is also well developed, being at least one-fourth as thick as the inner prismatic layer at all places except in the beak. Tongues of the nacreous layer may extend 2 or more mm. into the inner prismatic layer.

9 These shells contain a fully developed inner prismatic layer and a weak nacreous layer with poorly developed tongues of

nacreous structure in the inner prismatic layer.

The distinction between most structural types is not difficult and can be done objectively. Unusual structures such as discontinuous inner prismatic layers and an unusually large amount of aragonite in the beaks of shells with extensive inner prismatic layers cause some difficulty. The rule followed in these cases was to give the shells the higher of two possible type numbers.

Variation of Mean Structural Type with Temperature

In order to determine the correlation between structure type and temperature, a number of shells was examined from several locations, largely in the southern part of the study range. Figure 35 shows a plot of the mean structural type vs. mean annual temperature of the collecting locality. The vertical lines represent the probable error of the means. Since the structural types were arbitrarily selected, there is no reason to expect a straight linear trend from these points.

The structure type of large shells is usually slightly higher than in smaller shells. The crosses in fig. 35 represent the mean structural type of shells over 50 mm. in length. This may be due to the fact that M. californianus does not begin to develop an inner prismatic layer immediately after starting growth.

Larger samples would have been desirable in some cases, particularly at El Morro.

Geographic Variation in Growth Rates in M. californianus

As discussed above in the section on shell structure in Mytilus, determining the age of a specimen of M. californianus from the

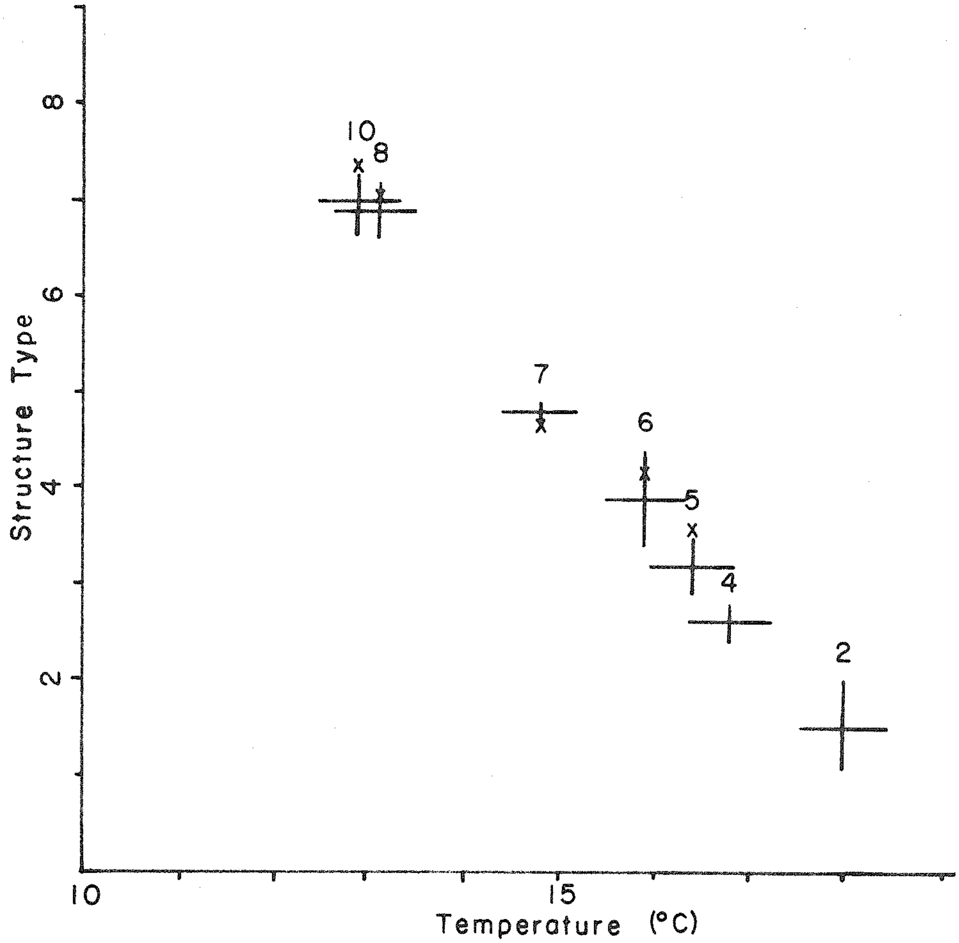

Figure 35. - Variation of mean structural type with mean annual temperature of collecting locality. The vertical bars represent the standard error of the mean. The x's are means for shells greater than 50 mm. in length. The numbers above the points are station numbers taken from fig. 1.

relationship between the nacreous and inner prismatic layers is often possible. Thus a generalized interpretation of growth rate can be made. Finding a method of expressing growth rate quantitatively presents a problem. As shown in fig. 9 above, the log of age plotted against length of M. californianus from La Jolla forms a straight line for the greater part of the range. If this relationship holds at all locations, points of log age vs. length plotted for mature specimens can be used to characterize growth rate for the whole range of sizes.

Figure 36 shows such a graph for a number of stations. Data from Avila Beach and Port Hueneme give growth rates essentially the same as that at Pacific Grove. These data were not included in fig. 36 in order to avoid a confusion of points. The La Jolla results of Coe and Fox (1942) and the results from the Corona del Mar growth series described above have also been plotted for comparison.

The relationship of decrease in growth rate with increase in latitude shows clearly. Fox and Coe (1943) have indicated that growth rate in M. californianus is probably greater in southern latitudes than farther north. This relationship has been found in many other species and is apparently related to the greater rate of biological activity at higher temperatures (Allee et al., 1949). If this relationship holds, a correlation should exist between mean annual temperature at a given locality and the growth rate. This correlation may be greatly modified by other factors such as variation in intertidal exposure time, food supply, oxygen tension of the water, and possible variation in many other ecological factors. Swan (1952) discusses a number of factors such as temperature, salinity, food supply, nature of

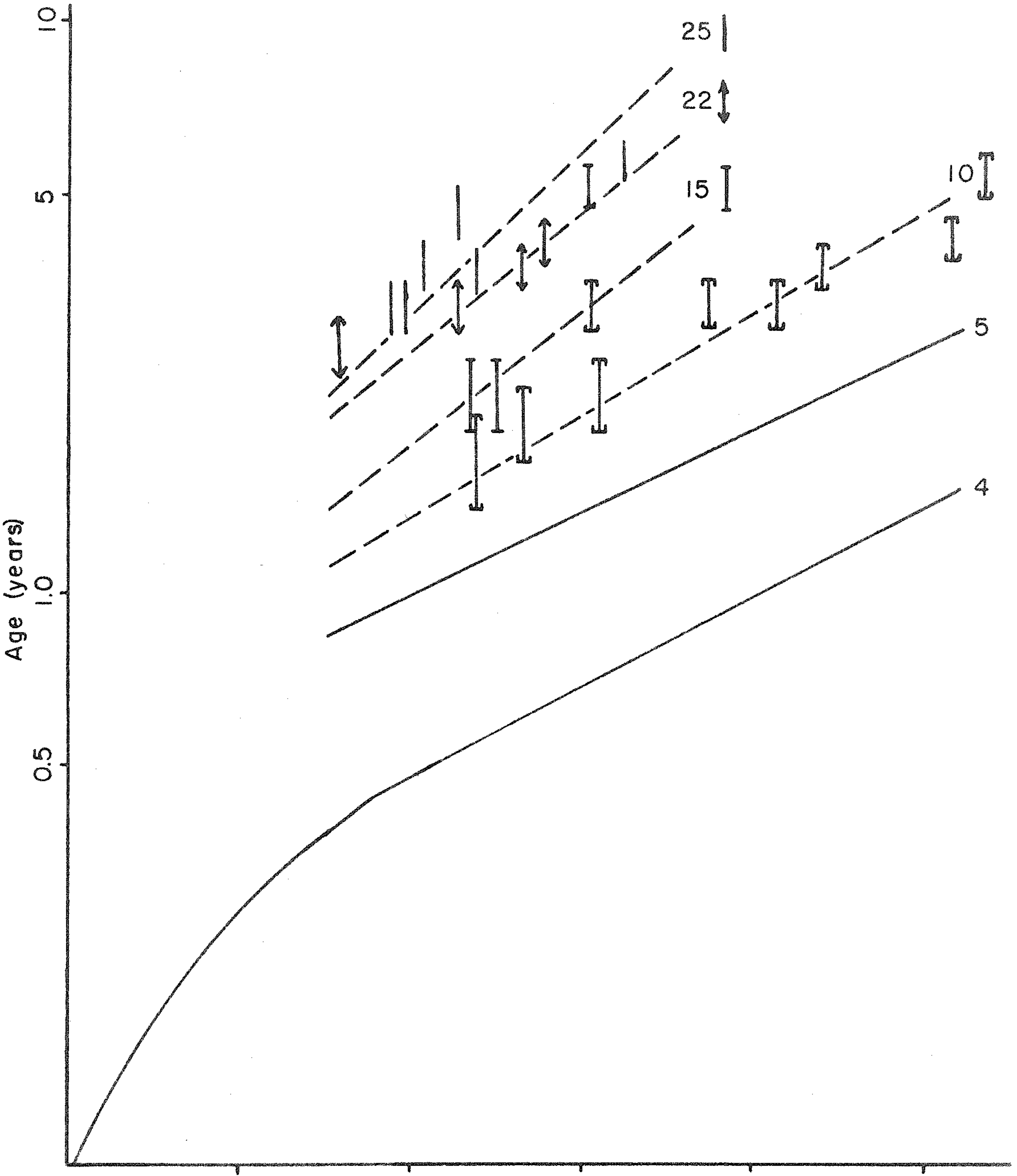

Figure 36. - Growth rate of M. californianus at selected stations. The vertical bars indicate the uncertainty in the age determination. The lines were drawn by sight to best fit the data. The numbers at the right end of the lines are station numbers taken from fig. 1. Following the station number is the symbol used for that station. The lines from fig. 9 are included for comparison.

the substrate, and amount of dissolved oxygen which might affect the growth rate of pelecypods.

The limitations of this study of growth rates should be borne in mind. It is impossible to determine the age of a specimen of *M. californianus* more precisely than a half year. A mistake of one year in the age can be made if a color zone or nacreous wedge is not developed for a particular year. Growth rate is not necessarily the same for all individuals at a given locality. To obtain an accurate estimate of mean growth rate, larger samples would be needed. Factors other than temperature may be operating to affect growth rate. This may explain the fact that the Pacific Grove rate is not lower than that at Avila Beach and Port Hueneme although the Pacific Grove temperature is lower. The results for the growth rate at Pacific Grove are similar to that suggested by Richards (1928) for that location.

Structural Variation in *M. edulis diegensis* and *M. edulis edulis*

The variations in shell structure discussed above apply only to *M. californianus*. No great variation in structure is found in the subspecies of *M. edulis*;although percent aragonite in longitudinal section does vary in the same general manner as the x-ray determined percent aragonite. As noted in the first section, northern specimens have more calcite in the beak area than southern specimens (Plate VIa and b, Appendix II, p. 220). No intermediate forms between these end members have been found. This suggests that this difference in structure is a subspecific difference. All specimens examined from San Francisco and further south had the beak structure which seems to be characteristic of *M. edulis diegensis*. Those from the Pacific northwest appear to have the beak structure characteristic of *M. edulis edulis*. Before the rapid spread of *M. edulis diegensis* in the early 1940's, the southern limit of abundant numbers of *M. edulis edulis* was in San Francisco Bay. The present subspecies there apparently is *M. edulis diegensis* (at least all of those specimens examined from that area in this study were *M. edulis diegensis*). This suggests that a radical change of the makeup of the *M. edulis* population had occurred in the San Francisco Bay area. To check this, a museum specimen of *M. edulis* collected before 1940 from San Francisco was sectioned. It showed the characteristic beak structure of *M. edulis edulis*. A more extensive study of this species in the San Francisco Bay area may prove to be informative. Perhaps both subspecies are still present in separate places in the area. Perhaps some very old specimens of *M. edulis edulis* still live in the bay but no young individuals. Apparently *M. edulis diegensis* is for some reason better adapted for this environment and has filled the niche formerly occupied by the other subspecies. A study of shells collected at various times since the 1940's (if such collections exist) would be useful in studying the rate of this change.

Growth rates in *M. edulis edulis* and *M. edulis diegensis*

The small inner calcitic wedge in *M. edulis edulis* sometimes intertongues with the nacreous layer. This apparently is the same relationship as in *M. californianus* with the aragonitic projections representing summers. Not enough sections showing this relationship are available to make a detailed study of growth rates. The San

Francisco specimen of *M. edulis edulis* mentioned above, which is 53.5 mm. long, was apparently at least two years old. One of the Washington specimens which is 32.8 mm. long appears to be approximately three years old. This would indicate a slower growth rate at lower temperature just as in *M. californianus*. Both of these rates are slower than the 76 mm. for the first year found by Coe (1945) for *M. edulis diegensis* from La Jolla. The San Francisco rate is slower than that suggested by the growth series for *M. edulis diegensis* from Avila Beach.

STRONTIUM AND MAGNESIUM CONTENTS

Literature Review

The amount of magnesium and strontium in certain types of invertebrate shells has been shown by various workers to be temperature dependent. Clarke and Wheeler (1922) first demonstrated apparent variation in Mg content with temperature. Chave (1954) made a more detailed study of this variation in all major marine invertebrates. He noted that the Mg content was dependent on three factors: mineralogy, temperature, and phylogenetic level of the organism. Mg is more readily accommodated in the calcite than in the aragonite structure. Within a given group of organisms, a positive correlation exists between Mg content and temperature of growth. In general, organisms of lower phylogenetic level have a higher Mg content. In at least one group, the brachiopods, Lowenstam (1959) has found that, at a given temperature, a positive correlation exists between Mg content and the salinity of the water in which the organism grew. Pilkey and Hower (1960) made a study of the Mg and Sr content of the echinoid Dendraster. They found a positive correlation between Mg content and both temperature and salinity.

Until relatively recently, only scattered analyses of Sr content of invertebrate shells have been made. Many of these analyses have been compiled by Vinogradov (1953). More recently, several comprehensive studies of Sr in shells have been made. Odum (1950, 1951a, 1951b, 1956a) has shown that the Sr content of shells is largely dependent on the Sr/Ca ratio of the water in which they grew, Sr/Ca of the shell being directly proportional to Sr/Ca of the water. He also demonstrated a mineralogic effect, the Sr content of aragonite being higher on the average than the Sr content of calcite. This effect does not seem to be as pronounced as the mineralogic effect on the Mg content. Sr content is also dependent on the taxonomic position of the organism but not in the regular manner of the Mg content. Swan (1956) interpreted some of the data of Thompson and Chow (1955) as indicating that relatively faster growth rates within a species result in relatively lower amounts of Sr in the shells. Odum as well as several other workers including Kulp et al. (1952), Thompson and Chow (1955) and Krinsley (1960) looked for a variation in Sr content with temperature but found none. Turekian (1955) attempted to demonstrate that the Sr content of fossils was salinity dependent but did not directly do so. Lowenstam (1959) demonstrated that a positive correlation exists between the Sr content of brachiopod shells and both temperature and salinity. Pilkey and Hower (1960) showed a negative correlation between temperature and the Sr content of Dendraster. The Sr content of Dendraster is apparently independent of the salinity of the water in which it lived.

Several workers have investigated the Sr content of fossils to determine if a variation in Sr exists which would indicate changes in the Sr content of the oceans with time (Odum, 1951b; Kulp et al., 1952; Bowen, 1956a and b; Turekian and Kulp, 1956; and Lowenstam, 1959). The most recent evidence indicates that the Sr content of the oceans has been constant since the Mississippian (Lowenstam, 1959).

Spectrographic Techniques

Preliminary work on the Mg and Sr content of Mytilus was done by emission spectrography. Twenty-five mg. portions of the samples were dissolved in a 1% solution of HCl. An ammonium molybdate internal standard was added. The solutions were allowed to stand overnight before being diluted with 1% HCl to exactly 25 ml. Standard amounts of the solution were placed on copper electrodes and allowed to dry under infrared heat lamps. At least five electrodes were loaded with each sample. Standard amounts of a series of nine standard solutions ranging in value from 0.01 to 4.64 wt. % Mg and Sr were also placed on copper electrodes. The samples were then excited for 30 seconds by a D. C. spark in a Jarrel Ash emission spectrograph.

Percent transmission of light by the Mg 2803, Mo 2848, Mo 3903, Sr 4078, and Sr 4216 lines was determined. The percent transmission values were converted to intensities. The ratio of intensity of the Mg line to intensity of the Mo line on the same plate and intensity of the Sr lines to intensity of the Mo line on the same plate was determined for samples and standards. Working curves were made from the ratios and amounts of Mg and Sr for the standards. Values for the samples were taken from these curves.

The error of spectrographic methods is usually assumed to be approximately ± 10%. The standard deviation of six values for the Mg determinations is approximately ± 10% of the mean. The Sr determinations are considerably more precise with a standard deviation of approximately ± 5%. The uncertainty shown on the graphs of spectrographic data is the standard deviation of the determinations.

The spectrographic determinations give weight percent Mg and Sr. Weight percents of the elements were converted to weight percents of the carbonates. Mole percents of the carbonates were then determined from graphs of the functions:

$$\text{mole \% } SrCO_3 = \frac{\dfrac{\text{wt. \% } SrCO_3}{147.64}}{\dfrac{\text{wt. \% } SrCO_3}{147.64} + \dfrac{100\text{-wt. \% } SrCO_3}{100.09}} \times 100$$

$$\text{mole \% } MgCO_3 = \frac{\dfrac{\text{wt. \% } MgCO_3}{84.33}}{\dfrac{\text{wt. \% } MgCO_3}{84.33} + \dfrac{100\text{-wt. \% } MgCO_3}{100.09}} \times 100$$

Each of these functions assumes that the sample is composed entirely of the carbonates of that trace element and calcium. The error caused by the fallacy of this assumption is small and within the uncertainty of the measurement.

Seasonal Variation in Strontium and Magnesium Content of the Outer Prismatic Layer of *Mytilus*

Analyses were made of samples of *M. edulis diegensis* collected at varying times of the year from one locality, the Kerckhoff Marine Laboratory in Newport Bay at Corona del Mar.

The outermost one or two mm. of the calcitic outer prismatic layer was clipped from the sample so that only a few days growth immediately preceding the collecting time was represented. Small specimens (9-16 mm. in length) were used in this series. After the samples were clipped from the shells (several shells were used for each sample) they were placed in Clorox to remove as much organic material as possible. This treatment did not completely remove the protein matrix between the crystals. Weighing of acid insoluble residues indicated that 2% organic material remained in the treated samples. This small amount is within the analytical error of the technique so it was ignored.

The contrast between summer and winter temperatures is greater in bays than along the open coast. The temperature in the shallow water of the bay may be raised considerably above that of the open coast in the summer. The bay water may likewise be cooled to a greater extent in the winter. Since the specimens are intertidally exposed, they grow only at high tide when the water temperature may be different from the average of all tidal heights.

Figure 37 shows the variation of mole percent $MgCO_3$ with collecting date of the samples. The $MgCO_3$ content clearly shows a seasonal variation. The maximum value in late September and the minimum value in February correspond with the times of maximum and minimum temperatures at this locality. $MgCO_3$ content thus correlates with temperature at this locality. The salinity here is nearly constant throughout the year. Variation in this factor can be ruled out as a cause of variation in the $MgCO_3$ content. The value for April of the first year is much higher than expected. The reason for this is not known.

The variation in mole percent $SrCO_3$ with collecting date is shown in fig. 38. The $SrCO_3$ content also varies with temperature.

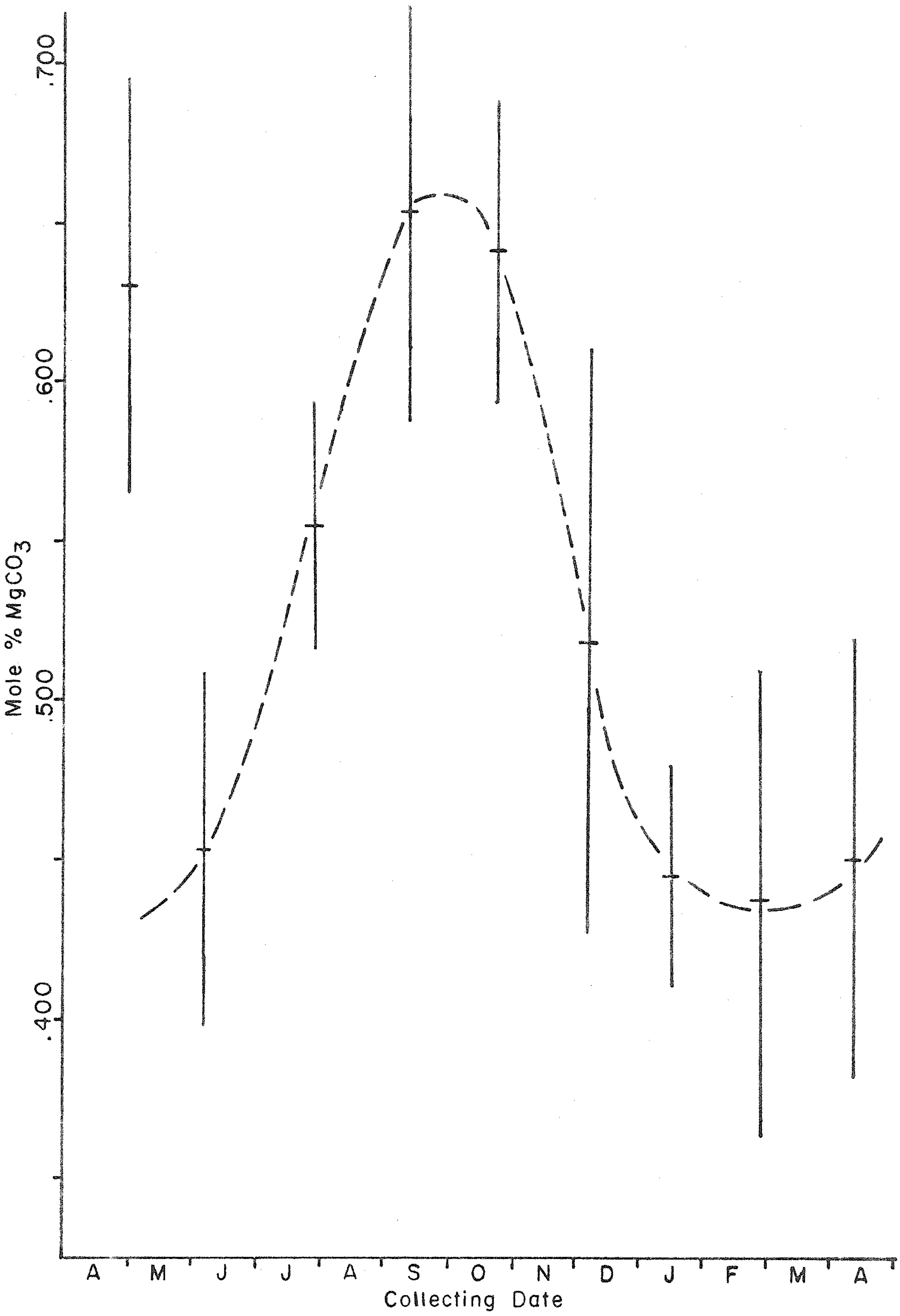

Figure 37. - Variation with collecting date of mole percent $MgCO_3$ in the calcite rims of M. edulis diegensis from Corona del Mar.

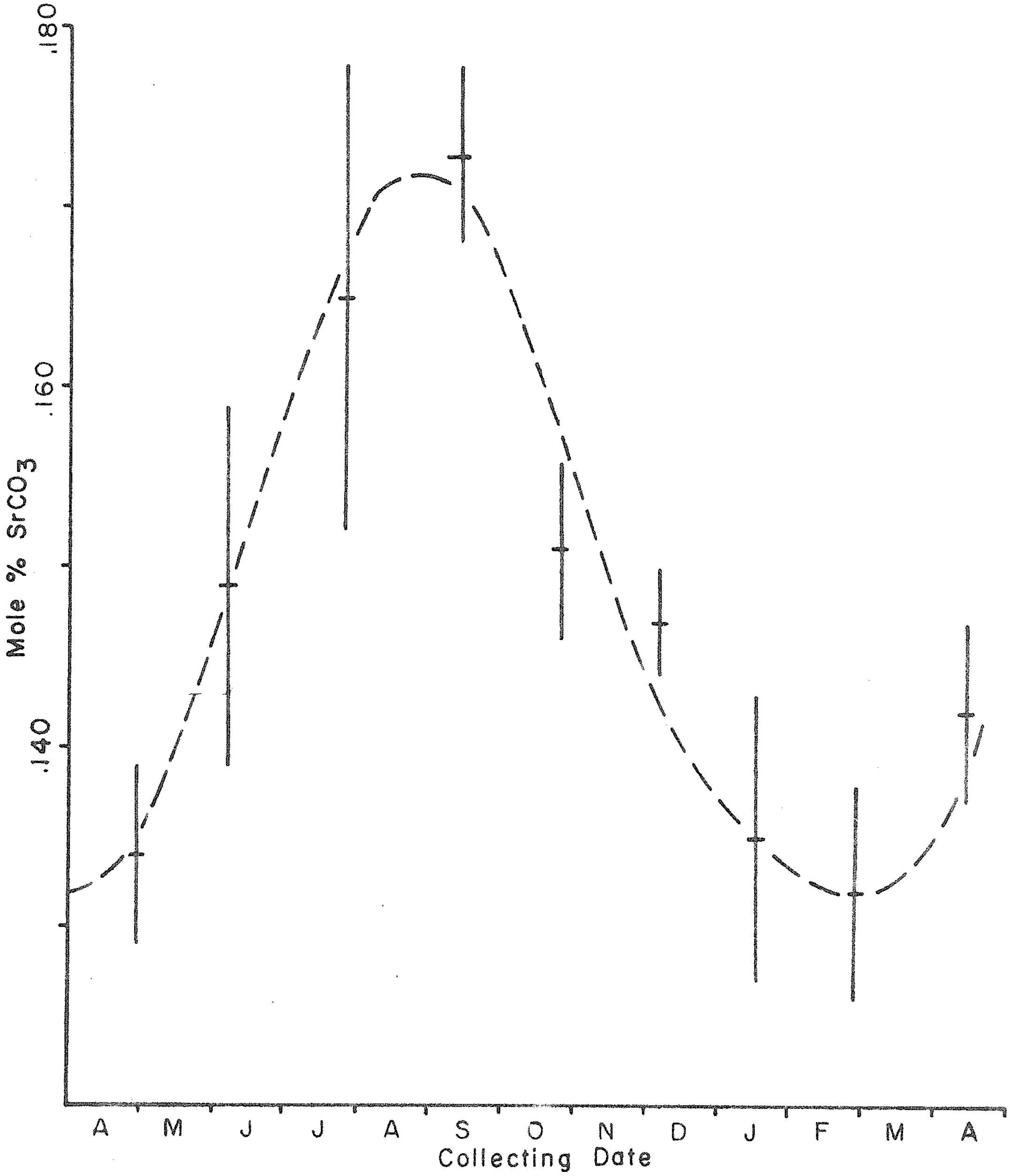

Figure 38. - Variation with collecting date of mole percent $SrCO_3$ in the outer calcite rims of M. edulis diegensis from Corona del Mar.

The two curves match in general terms although not in some details. One reason for this is the greater precision of the analyses for Sr. Some of the minor irregularities shown in the $SrCO_3$ graph may be hidden by the experimental error in the $MgCO_3$ graph. The variation in $MgCO_3$ content in both absolute and percentage terms is greater than the variation in $SrCO_3$. None of the $SrCO_3$ values differs significantly from the expected.

Correlation between Temperature and Spectrographically Determined $MgCO_3$ and $SrCO_3$

Percent $SrCO_3$ and $MgCO_3$ was plotted against the mean temperature for one week at the collecting time. When the data were available, this was for the week preceding the collecting date. In other cases it is for the week following or including the collecting date. These temperatures are uncertain. They were obtained from a recording thermometer in a 15 gallon aquarium through which water continuously circulated. This water was pumped from the bay into a large storage tank from which it circulated through the aquariums. The water in the storage tank may warm slightly in the summer or cool in the winter according to the atmospheric temperature.

The temperature recorded at the Laboratory varies considerably with the tidal cycle. The Laboratory is located near the mouth of the extensive, shallow Newport Bay. The water in the shallow upper reaches of the bay is heated considerably. When the tide goes out, this warm water flows out of the upper bay, raising the temperature in the lower Newport Bay. When the high tide comes in, it brings cool, open ocean water and pushes the warmer water back into the upper bay. The magnitude of this effect can be readily observed by recording the temperature on the bay and open ocean side of one of the breakwaters at the mouth of the bay. On the morning of July 9, 1958, the temperature on the bay side was 20.8°C and on the ocean side, 15.5°C, a difference of 5.3°C. Temperature differences recorded in the laboratory within a 12 hour period are as great as 2.5°C but are often considerably less.

Particularly considering all the uncertainties in the temperatures, the points in fig. 39 for mole percent $SrCO_3$ vs. temperature fall remarkably close to the curve. The curve was drawn by sight to best fit the data. This curve has the same general shape as the curve for mole percent $SrCO_3$ vs. temperature in brachiopods (Lowenstam, 1961) although the absolute values differ. A similar plot for $MgCO_3$ (fig. 40) shows a poorer correlation of $MgCO_3$ with temperature. The sight curve is problematical, but it also has a shape similar to the curve for mole percent $MgCO_3$ vs. temperature in brachiopods (Lowenstam, 1961). This shows a low correlation of $MgCO_3$ with temperature at relatively lower temperatures but a marked correlation at higher temperatures. The poor fit of the $MgCO_3$ temperature curve is in part due to the poor precision of the technique as well as the uncertainty of the temperature data. The shape of the two curves for $SrCO_3$ and $MgCO_3$ suggests that $SrCO_3$ determinations may be more useful for paleotemperature studies. Temperatures above 20°C are uncommon except in the extreme southern part of the range of this study and in embayments. Below this temperature, the slope of the $MgCO_3$ curve may be too low to

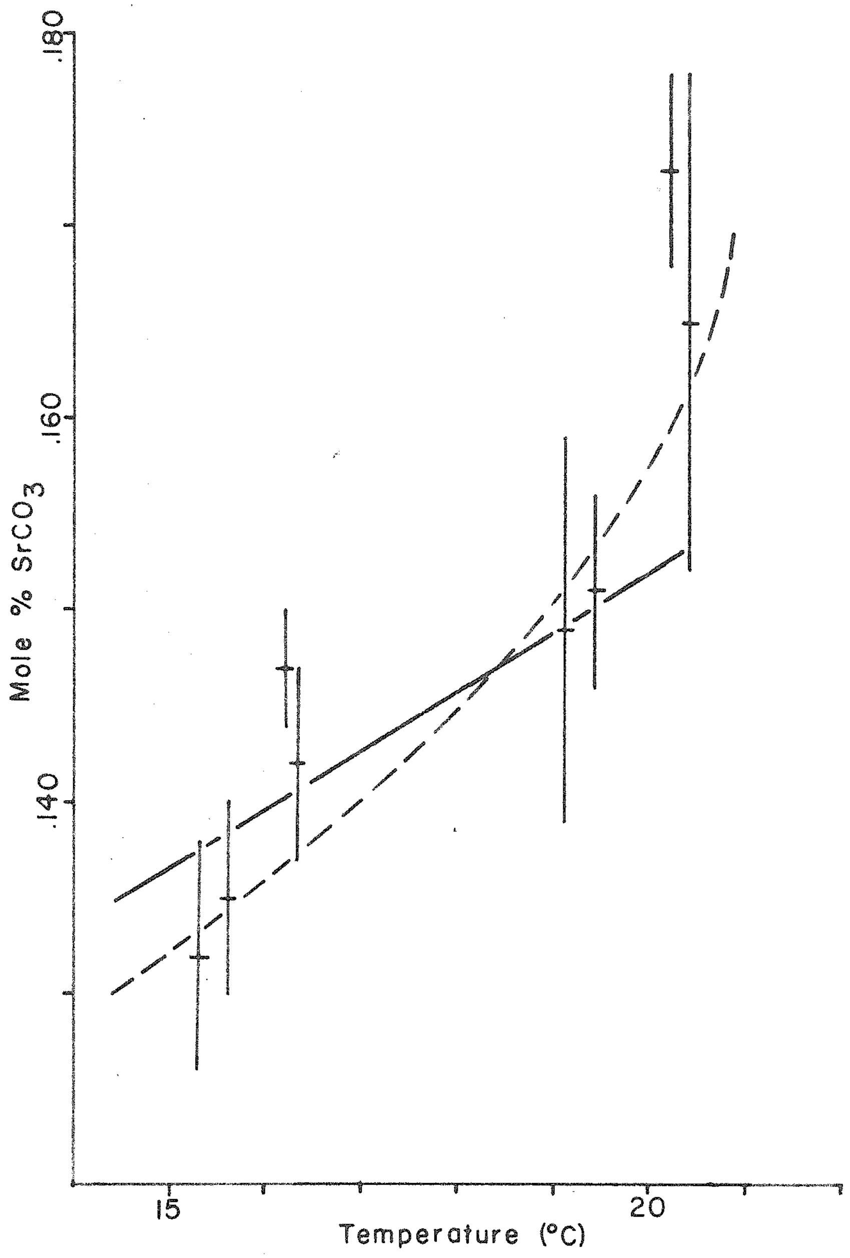

Figure 39. - Variation with estimated mean temperature for two weeks at collecting time of mole percent $SrCO_3$ in the outer calcite rims of *M. edulis diegensis*. The straight line is taken from fig. 42.

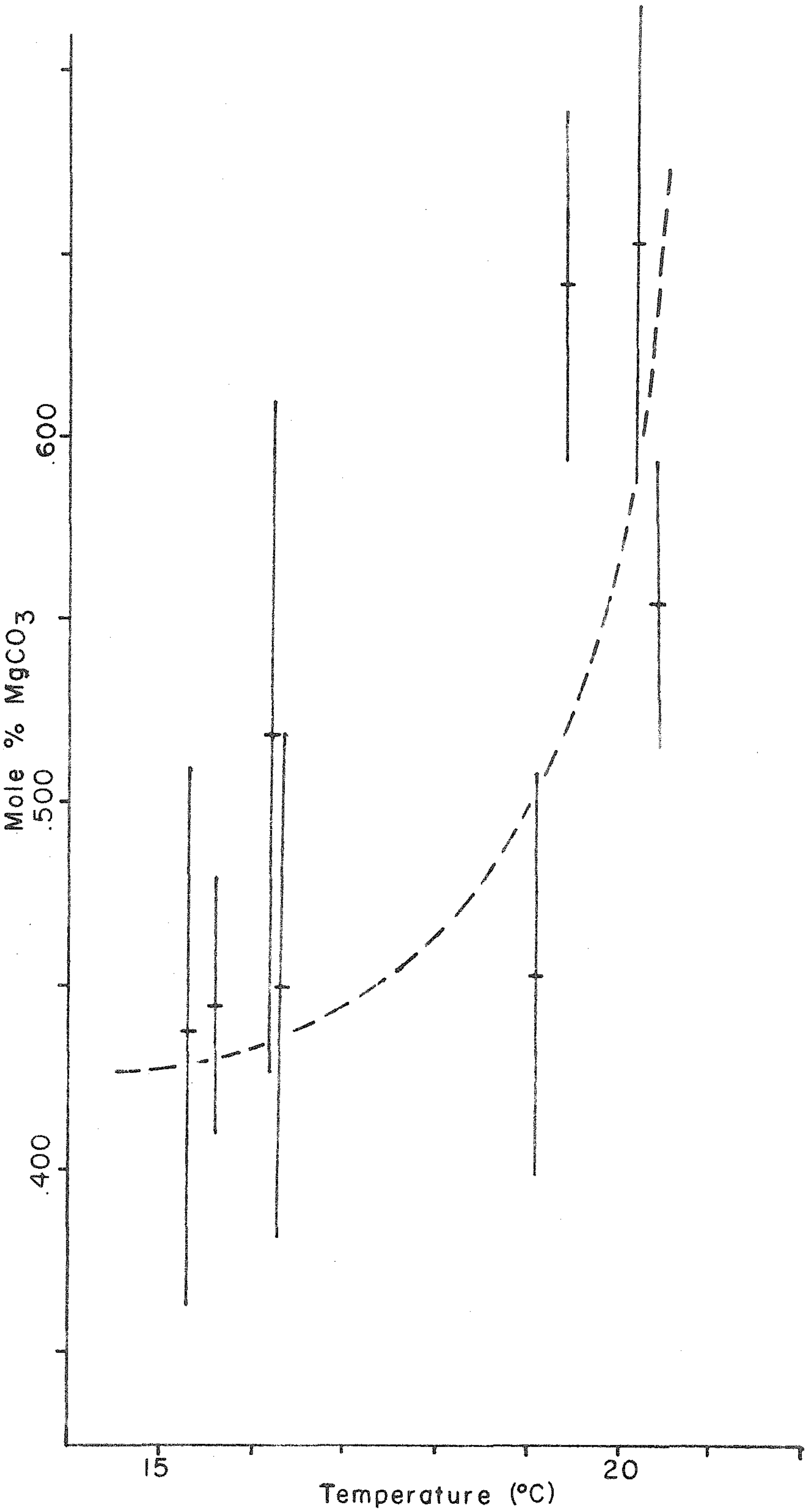

Figure 40. - Variation with estimated temperature for two weeks at collecting time of mole percent $MgCO_3$ in the outer calcite rims of *M. edulis diegensis*.

be of much use, even with a more precise method of analysis.

X-ray Fluorescence Analysis Technique

Due to the low level of the variation of $SrCO_3$ content of the outer prismatic layer, a more precise technique of analysis than emission spectrography is desirable. An x-ray fluorescence technique was developed which gave considerably greater precision than emission spectrography.

Samples were prepared by clipping or grinding with a dentist's drill portions of the outer prismatic layer parallel to the growth lines. These samples were ground in an agate mortar. The sample was packed into an opening a quarter inch in diameter in an aluminum sample holder. The sample was placed in the x-ray beam of a modified North American Phillips x-ray fluorescence spectrometer set at 50 kv. and 35 ma. The $K\alpha_1$ radiation of the Sr was measured by a flow proportional counter. No correction was made for background. One hundred thousand counts were taken on each sample and the times converted to counts per second.

A series of standard samples ranging in value from 0.12 to 0.78 weight percent Sr was run six times. The standards were shell samples which had been repeatedly analyzed for Sr content. The values for the standards are not as accurately known as desirable. This limits the accuracy of the technique, but the precision is nevertheless high. Therefore, the results obtained from these analyses are internally consistent although analysis with other standards or by other techniques might give quite different absolute values. To minimize the effect of gradual changes in the stability of the machine, a standard was run between each sample. A correction determined from average reading for the standard run before and after the sample was added or subtracted to the reading for the sample.

Subtracting background from standards and samples did not increase precision. Taking the ratio of Sr to Ca intensities gave poorer results.

A lower limit exists to the size of a sample which can be analyzed by this technique. Figure 41 is a plot of the weight of sample used against the difference in counts per second between the sample and a standard. A decrease in the difference for samples below the 35 mg. size indicates a decrease in the apparent amount of Sr in the sample. Thirty-five mg. was thus set as the minimum sample size for these determinations. Most samples weighed at least 50 mg. Three separate packings of most samples were run, in some cases only two.

Separate packings of one sample were run 20 times over a period of six months. The mean of all these runs was 0.117 wt. % Sr with a standard deviation of 0.0017. The precision of the method is probably better than this would indicate. Many of these packings were run before certain details of the technique were established. This sample was usually the first run of a group of samples, and the machine may have on occasion not been thoroughly warmed up. For example, five packings of one sample run under more ideal conditions gave a mean of 0.115 wt. % Sr with a standard deviation of 0.0005. The precision of the analyses done later in the study was better than those done earlier. The uncertainties shown in the graphs are the standard deviations of

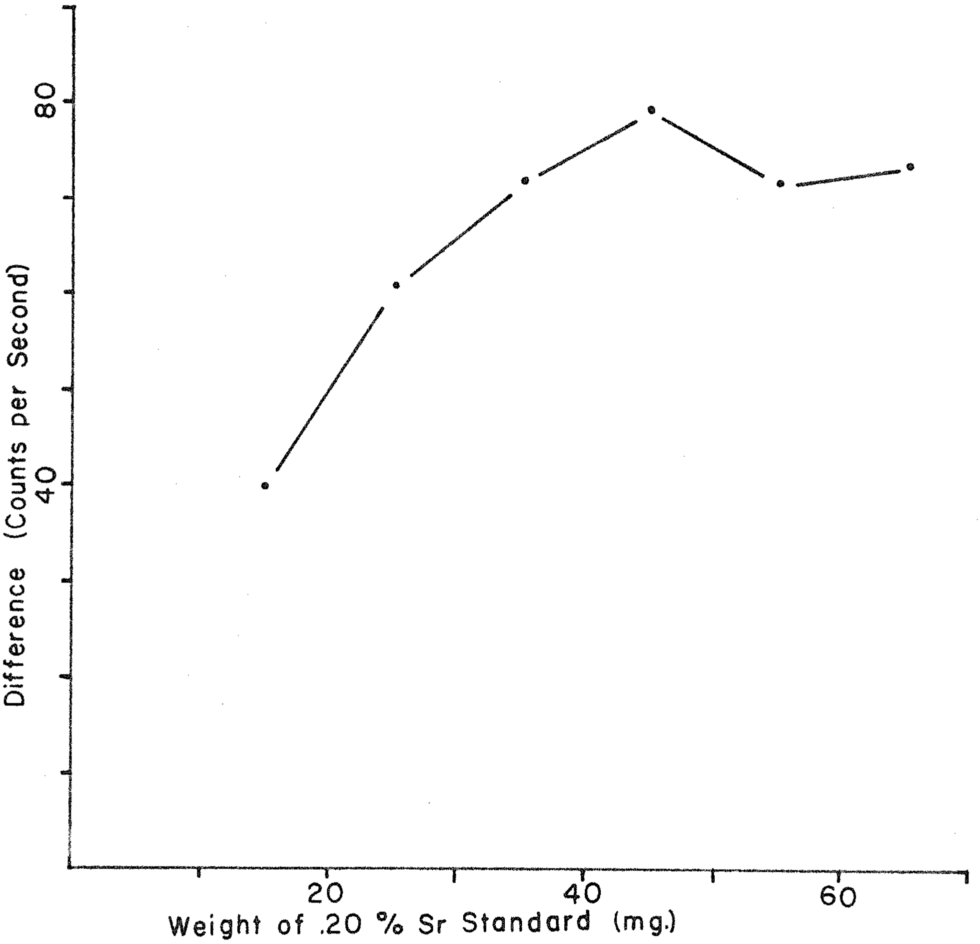

Figure 41. - Effect of sample size on x-ray fluorescence analyses of Sr content. The abcissa shows the weight of portions of the 0.20% Sr standard used. The ordinate shows the difference in counts per second between the 0.20% Sr samples and the 0.12% Sr standard.

the runs on that particular sample to the nearest thousandth of a percent. In those cases where the standard deviation was less than 0.0005, an uncertainty of 0.001% was arbitrarily assigned.

The precision of this technique was high enough that the 2% organic material in some of the samples could affect the results. As the blue color characteristic of the organic portion of the outer prismatic layer of Mytilus disappeared after short exposure to the intense x-radiation, it was assumed that the organic material was destroyed in the process. No change in the intensity of the fluorescence of the sample with time was noted; apparently the presence of a small amount of organic material does not affect the results.

Correlation between Temperature and $SrCO_3$ as Determined by X-ray Fluorescence

In order to establish a scale of variation of $SrCO_3$ content with temperature, samples were selected from several stations with normal salinity and where detailed temperature data were available. Three to three and one-half mm. of the edges of the outer prismatic layer of several individuals averaging approximately 20 mm. in length were used.

No difference was noted in the $SrCO_3$ content of the outer prismatic layer between M. californianus and the two subspecies of M. edulis which were collected at the same place and time. Both species were used in determining the relationship of $SrCO_3$ content to temperature.

Figure 42 is a plot of mole percent $SrCO_3$ against the average temperature for the preceding half month. This should represent the approximate time required for the outer rims to grow. The uncertainty

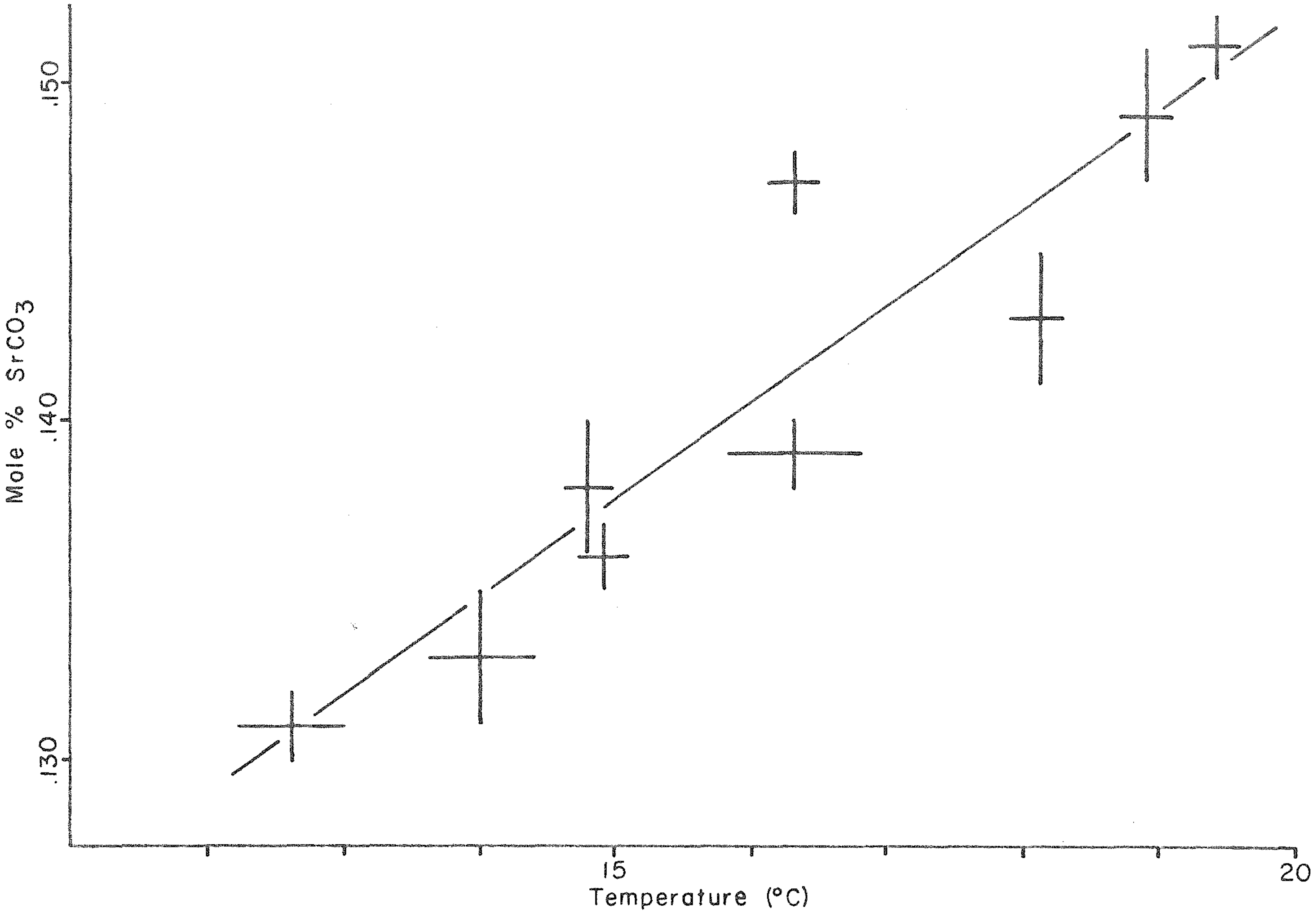

Figure 42. - Variation with temperature of mole percent $SrCO_3$ in the outer prismatic layer of *Mytilus*.

in the temperature shown in the graph is an estimate of possible error in determining the averages. The correlation coefficient for these data is 0.916. The equation of the least squares line is:

$$\text{mole \% } SrCO_3 = 0.0028 \times \text{temperature } (^{\circ}C) + 0.096.$$

This line is compared with the spectrographic data in fig. 39. The temperature data used with the fluorescence samples are better than those used for the spectrographic samples. No samples with good temperature data were available in the higher temperature range to determine if the upward inflection suggested by the spectrographic curve occurs.

A larger number of samples for the temperature vs. mole percent $SrCO_3$ curve would have been desirable. Using material from specimens grown in the aquariums was originally planned. However, sufficient amounts of this material for use with the fluorescence technique were not available.

A series of five samples from the open coast at Corona del Mar was analyzed with the intent of including them in the temperature-mole percent $SrCO_3$ graph. The results for these (Table 16, Appendix I, p. 205) proved to be completely inconsistent with the results from samples from other stations. Inclusion of these samples in the graph would appear to largely invalidate the concept of temperature control of $SrCO_3$ content. All other evidence indicates that $SrCO_3$ content is clearly related to temperature. Exclusion of these anomalous results therefore seems justified. No explanation can be offered as to why these samples do not conform to the usual pattern. Since these samples did give anomalous results, the possibility that this is not an isolated case should be considered in making temperature interpretations from $SrCO_3$ content.

Effect of Shell Size on $SrCO_3$ Content

Figure 43 shows the mole percent $SrCO_3$ in the outer rims of shells of M. californianus of various sizes collected in late October from Santa Monica. Narrower rims were taken from larger shells to take the slower growth rate of larger individuals into consideration. The $SrCO_3$ content decreases with increasing size of the individual. The total decrease is slightly less than 5% of the value for the 23 mm. individuals. The amount of decrease in shells of 70 to 90 mm. in length from two other locations is 4%.

The reason for this decrease can only be speculated on at this stage. It may result from the slower growth rate of larger individuals. This interpretation may explain the entire temperature effect on $SrCO_3$ content. Temperature may directly affect the growth rate and only indirectly the $SrCO_3$ content of the outer prismatic layer. This may explain the two points in fig. 42 which fall considerably off the curve. The point falling on the low side is for thicker than average shells, suggesting a possible slow growth rate; and the point falling on the high side is for shells thinner than average, suggesting a possible fast growth rate. Some factor other than temperature may have caused this variation in growth rate. One method of checking this interpretation would be to vary the growth rate of individuals grown in aquariums by varying the amount of food while keeping the temperature constant.

This interpretation is opposite that of Swan (1956), who suggested a negative correlation between Sr content and growth rate. Swan was

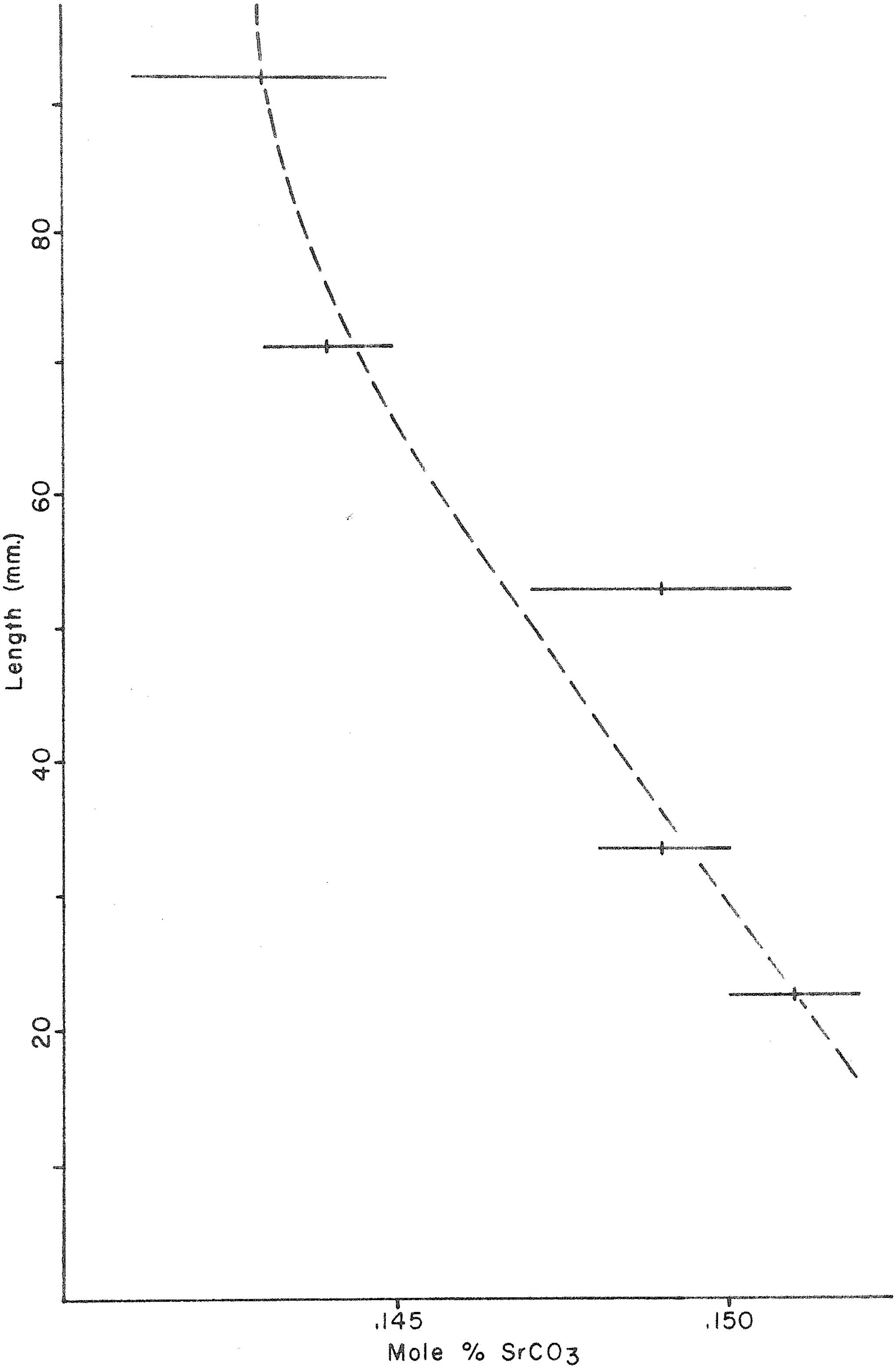

Figure 43. - Variation with length of specimen of the $SrCO_3$ content of the outer prismatic layer. All samples grew at the same temperature.

handicapped in his interpretation by the fact that total shells were used. Two of the species used by Swan in his interpretation are forms containing both calcite and aragonite. The thicker shells which he indicates are representative of slow growth rate possibly contained a relatively larger amount of aragonite. Aragonite usually contains a larger amount of $SrCO_3$ than the calcite.

Before $SrCO_3$ content can be used to estimate temperatures of growth, a method must be devised to take differences in size into consideration. Temperatures taken from the curve in fig. 42 for 70 to 90 mm. individuals would be almost two degrees too low. Figure 44 shows an idealized approach to this problem. The solid line is the least squares line from fig. 42. The broken lines have been moved over percentage-wise in accordance with the apparent linear trend of decrease in $SrCO_3$ content with increase in size shown by fig. 43. The scatter of points about the least squares line makes this approach applicable only in a generalized way.

The limitations of this technique for estimating shell deposition temperatures must be borne in mind. The original curve is based on a limited number of samples. Some uncertainty exists about the exact temperature at which the analyzed shell portions grew, perhaps more uncertainty than is indicated in the graph. The scatter of at least two of the samples is too great to explain as due to temperature, thus some other factor (perhaps growth rate) must be affecting the $SrCO_3$ content of the shells. The one group of specimens which grew at known temperatures fell far off the curve for some unknown reason. With all these uncertainties, it is apparently not possible to estimate

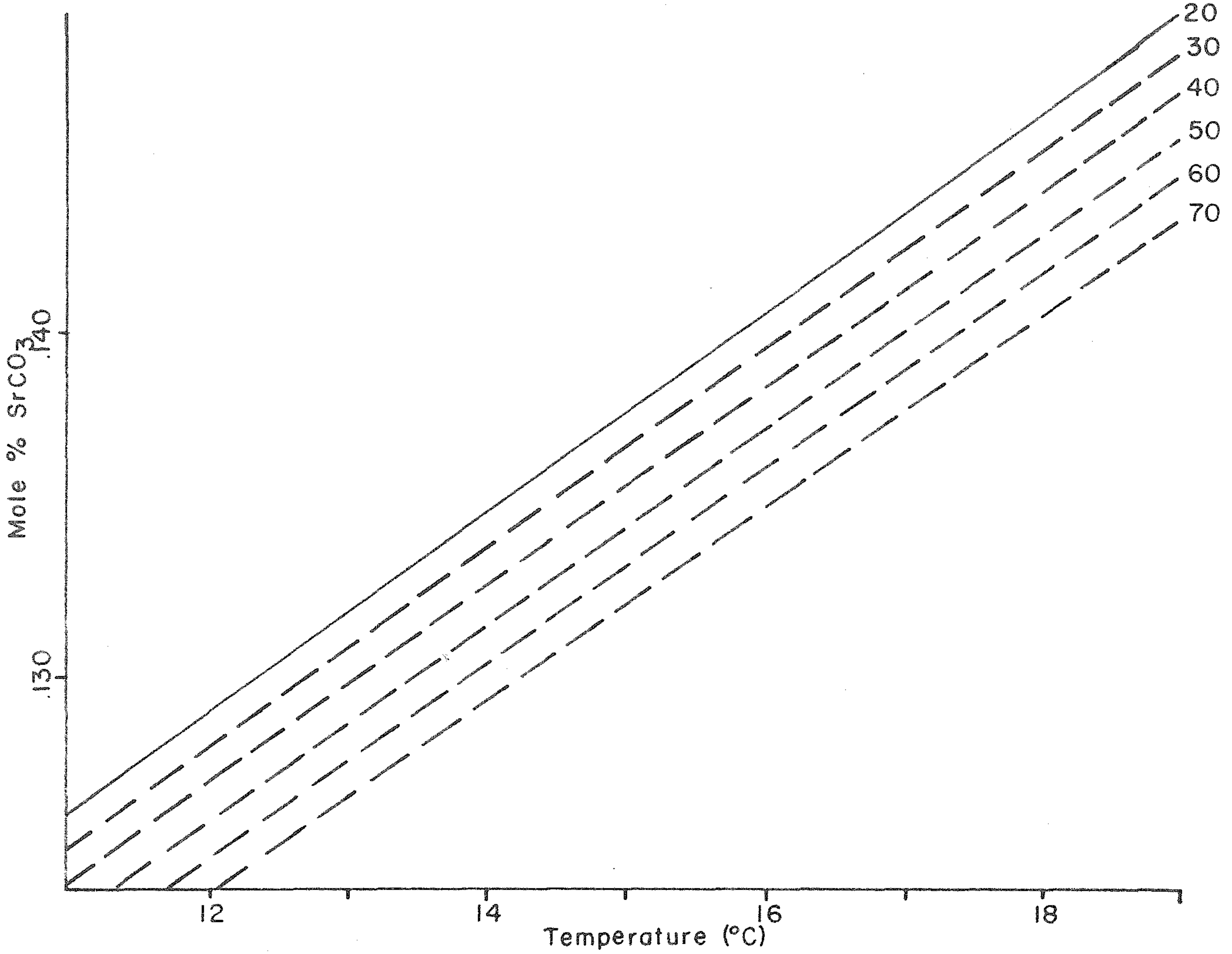

Figure 44. - Idealized representation of the relationship between $SrCO_3$ content and temperature in *Mytilus*. The solid line is taken directly from fig. 42. The dashed lines represent individuals of differing sizes. The numbers at the right ends of the lines are the lengths of specimens represented.

temperature of shell deposition from the $SrCO_3$ content better than ± 1°C. Occasional samples may give even less accurate results than this. In the following discussions when temperatures are estimated from $SrCO_3$ content, an uncertainty of ± 1°C is implied.

Variation of $SrCO_3$ Content with Salinity

Samples of M. edulis edulis were collected from the Hood Canal area of Washington and M. edulis diegensis from the San Francisco Bay area. The samples were prepared in the same manner as those for the temperature study. The samples from the Hood Canal were excellent for this purpose because temperature was apparently nearly constant at all stations. Specimens used for these analyses came from the same stations discussed above in considering the effect of salinity on shell mineralogy. Figure 45 shows the results of the Washington analyses. The values do not differ greatly. They have a random scatter with no trend noted with salinity. Variation in the values is probably entirely due to the temperature effect. As mentioned above, the temperatures at these stations depend to a large extent on the time of day (highest temperatures occurring in the mid-afternoon and lowest in early morning). Temperatures varied from 13.7 to 25.0°C at collecting time. Shell growth temperatures of 17-19°C suggested by the $SrCO_3$ content are reasonable.

The results for the two samples from the San Francisco area are not so clear.

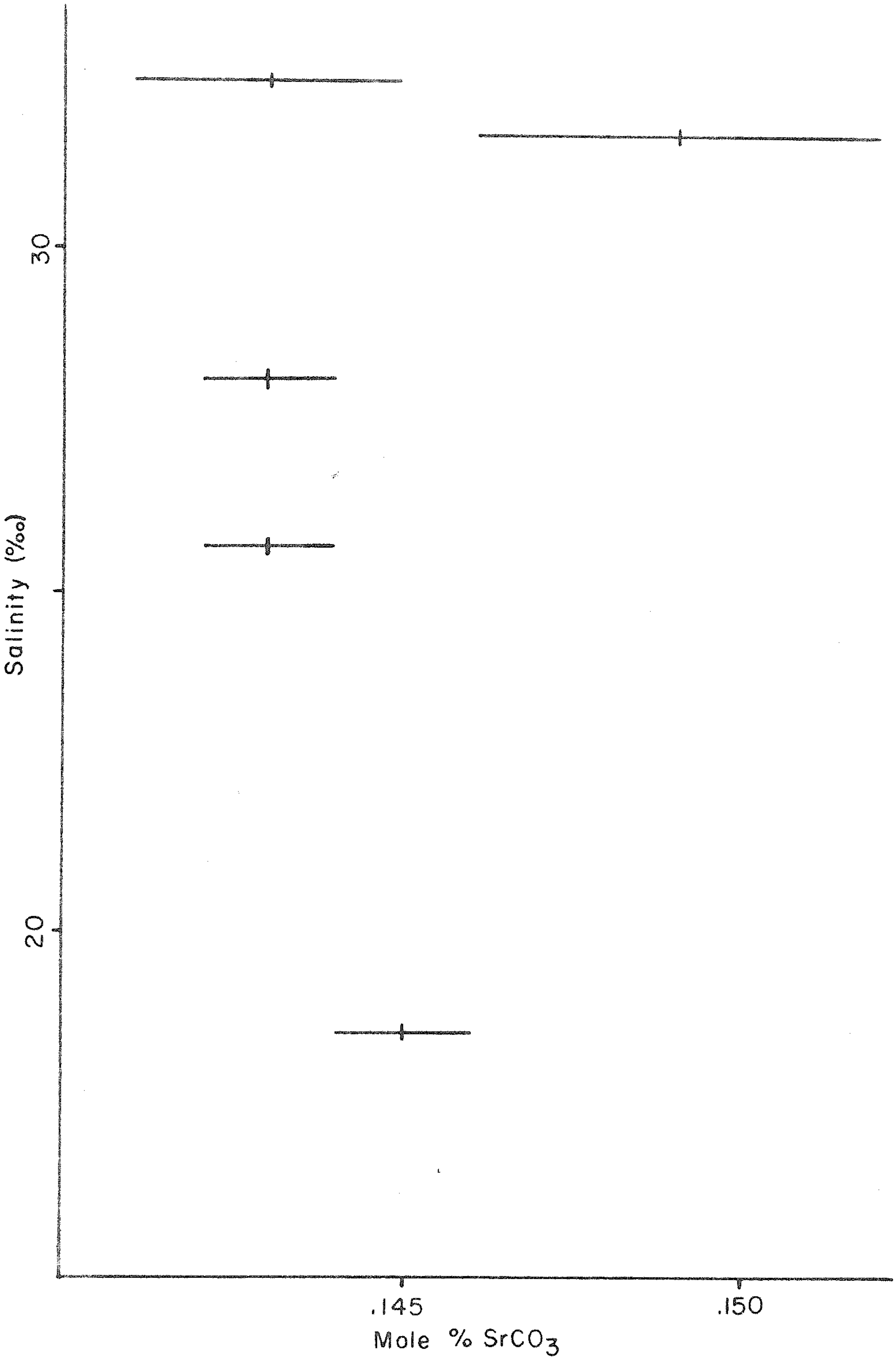

Figure 45. - Variation with salinity in mole percent $SrCO_3$ in the outer prismatic layer of M. edulis edulis.

Location	Salinity at Collecting Time	Temperature at Collecting Time	Mole % $SrCO_3$
Sausalito	28.75	16.1	0.131
China Camp	19.96	22.5	0.148

The $SrCO_3$ content of the samples appears to increase with decrease in salinity, but temperature is higher at the low salinity station so it is not possible to determine with certainty what causes the change in $SrCO_3$ content from these two samples alone. If any possible salinity effect is ignored, the value for Sausalito indicates a temperature of shell deposition of 12.5 to 13°C. Although the temperatures in this part of the bay are comparable to open coast temperatures, this value is too low for late July, when the samples were collected. The possibility exists that the Sr/Ca ratio of the water in this partially restricted area was not that of open ocean water. The China Camp sample has a $SrCO_3$ content which indicates a temperature of 18.5°C. This locality is back in San Pablo Bay where late July mean temperatures of this order are probable.

Under certain conditions $SrCO_3$ may vary with salinity. Presumable variation in the Sr/Ca ratio of the water would cause variation of that ratio and thus the $SrCO_3$ content in the shell. Investigation of the Sr/Ca ratio of the water in areas of reduced salinity in connection with investigation of the $SrCO_3$ content of the shell would be desirable.

Seasonal Variation Series from Single Shells

Figure 46 shows where a series of samples was taken parallel to growth lines from a number of modern and fossil shells. Figure 47

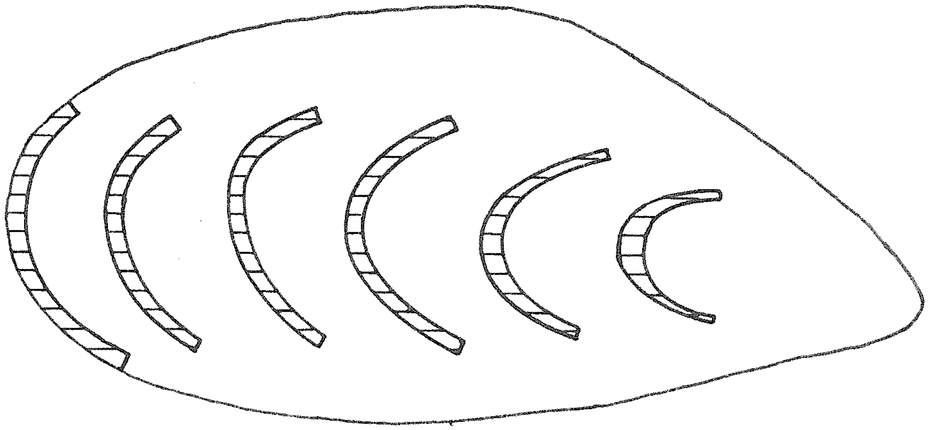

Figure 46. - Location of samples used in seasonal variation studies of the $SrCO_3$ content of individual shells. The samples were removed from the cross-hatched areas which parallel growth lines.

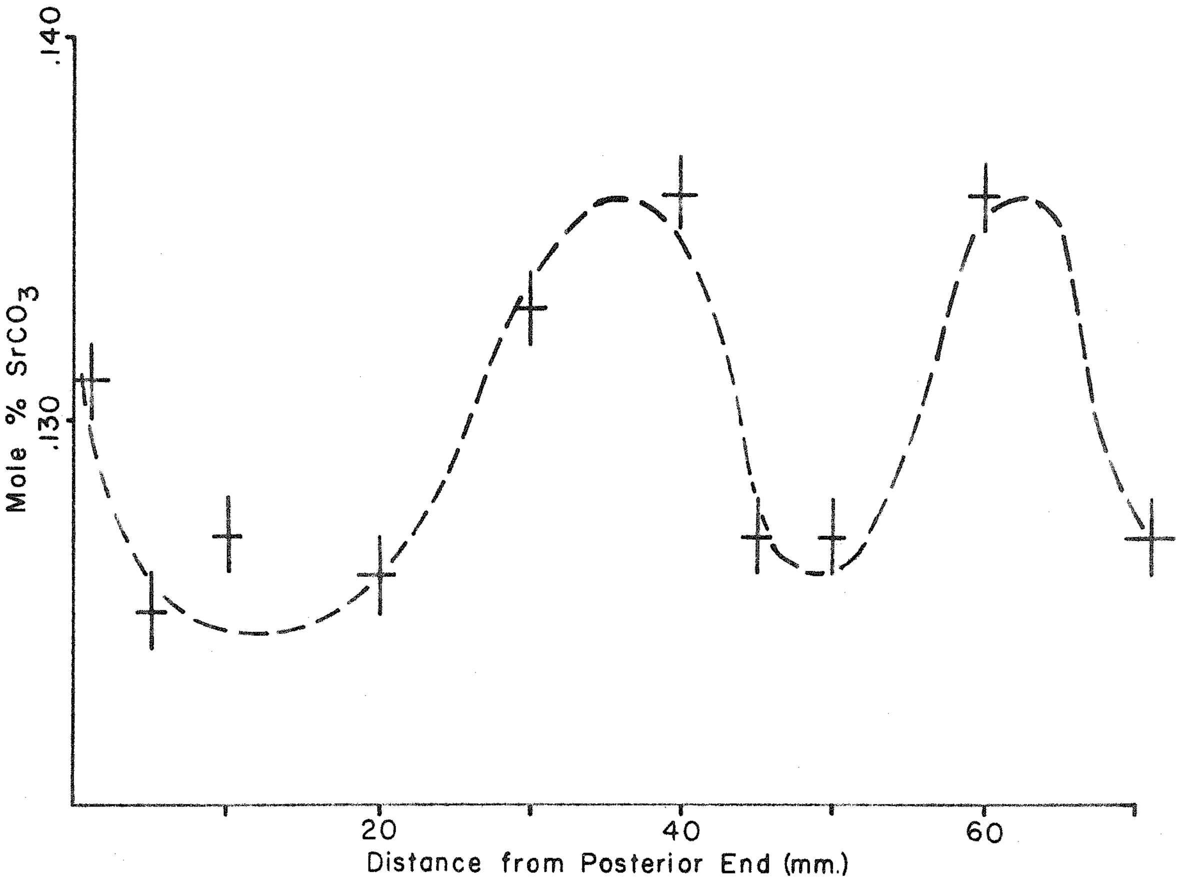

Figure 47. - Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a specimen of M. californianus from Pacific Grove.

is a plot of the mole percent $SrCO_3$ against the distance from the posterior end of a specimen of M. californianus from Pacific Grove. The specimen was 87 mm. long.

Since the $SrCO_3$ content of the outer prismatic layer appears to be temperature dependent, the series of samples should show seasonal variation. This series shows three maxima in $SrCO_3$ content separated by minima. The maxima represent summers and the minima winters. The final maximum is not as high as the preceding two because of the size effect on $SrCO_3$ content discussed above. The $SrCO_3$ content of the initial portion of shells cannot be determined because the outer layer is very thin and narrow in this area of the shell so that a sample of sufficient size cannot be obtained. This series indicates that the specimen was approximately three years old. A study of the shell structure of the opposite valve of this individual also indicates that this specimen is three years old. Thus, these data lend support to the interpretation that certain structural features of the shell reflect seasonal changes. This sample series indicates that the growth rate during the final year was greater than in preceding years. This is contrary to the expected result.

The range of values of mole percent $SrCO_3$ from this shell is not great. This would indicate a narrow temperature range at this location. The range indicated from the $SrCO_3$ content is approximately 11 to 16°C with a mean annual temperature between 13 and 14°C. The actual range in temperatures at Pacific Grove during the life of this specimen was 10.8 to 18.2°C. These temperature extremes persisted for very brief periods and would be lost in the averaging process of taking samples representing as much as a month's growth. An estimate of the effective range of temperatures which would be recorded by samples of this type would be 11.5 to 17.0°C. The mean annual temperature at Pacific Grove during the life of this individual was approximately 13.9°C.

A M. californianus shell 92 mm. long from the open coast at Corona del Mar was used to prepare a similar series of samples. The results of the analysis of the samples are shown in fig. 48. The interpretation of the series is not as obvious as in the case of the Pacific Grove specimen. It is not certain whether one or two maxima are represented. An anomalous growth pattern is indicated if an interpretation of two maxima is made. If there is really only one maximum, it is difficult to explain the two low values at 45 and 50 mm. If only one maximum is present, this indicates that the shell is not much over one year old and has grown much faster than suggested by the other data presented above. This shell came from the same location as the series of samples which fell completely off of the temperature curve. Temperature interpretations based on this series of samples are not unreasonable, however. A temperature range of 14 to 19°C with a mean of 16 to 17°C is indicated. The effective range in temperatures at Corona del Mar which might be represented in samples during this period is 15.0 to 20.5°C and the mean annual temperature was 17.7°C. Neither the Corona del Mar nor the Pacific Grove samples show such a large variation in $SrCO_3$ content as the series of samples from the Kerckhoff Marine Laboratory in Newport Bay. This appears to be due to the heating of the water in the shallow bay mentioned above.

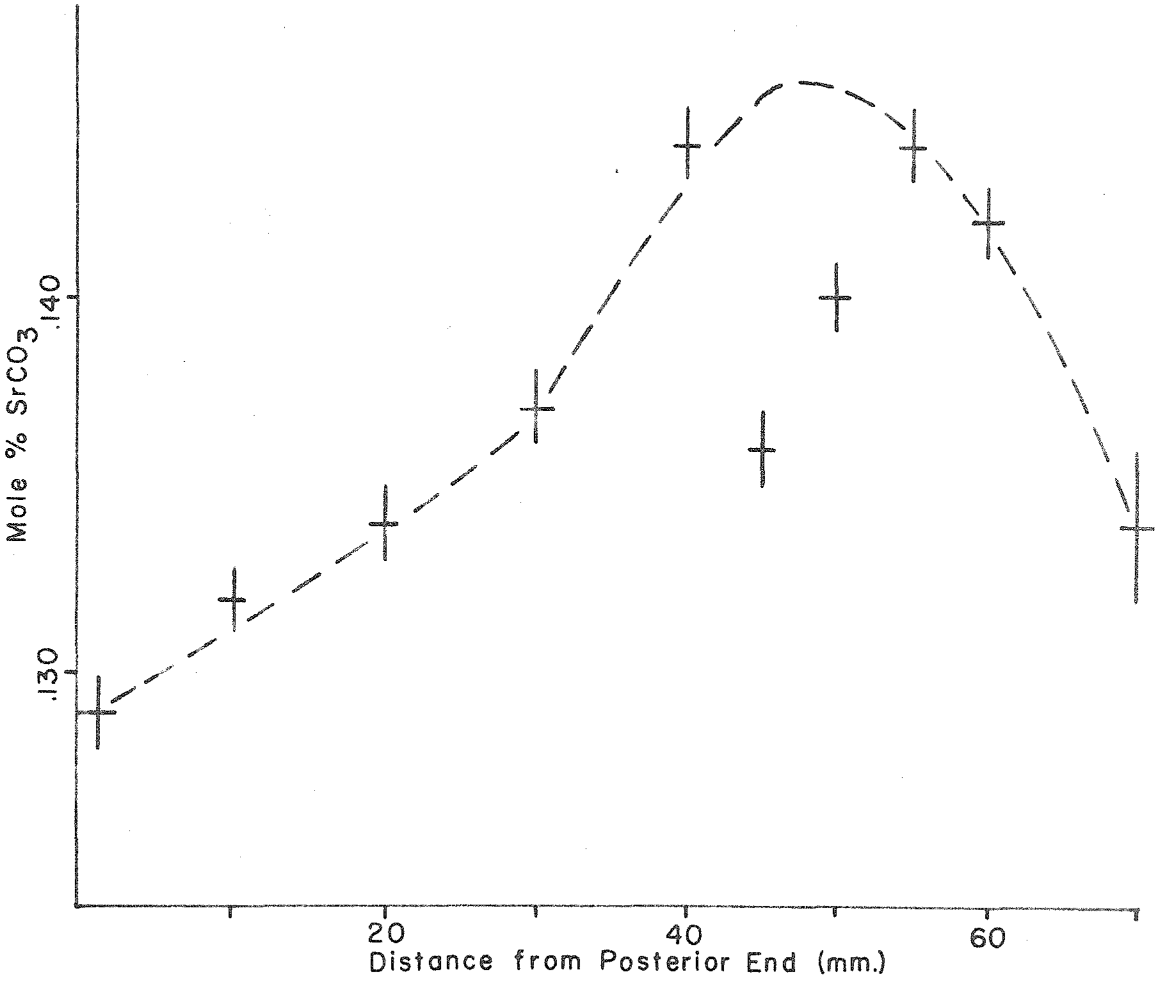

Figure 48. - Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a specimen of M. californianus from Corona del Mar.

Similar sample series were prepared from fossils. They will be discussed in detail in a later section. The fossil series in fig. 51 shows the seasonal variation even better than the modern samples.

$SrCO_3$ Content of Other Layers

The above discussion has been limited to the outer prismatic layer of Mytilus. No extensive study of the $SrCO_3$ content of the other two layers was made. One reason for this is the difficulty in preparing samples from the nacreous and inner prismatic layer. Preparing a sample of sufficient size presents no problem, but knowing the period of time during which this sample has been growing is difficult. Ideally, it would be best to skim thin samples off the inner surface of the shells. Such samples should represent a relatively short period of growth immediately preceding the collecting time.

One analysis of the inner prismatic layer of M. californianus was made. The sample was prepared by scraping the surface of this layer with a dentist drill. The $SrCO_3$ content of this sample was 0.123 mole %. This is a lower value than that for the outer prismatic layer of the same shell which contains 0.136 mole %.

The nacreous layer was sampled by two methods. In one case the inner surface was scraped with a dentist drill. In other cases, the shells were put in Clorox. This removes the organic material from between the first few layers of the nacreous structure and frees flakes of aragonite.

The results of the analysis of five samples prepared in this way are shown in fig. 49. A negative correlation apparently exists between

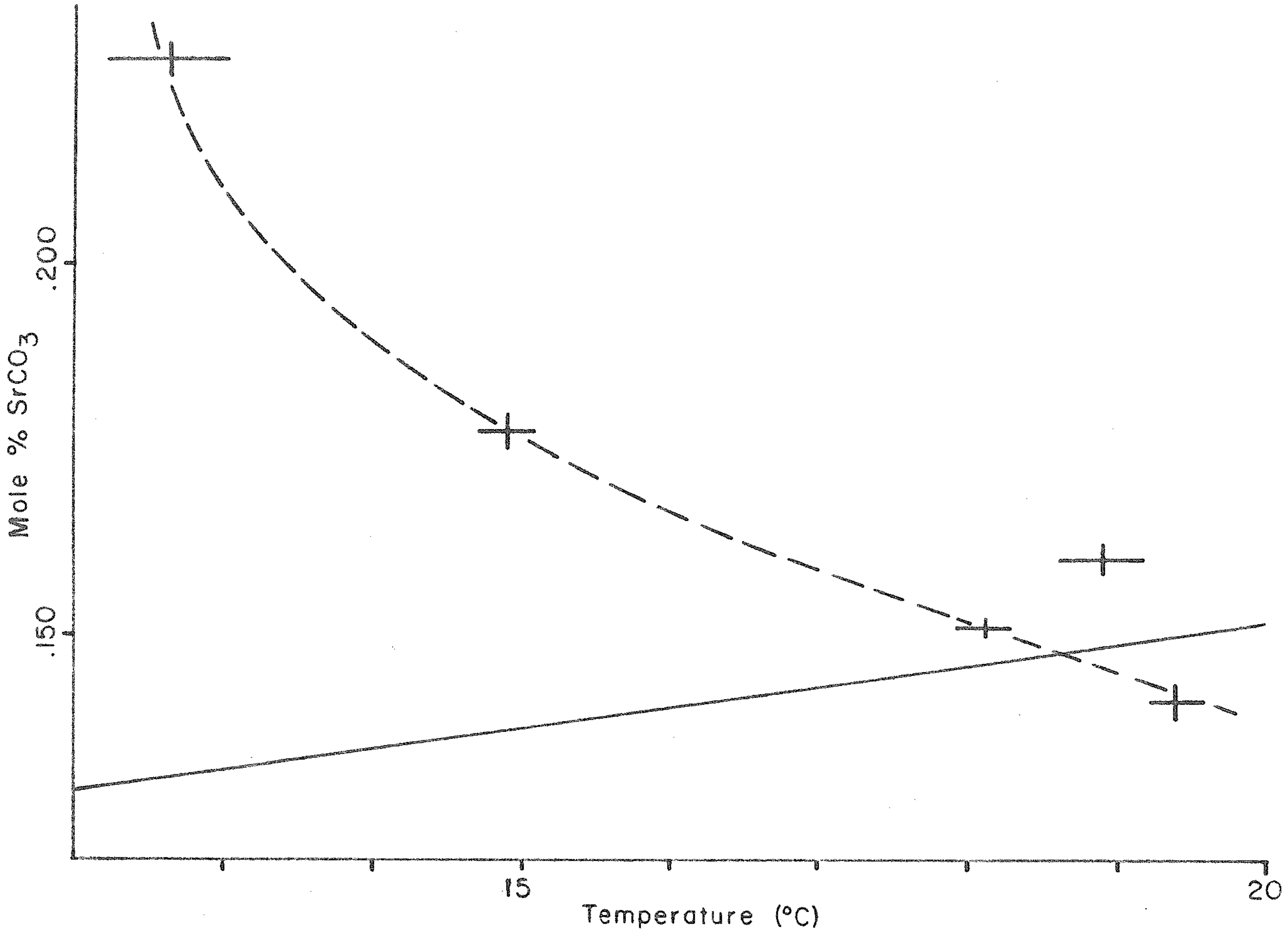

Figure 49. - Variation with temperature of mole percent $SrCO_3$ in the nacreous layer of _Mytilus_. The lower, solid line is taken from fig. 42 showing the relationship between $SrCO_3$ and temperature in the outer prismatic layer.

temperature and $SrCO_3$ content. The magnitude of the temperature effect is much greater in this layer than in the outer prismatic layer. A negative correlation between temperature and $SrCO_3$ content was found by Pilkey and Hower (1960) in the echinoid Dendraster. The solid line in fig. 49 is the least squares line for the correlation between $SrCO_3$ content and temperature in the outer prismatic layer. The usual relationship of higher $SrCO_3$ content in aragonite than in calcite (Odum, 1956a) thus apparently does not hold in all cases.

Due to the sampling technique, the estimated temperatures shown may differ appreciably from the actual growth temperature. The apparent correlation between temperature and $SrCO_3$ content may thus not be as obvious as it appears from these results. The possibility exists that the Sr taken up by Mytilus is partitioned between the nacreous and outer prismatic layers in such a way that the total Sr content per unit weight of shell deposited is approximately constant. This would explain why previous workers found no temperature effect on the $SrCO_3$ content of total Mytilus shells.

PALEOECOLOGICAL INTERPRETATIONS

Comparison of Paleotemperature Methods

Several techniques have been developed in this study which can be used to indicate past temperatures. Some of these methods are more satisfactory than others. Some are effective under certain conditions and not under others. Before illustrating the use of these techniques to determine paleotemperatures, a discussion of the relative merits of each is in order.

Perhaps the most effective method developed in this study is the use of the mean structural type. Since it is based on a number of shells, one non-representative shell will not affect the results unduly. No cases have been found in modern shells where this technique gave inconsistent results. This method is not subject to instrumental errors. It is the easiest to use and requires the least amount of equipment. General approximations of paleotemperatures could even be made in the field. Diagenesis cannot produce unsuspected alterations in structural type; however, diagenesis can complicate the use of this technique in some cases as discussed below. Even if the aragonitic nacreous layer had converted to calcite or been dissolved and replaced by secondary calcite, this technique will still work if the layers can be distinguished.

This method does have certain disadvantages, however. It cannot be used on shells which have been subjected to wear during the life of the individual (this often includes a large proportion of the specimens at a given locality). It will not work for mean annual temperature below 13°C. At this temperature the inner prismatic layer of most specimens is fully developed so that further lowering of temperature does not produce changes which can be measured by this method. It would probably not work above a mean annual temperature of about 18°C. It gives no measure of maximum or minimum temperatures during a given year. This method cannot be used for M. edulis edulis or M. edulis diegensis.

The second most effective method of determining paleotemperatures is by the $SrCO_3$ content of the outer prismatic layer. In some respects this is the most effective. This technique gives maximum and minimum as well as mean annual temperatures. It can be used to tell temperatures for one particular year and can thus be used to study variation in temperatures from year to year. Growth rates can also be determined. The demonstration of seasonal variation curves in the $SrCO_3$ content along the layer can be used to discount diagenetic alteration. This method works for both west coast species of Mytilus.

Some disadvantages are connected with use of this method. Only well preserved material can be used. Unless a seasonal variation curve can be demonstrated, a small loss of Sr which would give lower temperatures cannot be discounted. $SrCO_3$ content varies with size of the individual as well as with temperature adding an additional complicating factor. A few cases in modern shells have been found in which $SrCO_3$ content did not seem to be correlated with temperature. Such cases may occur in fossils. Demonstration of seasonal variation can eliminate this possibility. Elaborate equipment is required to make the determinations. The $SrCO_3$ contents are low enough and differences between samples grown at different temperatures are small enough that a small amount of contamination of samples can invalidate the results.

The $SrCO_3$ content of the nacreous layer is a potentially effective method of determining paleotemperatures. Sample preparation is the main obstacle to using this technique.

Determination of shell mineralogy by x-ray diffraction can be used as a method of paleotemperature determination in some cases. This method involves some uncertainties, however. The variation in mineralogy at any one locality is often large compared to variation between localities. Shell thickness, and other unknown factors, affect shell mineralogy. Only large, complete, unworn, very well preserved fossils can be used. In some cases shell mineralogy in modern shells could not be explained by factors measured in this study. This method probably should only be used in conjunction with the above two more reliable methods.

Growth rate as determined from shell structural and seasonal variation curves in the $SrCO_3$ content of the outer prismatic layer gives some indication of temperature. Factors other than temperature may also affect the growth rate, however. This method should not be used for worn shells as their growth rate may be slower at a given temperature than unworn shells. Shells from differing microenvironments may also have varying growth rates. For instance, specimens which are continually submerged grow faster than those which are intertidally exposed. This method cannot at present be used to precisely determine actual temperatures. It can be used to support or cast doubt on values determined by more precise methods.

Review of California Upper Pleistocene Faunas

The faunas of the California Pleistocene have received a great deal of attention in the last 100 years, particularly since Arnold's (1903) monograph on the Pleistocene of San Pedro. Valentine (1958a) has reviewed previous work on the Pleistocene faunas of the Pacific Coast as well as added much additional information. Upper Pleistocene faunas have been described from numerous locations along the southern California and northern Baja California Coasts. These are practically all found in terrace deposits formed at shallow depths. The exact age and correlation of these faunas is problematical. The relationship of the age of the California marine Pleistocene sediments to the age of the glacial drift in the midwestern United States is unknown (Woodring _et_ _al_., 1946). Attempts at radiocarbon dating of some of these fossils have shown that they are too old to date by this technique. Shells from the lowest terrace at San Pedro give an age of >30,000 years (Kulp _et_ _al_., 1952b). Bradley (1956) reported an age of >39,000 years for shells from Santa Cruz, California. The terraces on Santa Rosa Island are >33,000 years old (Orr, 1960).

Some question exists as to whether or not the deposits are glacial, interglacial, or both; and if the deposits are of approximately the same age. Some of the faunas containing elements characteristic of warmer temperatures than presently found have been provisionally correlated with interglacial stages (Gale in Grant and Gale, 1931; Smith, 1919). Some of the faunas have a cold water element. Recently, Valentine (1958a) has made the interpretation that all the faunas are glacial. Those on the open coast where intense upwelling of cold subsurface water has occurred are characterized by a cold temperature element. Those faunas in more protected situations have a warm water element (Valentine, 1954a and 1955). Emerson (1956a and b) and Addicott and Emerson (1959) suggest that intense upwelling explains the cold water faunas, but indicate that they are interglacial.

Care must be taken in making generalizations about these faunas. Any implication that all faunas from the Pleistocene terraces are of the same age must be viewed with skepticism. The tectonic instability of southern California makes such correlation impossible without detailed investigations. The safest course is to treat the fauna from each particular terrace as a separate entity.

Paleoecological interpretations based on these Pleistocene terrace faunas have been made by many writers. Since practically all the species listed in these papers are still living, these interpretations are based on known ecological requirements. Temperature interpretations have been particularly common. Most temperature interpretations are based on the present ranges of species. If the fossil species is south of its present range, this is considered as evidence of colder temperatures. Fossil species north of their present ranges are evidence of warmer temperatures. This technique is handicapped by the lack of complete knowledge of ranges. These species are often represented by few specimens and the limit to the presently known range may be only a few miles from the collecting locality.

Schenck and Keen (1937 and Schenck, 1945) developed a technique of estimating past temperatures by a comparison of the median of the latitudinal mid-points of species ranges with the latitude of the collecting locality. This method has several advantages over those based on fossils outside the present range of the species, particularly in that it considers all species present.

The extent to which the fossil fauna at any particular locality may represent the fauna at any given instant of time is questionable. The time involved in the accumulation of these fossil faunas may be of the order of hundreds or even thousands of years. During such periods of time, rather large fluctuations in ecological factors, such as temperature can occur. Significant temperature fluctuations have occurred on the Pacific Coast in the last 100 years. Marked changes in the fish fauna have occurred in response to this variation (Hubbs, 1948). Thus, the existence of forms which are presently confined to the south or north of the particular collecting locality may represent temporary temperature fluctuations. Emiliani and Epstein (1953) demonstrated by oxygen isotope analysis what appears to be marked fluctuations in temperature during the deposition of the lower Pleistocene Lomita Marl. The total fauna thus cannot be considered as characteristic of any particular temperature regime. In large faunas, usually elements are present which are characteristic of both relatively colder and warmer temperatures than presently occurring at that latitude. The predominance of one type or another certainly does not mean that the temperature at that locality was always warmer or colder than the present. This problem of fossil faunas covering a considerable span of time is further complicated by the combination of all fossils from a particular terrace deposit. Confining collecting to one particular horizon would help to restrict the magnitude of the time factor.

Woodring (1951) suggests that some of the contradictory evidence in the upper Pleistocene may be due to physiologic evolution of species which is not expressed morphologically. Johnson (1960) discusses this possibility and also observes that factors other than temperature may be involved in limiting the present ranges of these species.

A study of these faunas which estimates paleotemperature on a basis other than faunal interpretation should help to clarify some of the contradictions. Woodring (1951) suggested that a study of paleotemperatures based on oxygen isotopes might be useful in clarifying the apparent contradiction of having warm and cold water elements in the same fauna. Such a study would be a major undertaking. Here it is only hoped to give some indication of the problems involved in, and the results that might be expected from, such a study. The main purpose here is to test the applicability to fossils of the techniques developed for modern shells.

Use of M. californianus for Paleotemperature Interpretations

M. californianus is abundant in many of the Pleistocene terrace deposits. For this study, specimens were collected from four localities from northern Baja California to central California. In addition, specimens of M. edulis edulis were collected from the lower Pleistocene of the Seven Mile Beach (Merced formation) in San Francisco. Figure 2 shows the collecting localities.

The ecology of M. californianus should be briefly reviewed in order to more satisfactorily evaluate the meaning of the paleotemperature results. This species is usually intertidal or occurs only a few feet below low tide. A few specimens have been found from greater depths (Berry, 1954), but they are apparently not abundant. Newcombe (1935) suggests that predators may place a lower depth limit on *M. edulis* from the Bay of Fundy area. This may also apply to *M. californianus*. *M. californianus* is only found on rocky shores which provide a hard substrate for attachment. They appear to be restricted to the open coast where the salinity is normal and the water is turbulent. Specimens may occasionally be found just inside bays. *M. californianus* should thus record the surface or near surface water temperatures of the open coast.

M. californianus Fossils from Rosarito Beach

Several specimens of *M. californianus* were collected from terrace deposits approximately 1½ miles south of Rosarito Beach, Baja California. This was probably the same as UCLA location No. 2720 discussed by Valentine (1954b and 1957). The fossils were found immediately above the terrace platform which is cut into the basaltic bedrock. The elevation is from 15 to 20 feet above sea level. The sediment is poorly sorted with grain sizes all the way from silt or clay size to boulders a foot or more in diameter. The fossils were in a lens-shaped body extending for only a few feet laterally and two or three feet vertically. *M. californianus* is an abundant constituent of this fauna. The original crystalline structure of these shells is preserved. They are crumbly because most of the organic matrix which holds the crystals together is apparently gone. Two specimens were found with valves still articulated. To find fossil specimens of this species with both valves together is unusual. This indicates that little transportation at least of this species has occurred. A complete collection of all species was not made.

The estimated mean annual temperature at this approximate locality between 1949 and 1960 (from data supplied by C. L. Hubbs) was 15.6°C. Considerable upwelling of cold water occurs at this locality today, reducing the mean annual temperature below that of locations many miles to the north. Upwelling along many parts of the northern Baja California Coast is intense (Dawson, 1951) making temperatures here generally lower than those along most of the southern California Coast.

Study of the structure of 10 shells gives a range in structure type from 2 to 6 with a mean value of 4.4. This indicates a mean annual temperature approximately the same as or slightly lower than at Santa Monica. Thus a temperature of 15.5 to 16.0°C is indicated. On the basis of M. californianus shell structure, the mean temperature in the upper Pleistocene at this locality was no different from the present day value.

Figure 50 is a graph of mole percent $SrCO_3$ vs. distance from the posterior end of a 71 mm. long M. californianus shell. This shows a fluctuation which is apparently seasonal. This indicates a fairly rapid (but not unreasonable) growth rate. There are no minima in this curve to indicate with certainty what the winter values would be. If the low values at both ends of the curve are considered as minimum values, a temperature range of 13 to 17°C with a mean annual temperature of 15°C is indicated. This is the mean annual temperature for

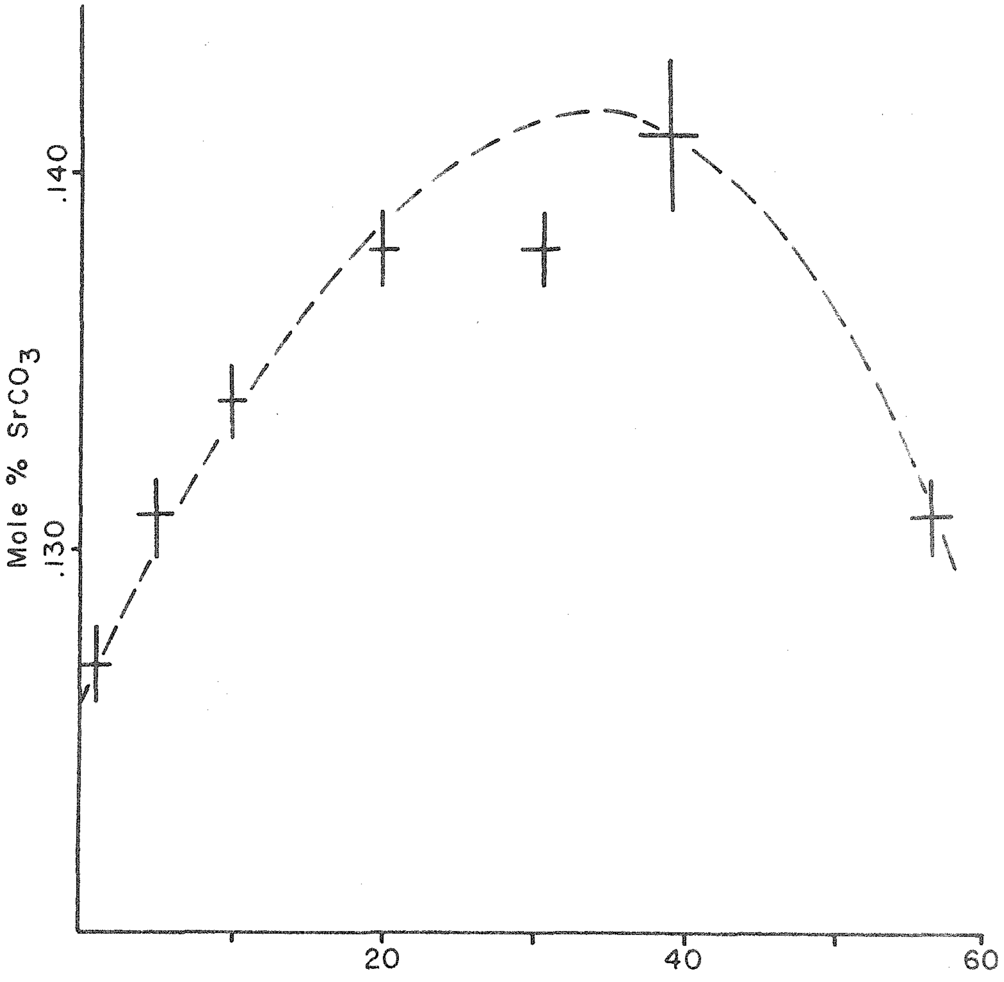

Figure 50. - Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Rosarito Beach.

only one year and should not be regarded as necessarily applicable to the whole deposit. To determine how temperature may have varied from year to year, it would be necessary to run series of samples from a number of shells. This temperature is a little lower than that given by the study of shell structure and may be due to variation in the mean annual temperature from year to year. In the two cases above, where seasonal curves were obtained for modern specimens, the indicated mean annual temperatures were slightly low. This is probably due to the inaccuracy of the original temperature vs. mole percent $SrCO_3$ line.

A value of 19.0% aragonite was obtained by x-ray diffraction for a 45 mm. specimen of M. californianus from this locality. This specimen was too small to be representative of the mean annual temperature of this locality, particularly in view of the growth rate suggested above. In addition a small portion of the shell was broken off. Although a number of beaks of larger shells were collected, only small complete shells were found at this locality. This is due to the fragile nature of the fossils discussed above. Also the lamellae of the nacreous layer tend to peel off very readily. For this reason, some of the aragonite originally in this shell may have been lost. As mentioned in the section on shell mineralogy above, this is not always a reliable method of determining paleotemperatures. In this case, it indicates a temperature of approximately 11°C which appears to be too low based on the evidence of the above two methods.

Data on growth rate are in general agreement with shell structure and $SrCO_3$ content. Two of the ten shells examined in section have a slower growth rate than the remainder. The rest of the shells indicate a growth rate slightly faster than that at Pacific Grove. This is weak evidence of temperature since it is based on a small number of samples. The slow growth rates in two shells are difficult to explain. Perhaps they grew during unusually cold periods. The slow growth rate may be due to some factor other than temperature. Detailed growth rates cannot easily be determined from fossils which may come from a variety of microenvironments. Some of the specimens may have been intertidal and others continuously submerged so that growth rate may vary considerably at any given locality.

The two most reliable methods of paleotemperature determination give temperatures between 15 and 16°C for this station. Growth rates do not in general contradict this suggested temperature. X-ray determined shell mineralogy gives a lower temperature, but this technique is not reliable and the sample used was far from satisfactory. On this basis, an estimate of 15.5 ± 1.0°C for the mean temperature during the deposition of this fossil deposit seems justified.

Valentine (1957) listed 32 species from his UCLA locality 2720. He lists 230 molluscan species and subspecies from the upper Pleistocene of the northern Baja California area. Nineteen of these have the southern limits of their present range north of this location. Three have their present northern limits to the south. Eleven of the 22 species and subspecies which are outside of their present range are less than 20 miles from the known endpoint of their range. Valentine interprets this as indicating that this locality was one with intense upwelling and colder temperatures than found at present. The fauna contains an admixture of a few species carried in from nearby protected sites which were characterized by warmer temperatures than those presently found. Since *M. californianus* is characteristic of exposed rocky shores and since the specimens show no sign of much transport, presumably they should have grown at the low temperatures if this interpretation is correct.

M. californianus Fossils from Torrey Pines

Pleistocene specimens of *M. californianus* were collected from the terrace deposits at Torrey Pines, north of San Diego, California. The locality is approximately 1 mile south of the north end of the Torrey Pines cliffs. This locality is probably the same as locality SDSNH No. 68 of Stephens (1929) and UCLA locality No. 3458 of Valentine (1958a and 1960). The terrace here is some 65-70 feet above sea level. It is a remnant of a terrace which once was presumably more extensive and which has been preserved in a re-entrant formed in the cliff by a hanging valley (Valentine, 1960). The fossils are embedded in sand which is better sorted than that at Rosarito Beach. Fragmented and worn specimens of *M. californianus* are more common than complete specimens. A distinction should be made in species such as *M. californianus* between pre- and post-mortem wear. As discussed above, living specimens of *M. californianus* are often extensively abraded, particularly in the beak area, from scraping against other individuals or the substrate. This can usually be distinguished from general abrasion of the entire surface and particularly the edges of the shells which has occurred after death. The fragmentation and post-mortem wear of these shells suggest that they were transported at least a short distance. That a suitable hard substrate for attachment was available at the site of deposition is unlikely. The terrace is cut in a relatively soft sandstone which does not stand up under the erosive action of waves. The abundance of specimens indicates that M. californianus did not live far from the depositional site, however.

The preservation of M. californianus at this locality is different from that at the Rosarito Beach locality. Fossils here are harder, in fact harder than modern shells. They have a reddish coloration which is apparently related to the original blue pigment pattern of modern specimens. The original crystals are apparently preserved.

This locality is only a few miles north of La Jolla along a straight coast. The present mean annual temperature should be approximately the same as at La Jolla (16.9°C).

Determination of the structural type of nine shells from this locality gave a range of 2 to 4 and a mean value of 3.2. This is approximately the same as Corona del Mar and indicates a mean annual temperature of about 16.5°C. This would indicate that the mean annual temperature during this period of the upper Pleistocene was about the same as at present. The slight difference indicated is not significant.

A plot of the mole percent $SrCO_3$ vs. distance from the posterior edge of the shell of a 85 mm. long specimen gives a better seasonal curve than was found in the modern shells used (fig. 51). Two maxima and two minima are present indicating that this individual was slightly more than two years old. A study of the structure of this shell indicates a probable age of $2\frac{1}{2}$ years. The peak in the anterior portion of the shell is higher (younger shells have relatively more $SrCO_3$ at a

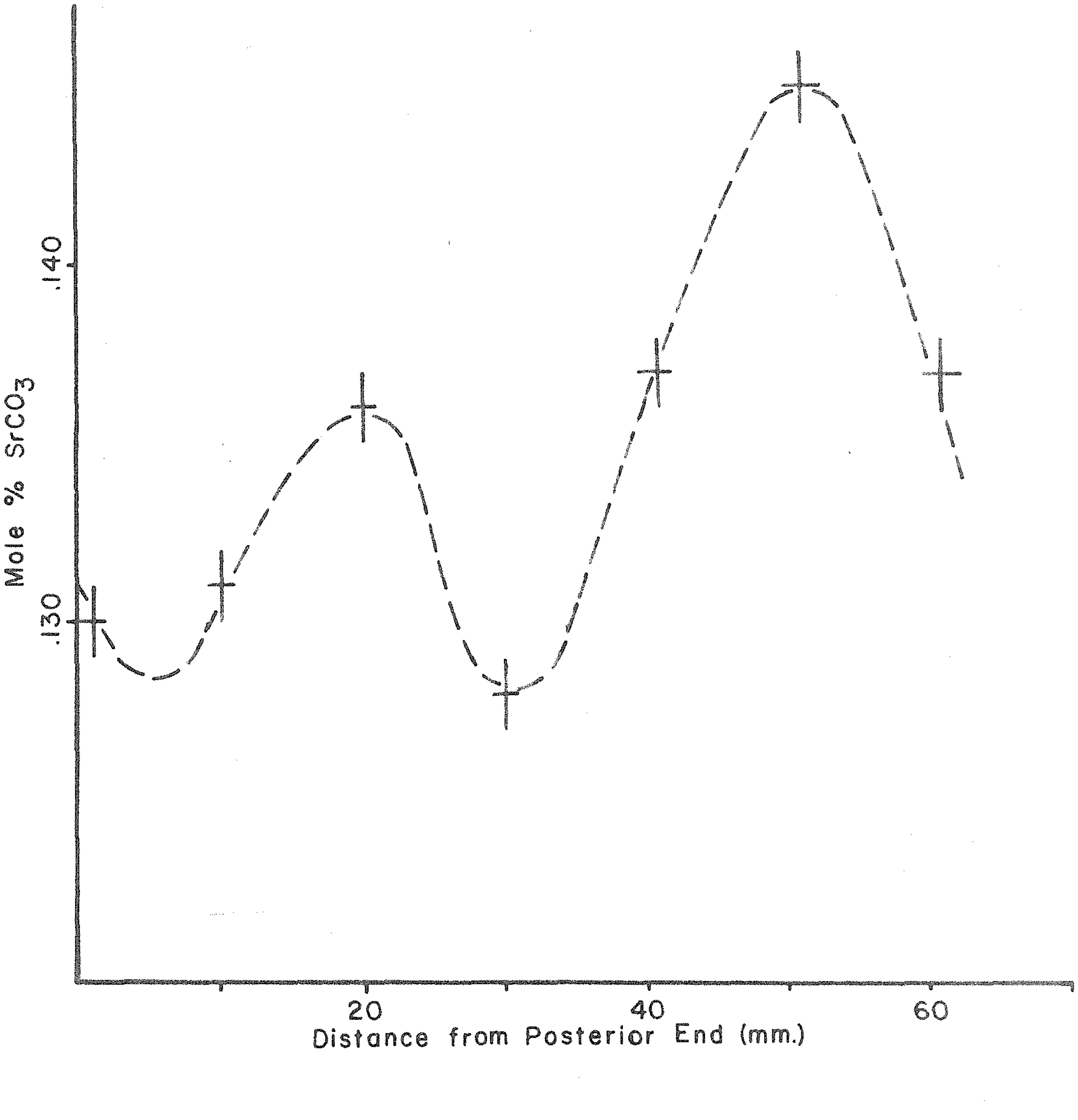

Figure 51. - Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Torrey Pines.

given temperature) and broader (growth rate is faster in younger shells) than the peak in the posterior portion. These values indicate a temperature range of 14 to 18°C and a mean annual temperature of 16°C. As was the case with the Rosarito Beach fossils, this gives a mean annual temperature slightly lower than that indicated by the shell structure. The difference is not outside the range of uncertainty, however. The discussion of the reasons for this at Rosarito Beach is appropriate here also.

X-ray diffraction determination of the mineralogy of a 100 mm. long specimen shows that it is composed of 27.2% aragonite. This specimen was more satisfactory for this purpose than the one from Rosarito Beach. This specimen was complete and unworn. A few bryozoans growing on the inner surface indicated that not much of the aragonite could have flaked off the inner surface after deposition. Nevertheless, the value of 27.2% aragonite indicates a mean annual temperature of only 14°C or slightly higher. As in the Rosarito Beach fossils, there is no indication of conversion of aragonite to calcite. No explanation can be offered as to why this temperature should be so much lower than the other two except that unknown factors apparently influence the mineralogy.

Approximate ages were determined for five shells. All shells indicated a relatively rapid growth rate (similar to that at Corona del Mar).

The two most reliable methods of paleotemperature determination give temperatures between 16 and 17°C. Growth rates do not contradict this estimate. Shell mineralogy suggests a lower temperature. A temperature of 16.5 ± 1.0°C would appear to be the best estimate of the mean temperature during the time of deposition of this fauna.

Valentine (1960) recognized that much of this fauna must have been transported from some other locality. He postulated that longshore currents carried shells north from the La Jolla region. From his study of the fauna, Valentine estimated that the mean annual temperature of this locality, unlike most open localities, was about the same as it is today. He identified only one species north of its present range. That species is a rare constituent of the fauna. No species were identified which are south of their present range.

M. californianus Fossils from Newport Bay

The third locality from which specimens of M. californianus were collected for this study was near upper Newport Bay near Corona del Mar, California. These specimens were collected from the lower terrace some 60-70 feet above sea level. The locality is in a gully cut in the terrace some 200 yards from upper Newport Bay. The locality is the same as locality 66 of the Los Angeles County Museum (Kanakoff and Emerson, 1959). In fact, some of the specimens used in this study were supplied by Mr. Kanakoff. The fossils here are found in a predominantly sandy sediment. M. californianus is common but not as abundant as in the preceding localities. Most of the specimens show no post-mortem wear indicating only very short transport from the actual life site. The general condition of the fossils is much like that at Torrey Pines. The original crystals of these shells are preserved. The shells are hard and some are discolored.

The mean of the structural type of eight shells of M. californianus from this locality is 3.4 with a range of 1 to 4. This is about the same as at Corona del Mar and indicates a temperature of approximately 16.5°C or about the same as at this locality today. The total fauna represents a diverse number of environments. It is not suggested that this temperature is characteristic of all of them. Since M. californianus is never found far from the open coast, probably the temperature indicated by these shells is for the surface water of the exposed coast in this area. The temperature in a hypothetical upper Pleistocene Newport Bay may well have been warmer than the open coast.

Analyses for $SrCO_3$ content of the outer prismatic layer at this locality are inconclusive. Figure 52 is a plot of mole percent $SrCO_3$ vs. distance from the posterior end of a 105 mm. shell. No well defined seasonal cycle can be seen. With the exception of the one high value at 90 mm., all the values fall within a narrow range of variation. This indicates some loss of Sr in diagenesis. A spectrographic analysis shows that the iron content of at least some of these shells is four times higher than in modern shells. This indicates the addition of some material. Perhaps these shells are similar to the group of modern shells from Corona del Mar discussed above which apparently were not temperature sensitive in their $SrCO_3$ content for some unknown reason. If these $SrCO_3$ values do reflect temperature, the values for this shell suggest a range of 12 to 14.5°C with a mean annual temperature of 13.5°C. This excludes the one high value which gives a temperature of 17.0°C.

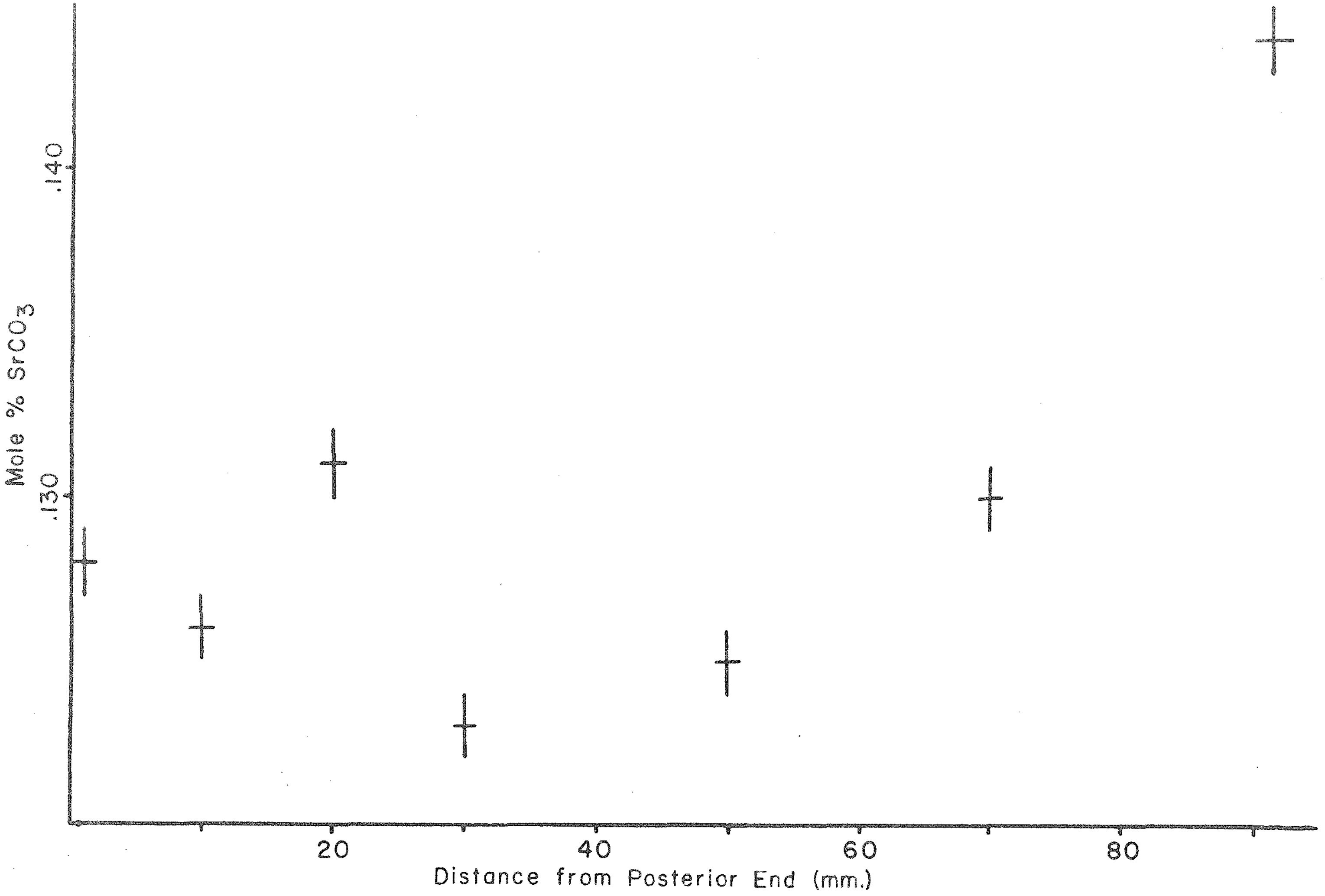

Figure 52. - Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Newport Bay.

An 89 mm. long specimen contains 27.9% aragonite as shown by x-ray diffraction. This indicates a temperature of 14 to 14.5°C. This temperature appears to be too low as in the case of the temperature based on mineralogic determinations of shells from the other localities.

Age determinations of five specimens at this locality indicate growth rates of from approximately that at Pacific Grove to rates comparable with those occurring presently at Corona del Mar.

The most reliable method of determining paleotemperatures gives a value of 16.5°C. Growth rates suggested by shell structure study do not contradict this. The $SrCO_3$ content is apparently altered or at least not a reflection of temperature. The shell mineralogy gives a low temperature as in the case of other localities. Since structurally determined temperatures are apparently the most reliable, a value of 16.5 ± 1.0°C is a reasonable estimate of the mean temperature of the open coast surface waters during the formation of this deposit.

Three papers have appeared on the upper Pleistocene paleontology of this area. Bruff (1946) collected fossils from several localities in the Newport Bay area. He determined the median of mid-points of the range of all the species in his collection. This median was at the latitude of San Diego. He concluded that the mean annual temperature was the same as at San Diego today. Schenck and Keen (1937) warned against using this technique to put such precise values on the temperature. The median of mid-points at best suggests that the temperature during deposition of these faunas was not significantly different from that of today. Modern faunas collected in the San Pedro area a few miles north of Newport Bay give medians of mid-points south of the actual latitude of San Pedro (Schenck and Keen, 1937).

Valentine (1958a) interpreted the fauna of this area as indicating warmer temperatures than occur in this region today. His interpretation was based on the presence of several species north of their present range. He indicated that the warmer temperatures were due to the absence of upwelling at this point and the presence of insolated water.

Kanakoff and Emerson's (1959) interpretation of the fauna is essentially the same as Valentine's. The fauna indicates a generally warmer but more diversified climate than exists at this point today. They base their interpretation on the presence of 47 species (12% of the fauna) which today do not range this far north. They conclude that the temperature in protected embayments in this area must have been at least 4°F (2.2°C) warmer than today. Six species (less than 2% of the fauna) were observed which today occur only north of this locality. They interpret this as meaning that nearby areas were characterized by low temperatures and strong upwelling of cool, subsurface water.

M. californianus Fossils from Cayucos

The most northerly locality at which M. californianus was collected in this study was at Cayucos, California. The fossils were collected from exposures of the terrace deposit in the low sea cliffs in the town of Cayucos from a point 50 feet south of the foot of 5th Street to a point south of the end of 7th Street. This probably includes Valentine's (1958b) UCLA localities 3389, 3390, 3391 and 3392. A fossiliferous bed immediately above the terrace platform is continuous throughout this area. The elevation is 10-15 feet above sea level. The fossils occur in a sandy sediment.

The preservation of M. californianus is different at this locality. The aragonitic nacreous layer has been completely dissolved from every specimen. The only aragonite found in any of the shells is in the form of small flecks within the inner prismatic layer. Not all of the other aragonitic fossils are dissolved, however. Evidently the nacreous structure is most susceptible to solution. With the middle layer missing, collecting shells with outer and inner prismatic layers intact is extremely difficult. The thin outer prismatic layer of the beak region is always lost. Had the aragonite which was removed by solution been replaced by secondary calcite, structural interpretations could have been made as readily as if the actual nacreous layer were still present. The crystal structure of the prismatic layers is preserved.

Sections were made of the beaks of four specimens of M. californianus. The extent of development of the inner prismatic layer was observed. Tongues of nacreous structure within this layer were observed as voids within the layer. The mean value of the structural type was 8.0 with a range of 7 to 9. This indicates a mean annual temperature slightly lower than that at Pacific Grove (12.9°C).

Structural studies of M. californianus from this locality are difficult due to the absence of the nacreous layer. The main problem is deciding whether or not a given shell had been worn in the beak region during the life of the individual. Worn specimens almost invariably have better developed inner prismatic layers than unworn ones. Thus if whether or not the specimen was worn cannot be determined, structural type is of limited value in determining temperatures. With a well developed inner prismatic layer, paleotemperature determinations from structural type are reaching the limit of sensitivity. An estimation of temperature is hardly justified since no estimate of the amount of shell wear can be made, and since the sample is small.

The results of $SrCO_3$ determinations for this locality are inconclusive. Figure 53 shows the variation in $SrCO_3$ content along the outer prismatic layer of a 82 mm. long shell. With the exception of one high value, the $SrCO_3$ content is nearly constant. This indicates that loss of Sr in diagenesis has destroyed the seasonal variation effect. The only other possible interpretation is that the temperature at this locality was nearly constant throughout the year and hence no seasonal variation appears in the $SrCO_3$ content. This is unlikely. Not much loss could have occurred because the values for mole percent $SrCO_3$ are still relatively high. In fact, the values are slightly higher than those for winter deposition at Pacific Grove. The possibility that the shell could have gained Sr in diagenesis is considered extremely remote. Equilibration with ground water, which almost invariably has a relatively low Sr/Ca ratio (Odum, 1956b), always causes a loss of Sr (Lowenstam, 1960). The minimum possible change in $SrCO_3$ content would occur if those portions of the shell having a low $SrCO_3$ content were unaffected and only those portions with high values reduced. At any rate, these values would then represent a minimum

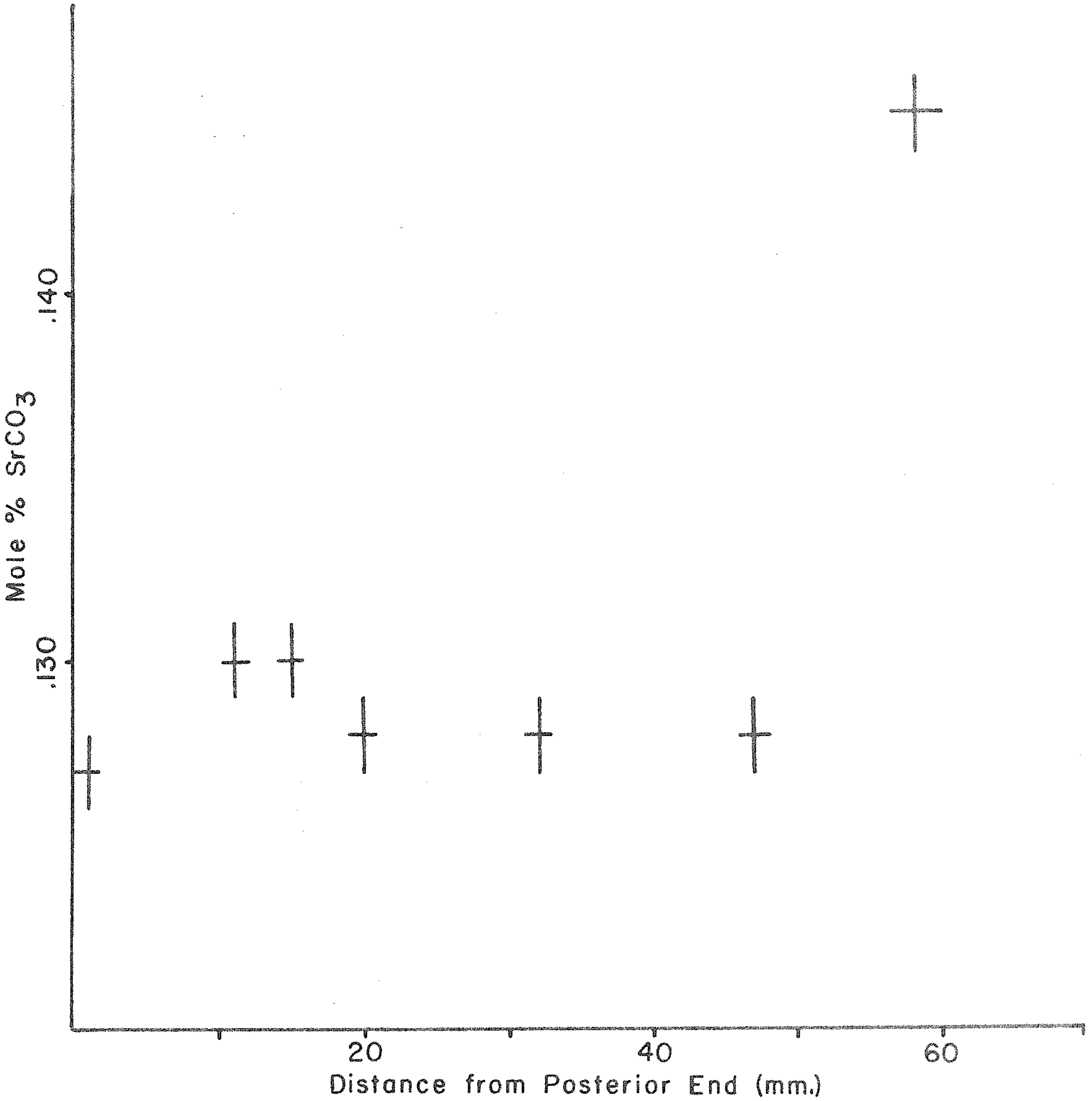

Figure 53. - Variation with distance from the posterior end of the shell of mole percent $SrCO_3$ in the outer prismatic layer of a fossil specimen of M. *californianus* from Cayucos.

possible mean temperature for this locality of 13°C. The one high value could perhaps be an unaltered portion of the layer. This indicates a temperature of 17-18°C.

Age determination of three shells from this location indicates a slow growth rate. Rates between those at Westport and Waldport are suggested. These may be worn shells. The effect abrasion may have on growth rate is unknown, but may cause a slower growth rate. Ages determined on worn shells are thus of doubtful value.

None of the paleotemperature determining techniques gives the exact temperature of this location. Study of structural types indicates a mean temperature of the order of 12°C. This should be regarded as a minimum value. $SrCO_3$ content indicates 13°C as a probable minimum value for the mean temperature and one temperature as high as 17.5°C. Growth rates, which are probably not reliable in this case, indicate lower temperatures.

On the basis of these data the most reasonable interpretation is that temperatures were probably at least as warm as the present temperatures at this locality and may have been slightly higher.

Valentine (1958a and b) listed 130 species from the Cayucos region. Most of them are characteristic of a rocky, open coast environment. He listed four species as north of their present ranges and two south of their present ranges. Valentine states that this indicates a greater range in temperature than at present. He infers that the mean temperature did not differ greatly from the present value.

M. edulis edulis Fossils from San Francisco

A number of specimens of *M. edulis edulis* were collected from the upper Merced formation exposed in the cliffs at the Seven Mile Beach just south of the San Francisco city limits. The fossils were collected from a fossiliferous bed some five feet above the base of the cliff at a point immediately west of the intersection of Skyline and Alemany Boulevards in the Thornton Beach Park. It is near locality B-4810 of Glen (1959). The fossils were found in an unconsolidated, fine sand. The fossils were fragile and difficult to collect intact. The material is apparently well preserved. The original crystals are still present.

The exact age of the upper Merced is uncertain. It has been assigned both to the upper Pliocene (Martin, 1916) and the lower Pleistocene (Woodring, 1952). Glen (1959) considers this fossil zone to be in the lower Pleistocene. Both valves of *M. edulis edulis* were usually intact and many of the other pelecypods were apparently in their life position. Although this is presently an exposed coast, this bed was deposited in a protected situation.

Study of structure of *M. edulis edulis* does not give information on environmental conditions. The structure of these fossil specimens does confirm that the subspecies *M. edulis edulis* is represented here.

These fossils are too small to allow preparation of samples along the outer prismatic layer of sufficient size to make $SrCO_3$ determinations to show seasonal variation. One composite sample was made of portions of the outer prismatic layer from six individuals.

Provided this is a representative sample and diagenesis has not changed the composition, the amount of $SrCO_3$ should be an indication of the mean temperature of shell deposition during the lives of these specimens. This sample contained 0.127 mole % $SrCO_3$. This indicates a temperature of 11.5°C. This is 2°C colder than San Francisco (Fort Point) mean annual temperature today. There is no way to tell with certainty that diagenesis has not lowered the $SrCO_3$ content.

X-ray determination of shell mineralogy for four separate valves of individuals approximately 10 mm. in length gave a result of 20.9% aragonite. This value is higher than that for individuals living at near normal salinities in both the San Francisco Bay region and northern Washington. Reduced salinities may thus be represented but no estimates of exactly what the salinity may have been can be made on the basis of these data.

Glen (1959) made a detailed study of the fauna of the Merced formation in this region. He concluded that the fauna indicated that the Merced formation was deposited at shallow depths in a "sheltered basin" with a probable reduced salinity. Glen made no statements about temperature implications of the fauna. Using the range data in Keen (1937), all the species from the upper Merced are apparently within their present range.

A more detailed study of paleotemperatures and paleosalinities of the upper Merced formation would be informative. A study of this type might help to indicate where the Pliocene-Pleistocene boundary should be placed in that formation.

Oxygen Isotope Analysis of Fossils

Oxygen isotope analyses were made of portions of the outer prismatic layer of fossil specimens from each of the above localities. Results of these analyses have not been included with those of the other paleotemperature techniques because these results are considered as only provisional. The mass spectrograph was not operating at peak efficiency during these analyses. More samples would be necessary to definitely establish the results obtained from this limited number of samples.

The advantages and limitations of this method have been extensively discussed elsewhere (Urey _et al_., 1951; Epstein _et al_., 1951 and 1953; Epstein and Mayeda, 1953; and Lowenstam and Epstein, 1954). Of particular importance in the fossils discussed in this study is the water correction. The California current lowers the present δO^{18} value of the surface water along southern California by as much as 0.4°/oo. Therefore, if a δO^{18} value of 0.0°/oo (mean ocean water) were used as the water correction for shells collected in southern California today, the resultant temperatures would be 2°C too high. During the glacial stages of the Pleistocene, the California current may have brought in a greater amount of glacial meltwater so that the δO^{18} values may have been even more negative. The δO^{18} values for the middle of the interglacial stages may have been nearer 0.0°/oo than today. Thus whether or not the faunas are glacial or interglacial is significant in the use of oxygen isotopic temperatures. Valentine and Meade (1960) did not consider this in their paleotemperature determinations for the California Pleistocene.

Oxygen isotopic paleotemperatures give the mean temperature of deposition of the shell. This is not necessarily the same as the mean annual temperature at the locality where the shell grew (Lowenstam and Epstein, 1953). Some organisms deposit shell only during parts of the temperature range. The rate of deposition varies with temperature in many species. Some of the shells used by Valentine and Meade (1960) are probably of this type. Some of their samples are southern species near the northern extremes of their range. They likely grow only during the warmer part of the year or at least grow faster then. They also used northern species near the southern extremes of their range. They likely grow most during the colder part of the year.

As has been discussed above, the rate of growth in the *Mytilus* species studied here is apparently in part temperature dependent (Coe and Fox, 1942). Therefore, oxygen isotope determination of complete *Mytilus* shells should give higher temperatures than the mean annual temperature because growth is faster in the summer. This was true for the modern shells analyzed.

If the temperature at which a shell or a portion of a shell grew can be determined by some other method, determination of the isotopic composition of the water in which it grew is possible. This would be useful in estimating the paleosalinity of the water in which the sample grew.

Oxygen Isotope Analyses of Portions of *M. californianus* Fossils

Table 23 (Appendix I, p. 213) shows the value of paleotemperatures at each fossil locality if the water is assumed to have a δO^{18} value of 0.0°/oo. The δO^{18} value of the water assuming that the temperature of growth was that indicated by the $SrCO_3$ content is also given.

Samples of the outer prismatic layer used for oxygen isotope analysis were also analyzed for $SrCO_3$ content. Those samples which have an $SrCO_3$ content indicating that they were deposited at near the mean annual temperature were used in some cases. In other cases, composite samples were made which should represent shell material grown throughout the year.

The sample from Rosarito Beach had a $SrCO_3$ content indicating a temperature of 15.0°C. This is approximately the mean annual temperature estimated on the basis of $SrCO_3$ content and shell structure. The uncorrected oxygen isotopic paleotemperature for this sample is 11.5°C. This is apparently too low and does not agree with temperatures estimated by other techniques with the exception of the mineralogy temperature, which was considered poor for this locality. This discrepancy can be explained in a number of ways. The sample may actually have been deposited at this temperature. This would mean that the other techniques of paleotemperature interpretation were inaccurate. This does not seem probable. The sample may have been deposited in water with a δO^{18} value of +0.8°/oo. That water of this composition could exist on the open coast at this location during the Pleistocene appears unlikely. This would indicate hypersaline water. Another possibility is that the shells established post-depositional equilibrium with water of this composition. The $SrCO_3$ content gives no indication of post-depositional alteration. More simply, perhaps the analysis was poor or the sample contaminated.

The sample from Torrey Pines has a $SrCO_3$ content which also indicates a temperature of 15.0°C. The uncorrected isotopic temperature agrees exactly with this value. This indicates that the water actually had a δO^{18} value of 0.0°/oo when this shell was deposited. This would be slightly different from the present water at La Jolla (δO^{18} = -0.4°/oo) and would indicate a lack of glacial meltwater in the California current and hence interglacial conditions. The specimens from Torrey Pines thus give the same paleotemperature results from shell structure, $SrCO_3$ content and oxygen isotope analysis with supporting evidence from growth rate. Only shell mineralogy conflicts.

The Newport Bay sample is a composite sample which should represent at least a year's growth. It has a $SrCO_3$ content which indicates a temperature of 13.0°C. The $SrCO_3$ content gives indications of being diagenetically lowered. The oxygen isotope temperature for this sample is 19.5°C. This temperature is higher than would be expected from the other techniques. This could most readily be explained as resulting from diagenetic alteration involving partial equilibration with ground water having a relatively more negative δO^{18} value than sea water. Diagenetic alteration would lower $SrCO_3$ temperatures and raise oxygen isotopic temperatures. If the $SrCO_3$ temperature is considered to be correct and no diagenetic alteration is assumed, the water in which the shell was deposited would have to have a δO^{18} value of -1.4°/oo. This would indicate reduced salinity. The fauna gives no evidence of this (Kanakoff and Emerson, 1959).

The Cayucos sample is a composite sample which should cover several seasons of growth. Since the size of the specimen from which this sample came is not precisely known, the temperature of 13.5°C represented by the $SrCO_3$ content of the sample should be considered as only approximate. The isotopic temperature of 13.0°C agrees with the $SrCO_3$ temperature and suggests that the isotopic composition of the water is not much different from that at present, although slightly more positive. This indicates interglacial conditions. The results of the oxygen isotope determinations give added confidence to the $SrCO_3$ temperatures from this locality. Since they do not vary much seasonally, at least the higher samples appear to have been lowered. The agreement of $SrCO_3$ and oxygen isotope paleotemperatures indicates that this lowering must have been slight.

The San Francisco sample is composed of several pieces of outer prismatic layer from small specimens of M. edulis edulis and should thus be representative of the mean temperature at this locality. The oxygen isotope temperature of 16.0°C is considerably higher than the $SrCO_3$ temperature of 11.5°C. This could either be the result of slight diagenesis or deposition in water of reduced salinity. Deposition in water of slightly lowered salinity would give apparently higher oxygen isotope temperatures when no water correction is made, but would not affect $SrCO_3$ temperatures. Glen (1959) suggested that this fauna did live under conditions of reduced salinity. If the $SrCO_3$ paleotemperature is considered to be correct, the water would have had a δO^{18} value of -1.1°/oo. What salinity this represents depends on the δO^{18} value of the fresh water which was diluting the normal sea water.

If the diluting water was glacial meltwater with a very negative δO^{18} value, the salinity would not be as low as if it were temperate zone rain water (Epstein and Mayeda, 1953). Using the relationship found between salinity and δO^{18} value of present surface water off the Pacific Coast of North America by Epstein and Mayeda (1953), a salinity of approximately 32.5^{o}/oo is obtained. There is no particular reason to believe that this relationship held in early Pleistocene time, however. Dilution with normal temperate rain water with a δO^{18} value of -7.0^{o}/oo would give a salinity of approximately 29.5^{o}/oo. These specimens probably grew in water which was in this salinity range of 29.5 to 32.5^{o}/oo.

CONCLUSION

A detailed description of the structure of the shells of *M. californianus*, *M. edulis edulis*, and *M. edulis diegensis* is included in this study. The *Mytilus* shell consists of three and sometimes four layers: periostracum, outer prismatic layer, nacreous layer, and inner prismatic layer. The inner prismatic layer is found in some specimens of *M. californianus* but not in *M. edulis edulis* or *M. edulis diegensis*. A blocky aragonite layer sometimes occurs in both species. The periostracum is composed entirely of organic material. The outer prismatic layer consists of elongate crystals of calcite. The long axes of these crystals recline at varying angles toward the beak and characteristically form cone-shaped aggregates. The nacreous layer is composed of tabular aragonite crystals arranged in lamellae parallel to the inner surface of the shell. The inner prismatic layer is composed of calcite crystals much like those of the outer prismatic layer. Cone-shaped aggregates are more common in the inner prismatic layer. The inner prismatic layer contains zones which are characterized by finer crystal texture than the rest of the layer.

The spatial relationship between the nacreous and inner prismatic layer can be used to determine the age of specimens of *M. californianus*. Tongues of nacreous structure in the inner prismatic layer, zones of fine texture in the inner prismatic layer, and tongues of the blocky aragonite layer in the inner prismatic layer apparently form during the summer.

Lowenstam (1954b) demonstrated on the basis of a growth series from La Jolla that percent aragonite in *M. californianus* is correlated positively with temperature. The present study demonstrates that the shell mineralogy of specimens less than 15-20 mm. in length is not affected by temperature. (Lowenstam's growth series did not include specimens this small.) This is indicated by the lack of variation in specimens collected seasonally from a single locality, the lack of geographic variation, and the lack of regular variation in growth series in specimens below this size range. That percent aragonite in the shells of larger specimens increases with temperature is indicated by growth series from Corona del Mar and La Jolla. Geographic variation in a large number of specimens also indicates this relationship. A quantitative relationship between temperature and shell mineralogy in *M. californianus* was determined. Factors other than temperature also affect the shell mineralogy of this species. Statistically, thick shelled specimens have a higher percent aragonite than thin shelled individuals. The factors causing shell thickening are unknown. Other unknown factors also affect shell mineralogy.

Lowenstam (1954b) demonstrated that percent aragonite in *M. edulis s. s.* from the Atlantic Ocean has a positive correlation with temperature. The present study shows the shell mineralogy of the Pacific Coast representatives of that species to be secondarily affected by temperature. Genetically distinct groups can thus be distinguished by shell mineralogy. Specimens of *M. edulis diegensis* collected seasonally from one location do not vary cyclically. No regular variation with latitude in larger specimens of *M. edulis edulis* and *M. edulis diegensis* was noted. An apparently distinct positive correlation between temperature and percent aragonite in small (less than 20 mm. in length) specimens of both subspecies, particularly in *M. edulis diegensis*, contradicts this evidence. A probable low level temperature effect was noted in the growth series from Avila Beach. Increase in percent aragonite with increased shell length is the dominant factor in *M. edulis diegensis* from Avila Beach. Decreased salinity causes increase in percent aragonite in both subspecies of *M. edulis*.

Variation in shell mineralogy is expressed as variation in shell structure. No previous study of the variation of shell structure within a species has been made. Variation in the percent aragonite in longitudinal sections of *Mytilus* reveals the same general relationships as shown by x-ray determinations of the total shell mineralogy. Shell structural types in *M. californianus* were established and found to vary in a regular manner with temperature. These structural types are based on the degree of development of the inner prismatic layer. The higher the temperature, the less developed is this layer. A study of shell structure was used to determine the age of specimens of *M. californianus* and thus the growth rate of the shell. A positive correlation exists between temperature and growth rate in both species of *Mytilus*.

The relationship of variation in magnesium and strontium to environment in pelecypod shells has not previously been determined. Mg and Sr content of the outer prismatic layer of both species is correlated positively with temperature. Spectrographic analysis of the rims of seasonally collected specimens of M. edulis diegensis show cyclical variation in the content of both of these elements. X-ray fluorescence analysis of Sr content of portions of outer prismatic layer grown at known temperatures at various localities was used to establish the quantitative relationship between temperature and $SrCO_3$ content. Analyses of specimens of M. californianus collected at one place and time indicate that $SrCO_3$ content is negatively correlated with the size of the specimen when that portion of the outer prismatic layer was deposited. The $SrCO_3$ content of the outer prismatic layer of M. edulis edulis was demonstrated to be independent of salinity. Seasonal variation in $SrCO_3$ content in samples of the outer prismatic layer taken across growth lines was demonstrated. Estimates of mean annual, maximum, and minimum temperatures of the collecting locality could be made from these analyses. On the basis of a limited number of samples, a negative correlation between temperature and $SrCO_3$ content was demonstrated for the nacreous layer.

The above relationships make possible four methods of quantitative paleotemperature determination from M. californianus shells. In order of apparent decreasing reliability, they are: shell structure type, $SrCO_3$ content of the outer prismatic layer, growth rate, and shell mineralogy. $SrCO_3$ content of the outer prismatic layer can also be used for M. edulis edulis and M. edulis diegensis. $MgCO_3$ content of the outer prismatic layer and $SrCO_3$ content of the nacreous layer are also potential paleotemperature determination methods but require additional work.

These methods of paleotemperature determination were used on fossils from five localities in California and Baja California. In all cases, shell structure type indicated temperatures approximately the same as exist today at the latitude of the fossil locality. In at least two and probably four localities, $SrCO_3$ content of the outer prismatic layer gave reliable temperatures. Diagenetic alteration has affected the fossils at one location (Newport Bay). Growth rates varied too much for a precise estimate of paleotemperatures but were in general agreement with shell structure temperatures in all cases but one (Cayucos). With one exception, shell mineralogy temperatures were lower than indicated by the other methods. The exception was at Newport Bay where low $SrCO_3$ temperatures resulted from diagenetic alteration of the fossils. The oxygen isotopic composition of the water in which the shells grew was estimated from oxygen isotopic analyses of shells and temperatures determined from $SrCO_3$ contents.

The results of these paleotemperature determinations and five oxygen isotope analyses indicate that the four upper Pleistocene terrace deposits investigated had temperatures approximately the same as found at that latitude today and were probably formed during interglacial stages. The lower Pleistocene fossils from San Francisco indicate a temperature $2^{o}C$ lower than presently found at that locality and a slightly reduced salinity.

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APPENDIX I

TABLES OF DATA

Appendix I

Tables of Data

Table 1

X-ray Determination of the Percent Aragonite in M. californianus
Collected Seasonally from Corona del Mar, California

Collecting Date	No. of Specimens	Length of Specimens (mm.)	Total Sample Weight (mg.)	Temperature at Collecting Time (^{o}C)	% Aragonite
6-30-58	4	11.8, 12.5, 13.7, 13.6	832.1	21.6	41.5
9-13-58	4	11.6, 11.0, 11.2, 11.0	517.0	20.2	39.0
11-14-58	4	12.8, 13.0, 12.0, 12.0	761.4	19.2	40.5
1-16-59	3	13.8, 12.5, 12.7	595.0	15.8	37.5
5- 7-59	3	12.0, 12.2, 12.2	521.8	18.6	46.0
6-30-58	1	20.4	874.4	21.6	40.2
9-13-58	2	19.7, 20.6	1299.4	20.2	43.7
11-14-58	1	21.7	755.0	19.2	37.9
1-16-59	3	17.7, 19.2, 18.3	1283.2	15.8	38.2
3-19-59	2	17.8, 17.6	878.4	17.8	47.8
7-24-59	1	26.6	1360.4	20.7	48.0
10-29-59	1	26.5	1280.0	19.7	38.9
12-16-59	1	28.6	1403.4	16.3	32.4
1-15-60	1	25.5	846.3	14.4	26.6
2-25-60	1	27.3	1105.0	13.6	32.4
5- 4-60	2	27.0, 27.8	2448.0	16.9	24.5

Table 2

X-ray Determination of the Percent Aragonite in <u>M. edulis diegensis</u>
Collected Seasonally from Corona del Mar, California

Collecting Date	No. of Specimens	Length of Specimens (mm.)	Total Sample Weight (mg.)	Temperature at Collecting Time (°C)	% Aragonite
6- 6-58	4	8.4, 9.3, 7.1, 9.0	187.7	19.8	31.0
6-30-58	4	8.3, 7.8, 6.2, 6.7	119.9	22.0	31.5
7-25-58	4	7.5, 6.8, 6.6, 8.3	103.2	19.2	25.5
8-11-58	4	8.4, 6.9, 7.2, 7.3	95.1	19.8	27.0
9-13-58	4	8.4, 8.4, 7.6, 7.9	128.5	21.5	27.0
10-10-58	4	8.0, 7.5, 8.2, 7.7	112.0	20.3	27.5
11-14-58	4	9.3, 8.5, 7.4, 7.8	141.4	19.2	27.5
1-16-59	4	7.3, 8.0, 9.1, 7.9	156.1	16.2	30.2
6- 6-58	3	13.7, 13.3, 14.0	576.4	19.8	28.0
8-11-58	2	15.3, 13.9	412.3	19.8	31.5
10-10-58	1	15.4	239.2	20.3	27.0
12- 5-58	3	16.3, 13.6, 13.5	504.6	17.4	22.0
12-27-58	4	16.5, 15.5, 17.3, 15.5	937.5	16.5	31.0
2-27-59	2	14.3, 14.3	378.2	15.5	28.0
5- 7-59	7	13.6, 13.5, 12.5, 12.5 13.5, 13.7, 13.7	554.4	19.3	26.5
7- 2-59	4	15.3, 14.8, 15.0, 15.4	984.9	24.2	30.5
9-16-59	1	29.8	1224.8	22.9	24.3
10-29-59	1	28.3	1801.0	19.9	31.0
12-16-59	1	31.6	1461.0	16.4	28.6
1-15-60	1	30.0	1548.0	13.4	33.7
2-25-60	1	32.1	1931.0	14.3	31.0
5- 4-60	1	30.1	1216.5	17.7	34.5

Table 3

X-ray Determination of the Percent Aragonite in Specimens of *M. californianus* Collected at Corona del Mar on October 29, 1959

Length (mm.)	Weight (g.)		% Aragonite
110.0	26.75	(one valve)	38.6
97.7	26.03	"	33.2
91.1	20.22	"	34.7
78.7	12.13	"	34.9
74.2	7.65	"	29.0
67.3	7.30	"	33.4
63.2	4.91	"	29.3
54.0	3.19	"	26.3
48.8	3.39	"	33.3
44.5	2.67	"	30.3
42.4	1.31	"	28.1
32.8	.810	"	32.9
20.2	.491	(both valves)	40.3
17.3	.389	"	36.5

Table 4

X-ray Determination of the Percent Aragonite in Specimens of *M. edulis diegensis* Collected at Avila Beach on October 16, 1959

Length (mm.)	Weight (g.)		% Aragonite
76.5	5.68	(one valve)	48.9
62.0	6.59	"	34.6
58.4	4.22	"	40.3
44.1	2.63	"	32.5
41.4	1.28	"	24.2
30.5	.650	"	16.1
18.3	.237	"	18.4

Table 5

X-ray Determination of the Percent Aragonite in Small Specimens of M. californianus from the Pacific Coast of North America (collected between July 15, 1958 and August 3, 1958)

Location	No. of Specimens	Length of Specimens (mm.)	Sample Weight (mg.)	Collecting Time Temperature (^{o}C)	Collecting Time Salinity (^{o}/oo)	% Aragonite
Bahía Sto. Tomás (1)	3	16.4, 14.0, 13.2	630.3	15.3	33.96	20.5
La Jolla (4)	2	20.4, 19.5	1211.0	20.8	34.40	30.5
Avila Beach (8)	4	15.0, 15.3, 13.6, 13.3	1091.5	16.8	34.23	25.9
San Francisco (10)	3	14.2, 14.7, 17.2	698.4	14.4	31.75	27.9
Westport (14)	2	15.8, 17.1	730.8	14.0	34.02	38.3
Bandon (19)	2	15.3, 15.8	519.2	11.0	34.18	27.9
Indian Beach (22)	3	15.5, 13.8, 13.4	519.5	12.9	33.84	27.6

Table 6

X-ray Determination of the Percent Aragonite in Small Specimens of M. edulis (both subspecies) from the Pacific Coast of North America (collected between July 15, 1958 and August 4, 1958)

Location	No. of Specimens	Length of Specimens (mm.)	Sample Weight (mg.)	Collecting Time Temperature (^{o}C)	Collecting Time Salinity (^{o}/oo)	% Aragonite
Halfway House (3)	3	13.8, 13.4, 14.6	452.4	19.8	34.00	24.1
La Jolla (4)	3	15.2, 13.4, 14.5	781.6	20.8	34.40	48.5
Santa Monica (6)	2	13.7, 15.0	417.9	18.8	34.05	32.1
San Martin (9)	3	11.1, 12.0, 11.0	356.1	13.4	34.00	21.6
San Francisco (10)	4	13.7, 11.8, 13.8, 12.3	396.4	14.4	31.75	16.8
Cape Mendocino (15)	3	14.8, 14.8, 12.7	401.8	12.8	34.24	28.9
Ophir (18)	3	15.2, 15.1, 13.0	450.8	12.8	33.77	19.7
Umpqua (20)	3	15.4, 15.7, 14.7	539.6	10.0	33.80	31.0
Waldport (21)	3	13.6, 15.3, 13.2	531.2	10.9	34.33	37.4
Point Grenville (23)	3	13.5, 13.9, 13.0	395.0	11.1	33.66	18.7
Hoh (24)	4	12.2, 11.5, 11.2, 11.8	278.8	12.8	33.66	26.6

Table 7

X-ray Determination of the Percent Aragonite in Larger Specimens of *M. edulis diegensis* and *M. edulis edulis* from the Pacific Coast of North America

Location	Length (mm.)	Subspecies	Weight (1 valve) (g.)	Collecting Time Temperature (^{o}C)	Collecting Time Salinity ($^{o}/oo$)	% Aragonite
La Jolla (4)	37.4	*M. e. d.*	1.42	20.8	34.40	37.2
Corona del Mar (5)	42.7	"	2.26	19.7	34.63	46.7
Santa Monica (6)	46.2	"	1.76	18.8	34.05	32.7
Avila Beach (8)	76.5	"	5.68	18.5	34.01	48.9
"	62.0	"	6.59	"	"	34.6
"	58.4	"	4.22	"	"	40.3
"	44.1	"	2.63	"	"	32.5
"	41.4	"	1.28	"	"	24.2
"	30.5	"	.650	"	"	16.1
"	18.3	"	.237	"	"	18.4
Point Grenville (23)	31.3	*M. e. e.*	.539	11.1	33.66	21.6
Hoh (24)	30.7	"	.539	12.8	33.66	28.4
Neah Bay (25)	30.3	"	1.19	15.8	32.48	12.0

Table 8

X-ray Determinations of Percent Aragonite in Larger Specimens of <u>M. californianus</u> from the Pacific Coast of the United States

Location	Length (mm.)	Weight (1 valve) (g.)	Collecting Time Temperature (°C)	Collecting Time Salinity (°/oo)	Mean Annual Temperature* (°C)	% Aragonite
La Jolla (4)	53.5	4.99	20.8	34.40	16.9	34.0
"	45.3	3.21	"	"	"	25.7
"	41.3	1.79	"	"	"	18.0
"	35.4	1.40	"	"	"	27.4
"	34.8	1.69	"	"	"	29.4
"	26.1	.577	"	"	"	28.8
"	23.1	.435	"	"	"	24.8
Corona del Mar (5)	110.0	26.75	19.7	34.63	16.4	38.6
Santa Monica (6)	65.3	6.27	18.2	33.78	15.9	32.3
Avila Beach (8)	69.2	9.48	18.5	34.01	13.1	22.7
"	60.1	9.20	16.8	34.23	"	20.9
"	47.6	5.25	"	"	"	23.0
"	47.0	4.21	"	"	"	19.6
"	39.0	2.69	"	"	"	26.4
"	35.7	1.92	"	"	"	24.9
"	34.2	1.79	"	"	"	26.6
"	24.4	.753	"	"	"	34.5
Pacific Grove (10)	91.7	27.62	14.9	34.01	12.9	23.5
Westport (15)	60.2	8.67	14.0	34.02	12.0	31.9

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* From U. S. Coast and Geodetic Survey (1956) or interpolated from this data.

Table 8 (con't.)

Location	Length (mm.)	Weight (1 valve) (g.)	Collecting Time Temperature (°C)	Collecting Time Salinity (°/oo)	Mean Annual Temperature (°C)	% Aragonite
Westport (15)	55.2	7.94	14.0	34.02	12.0	28.4
"	50.2	5.12	"	"	"	31.0
"	46.5	3.70	"	"	"	30.6
"	32.3	1.30	"	"	"	34.5
"	27.3	.739	"	"	"	34.1
"	22.3	.578	"	"	"	34.8
Waldport (22)	55.3	4.91	10.9	34.33	10.8	17.5
"	45.7	2.87	"	"	"	20.1
"	42.6	2.01	"	"	"	21.7
"	38.5	1.56	"	"	"	19.8
"	35.4	1.29	"	"	"	19.7
"	31.2	.771	"	"	"	16.4
"	23.9	.612	"	"	"	21.7
Hoh (25)	64.2	8.11	12.8	33.66	9.9	20.5
"	47.8	3.52	"	"	"	22.0
"	45.7	3.48	"	"	"	22.1
"	41.5	2.85	"	"	"	22.9
"	39.5	1.94	"	"	"	26.5
"	37.1	2.14	"	"	"	14.6
"	36.5	1.37	"	"	"	26.0

Table 9

Mean Temperatures of Growth as Determined by Oxygen Isotopic Analysis for M. _californianus_ from Various Points along the Pacific Coast of North America

Location	Length (mm.)	Weight (g.)	Mean Annual Temperature (°C)	% Aragonite	δ_{O}^{18} of Shell (°/oo)	δ_{O}^{18} of Water (°/oo)	δ_{C}^{13} of Shell (°/oo)	O isotopic Temperature (°C)
La Jolla (4)	53.5	4.99	16.9	34.0	-0.9	-0.4	+0.4	18.5
Corona del Mar (5)	110.0	26.75	16.4	38.6	-1.1	-0.4	0.0	19.5
"	67.3	7.30	"	33.4	-1.0	-0.4	0.0	19.0
"	54.0	3.19	"	26.3	-1.0	-0.4	+1.4	19.0
Avila Beach (8)	69.2	9.48	13.1	22.7	-0.3	-0.5	+0.5	15.5
Pacific Grove (10)	91.7	27.62	12.9	23.5	+0.3	-0.4	+0.6	13.5
Westport (15)	60.2	8.67	12.0	31.9	+0.2	-0.5	-0.7	13.5
Hoh (25)	64.2	8.11	9.9	20.5	-0.8	-0.8	-0.3	16.5

Table 10

X-ray Determination of the Percent Aragonite in Specimens of *M. edulis edulis* from Washington and San Francisco Bay

Location	Length (mm.)	Weight (1 valve) (g.)	Temperature at Collecting Time (^{o}C)	Salinity at Collecting Time ($^{o}/oo$)	% Aragonite
Neah Bay (26)	30.3	1.19	15.8	32.48	12.0
Port Townsend (27)	31.7	1.23	14.5	31.73	18.8
Brinnon (28)	30.5	1.33	23.8	28.15	23.1
Eldon (29)	30.7	1.03	23.5	27.56	25.2
Potlatch (30)	29.2	.932	25.0	18.60	24.0
San Francisco (11)	12.9 (ave.)	.099	14.4	31.75	16.8
Sausalito (12)	28.3	.787	16.1	28.75	25.5
San Pedro (13)	37.5	.669	22.9	26.65	25.8
China Camp (14)	25.1	.613	22.5	19.96	34.1

Table 11

X-ray Determination of the Percent Aragonite in Specimens of *M. californianus* and *M. edulis diegensis* from Corona del Mar Showing Microenvironmental Effects

Species	Collecting Date	No. of Specimens	Length (mm.)	Sample Weight (mg.)	% Aragonite	Remarks
M. e. d.	5- 7-59	1	13.6	80.5	29.0	Opposite valves of same specimen
M. e. d.	5- 7-59	1	13.5	82.0	31.5	
M. e. d.	5- 7-59	1	12.5	76.4	23.5	Opposite valves of same specimen
M. e. d.	5- 7-59	1	12.5	71.5	20.5	
M. e. d.	5- 7-59	1	13.5	79.3	29.0	
M. e. d.	5- 7-59	1	13.7	79.8	25.5	
M. e. d.	5- 7-59	1	13.7	84.9	25.5	
M. c.	7-24-59	3	22.3, 21.7, 18.5	1784.3	32.0	
M. e. d.	9-16-59	3	17.3, 19.1, 19.5	1150.9	27.5	High in intertidal
M. e. d.	9-16-59	2	20.2, 15.8	508.5	28.6	Low in intertidal

Table 12

Percent Aragonite in Longitudinal Sections of Shells of *M. californianus* from the Pacific Coast of North America

Location	Length (mm.)	Weight (g.)	Temperature at Collecting Time (°C)	Salinity at Collecting Time (°/oo)	Mean Annual Temperature (°C)	% Aragonite
Bahía Sto. Tomás (1)	45.0	3.03	15.3	33.96	14.5	30.4
El Morro (2)	49.5	4.32	18.9	34.22	18.0	38.0
"	39.9		"	"	"	30.5
"	38.7		"	"	"	28.0
"	31.8		"	"	"	40.3
La Jolla (4)	53.7	5.12	20.8	34.40	16.9	46.3
"	50.5	4.78	"	"	"	40.9
"	45.6		"	"	"	29.7
"	41.9	1.77	"	"	"	27.5
"	34.7		"	"	"	36.4
"	26.5		"	"	"	33.9
"	22.7		"	"	"	41.9
Corona del Mar (5)	111.7	26.77	19.7	34.63	16.4	44.9
"	79.0	11.89	"	"	"	37.4
"	73.2	7.72	"	"	"	33.8
"	63.1	5.01	"	"	"	42.8
Santa Monica (6)	40.4	3.25	18.8	34.05	15.9	51.5
"	65.3	6.23	18.2	33.78	"	39.8
"	53.0	3.24	"	"	"	35.1
"	51.6	2.52	"	"	"	33.5
Avila Beach (8)	70.8	9.39	18.5	34.01	13.1	26.1
"	47.0	4.16	16.8	34.23	"	20.2
"	47.3		"	"	"	19.1
"	34.9		"	"	"	32.9
"	33.8		"	"	"	27.3

Table 12 (con't.)

Location	Length (mm.)	Weight (g.)	Temperature at Collecting Time (°C)	Salinity at Collecting Time (°/oo)	Mean Annual Temperature (°C)	% Aragonite
Avila Beach (8)	23.7		16.8	34.23	13.1	49.8
Pacific Grove (10)	92.8	28.04	14.9	34.01	12.9	30.4
"	87.7	20.20	"	"	"	18.2
"	80.5	14.62	"	"	"	27.9
San Francisco (11)	50.6	5.56	14.4	31.75	13.2	13.5
Westport (15)	60.2	8.67	14.0	34.02	12.0	30.9
"	49.9		"	"	"	35.2
"	46.6		"	"	"	32.4
"	27.2		"	"	"	31.8
"	22.3		"	"	"	46.8
Trinidad (17)	46.8	3.17	14.7	34.38	11.6	28.0
Crescent City (18)	44.5	3.37	18.8	30.48	11.6	42.9
Ophir (19)	44.2	3.25	12.8	33.77	11.2	21.6
Bandon (20)	47.6	5.22	11.0	34.18	11.1	11.2
Waldport (22)	55.3	4.91	10.9	34.33	10.8	25.3
"	52.9	5.51	"	"	"	22.9
"	45.7	2.87	"	"	"	17.1
"	42.6	2.01	"	"	"	28.4
"	38.5	1.56	"	"	"	23.3
"	35.4	1.29	"	"	"	16.0
"	31.2	.771	"	"	"	14.9
"	23.9	.612	"	"	"	33.4
Indian Beach (23)	52.3	3.11	12.9	33.84	10.4	20.3
Hoh (25)	64.2	8.11	12.8	33.66	9.9	20.0
"	47.8	3.56	"	"	"	19.0
"	45.5	3.54	"	"	"	14.5
"	41.6	2.83	"	"	"	23.2
"	39.5	1.94	"	"	"	26.2
"	37.1	2.14	"	"	"	14.4

Table 13

Shell Structural Types in *M. californianus* from Southern California and Northern Baja California

Location	No. of Specimens	Longest Specimen (mm.)	Shortest Specimen (mm.)	Range of Structural Type	Standard Deviation	Mean Value (± Probable Error of Mean)
El Morro (2)	4	49.5	31.8	1-3	0.9	1.5 ± 0.4
La Jolla (4)	8	53.7	34.7	1-4	0.9	2.6 ± 0.2
Corona del Mar (5)	12	111.7	34.4	1-6	1.4	3.2 ± 0.3
Santa Monica (6)	8	76.0	40.4	2-6	1.9	3.9 ± 0.5
Port Hueneme (7)	13	67.1	39.3	4-6	0.6	4.8 ± 0.1
Avila Beach (8)	12	70.8	33.8	5-9	1.3	6.9 ± 0.3
Pacific Grove (10)	10	92.8	47.1	4-9	1.4	7.0 ± 0.3

Table 14

Emission Spectrographic Determinations of Strontium and Magnesium in the Outer Two mm. of the Outer Prismatic Layer in M. edulis diegensis from the Kerckhoff Marine Laboratory at Corona del Mar, California

Date Collected	Length of Specimens (mm.)	Estimated Growth Temperature (°C)	Weight % Mg	Mole % $MgCO_3$	Weight % Sr	Mole % $SrCO_3$
4-29-58	14.5, 13.4 13.6, 14.3	--	0.153 ± 0.016	0.630 ± 0.065	0.118 ± 0.004	0.134 ± 0.005
6- 6-58	11.2, 11.7 11.8, 11.8 12.3	19.1	0.110 ± 0.013	0.452 ± 0.053	0.131 ± 0.008	0.149 ± 0.010
7-25-58	11.9, 9.3 9.1, 9.3 9.0	20.4	0.135 ± 0.009	0.555 ± 0.039	0.145 ± 0.011	0.165 ± 0.113
9-13-58	16.0, 12.7 12.3, 13.2	20.2	0.159 ± 0.016	0.653 ± 0.065	0.152 ± 0.004	0.173 ± 0.005
10-24-58	13.8, 14.7 13.8, 14.2	19.4	0.156 ± 0.011	0.641 ± 0.047	0.133 ± 0.004	0.151 ± 0.005
12- 5-58	13.5, 12.0 11.5, 11.4 10.6	16.2	0.126 ± 0.022	0.519 ± 0.091	0.129 ± 0.002	0.147 ± 0.003
1-16-59	14.0, 12.8 13.4, 12.7 11.9	15.6	0.108 ± 0.008	0.445 ± 0.033	0.119 ± 0.007	0.135 ± 0.008
2-27-59	18.3, 13.1 13.5, 14.0	15.3	0.106 ± 0.018	0.437 ± 0.073	0.116 ± 0.005	0.132 ± 0.006
4-13-59	12.6, 12.5 11.1, 11.5 10.7	16.3	0.109 ± 0.017	0.450 ± 0.069	0.125 ± 0.004	0.142 ± 0.005

Table 15

X-ray Fluorescence Determination of the Strontium Content in the Outer Prismatic Layer of *Mytilus* from Various Points along the California Coast

Location	Date Collected	No. of Specimens	Species	Length of Specimens (mm.)	Estimated Growth Temperature (°C)	Weight % Sr $\pm\sigma$	Mole % $SrCO_3 \pm \sigma$
La Jolla (4)	7-15-58	4	*M. c.*	24.4, 19.6 19.2, 19.0	18.9 ± 0.3	0.131 ± 0.002	0.149 ± 0.002
Corona del Mar (5)	1-15-60	5	*M. e. d.*	20.5, 24.5 24.2, 24.1 18.8	14.0 ± 0.4	0.117 ± 0.002	0.133 ± 0.002
"	2-25-60	3	*M. e. d.*	30.3, 32.8 22.3	12.6 ± 0.4	0.115 ± 0.001	0.131 ± 0.001
"	4-13-59	7	*M. e. d.*	8.7, 9.5 9.7, 9.8 10.2, 10.1 10.5	16.3 ± 0.5	0.122 ± 0.001	0.139 ± 0.001
Santa Monica (6)	7-22-58	5	*M. c.*	23.7, 24.0 22.2, 19.9 17.0	18.1 ± 0.3	0.126 ± 0.002	0.143 ± 0.002
"	10-31-59	4	*M. c.*	23.8, 19.5 32.0, 16.-	19.4 ± 0.2	0.133 ± 0.001	0.151 ± 0.001
"	"	1	*M. c.*	33.7	" "	0.131 ± 0.001	0.149 ± 0.001
"	"	1	*M. c.*	53.2	" "	0.131 ± 0.002	0.149 ± 0.002
"	"	1	*M. c.*	71.7	" "	0.127 ± 0.001	0.144 ± 0.001
"	"	1	*M. c.*	91.7	" "	0.126 ± 0.002	0.143 ± 0.002
Avila Beach (8)	7-22-58	4	*M. c.*	20.5, 19.4 22.8, 22.6	14.8 ± 0.2	0.122 ± 0.002	0.138 ± 0.002
"	10-16-59	4	*M. c.*	25.6, 21.4 17.5, 16.8	16.3 ± 0.2	0.133 ± 0.002	0.151 ± 0.002

Table 15 (con't.)

Location	Date Collected	No. of Specimens	Species	Length of Specimens (mm.)	Estimated Growth Temperature (°C)	Weight % Sr ± σ	Mole % $SrCO_3$ ± σ
Avila Beach (8)	10-16-59	1	*M. c.*	69.5	16.3 ± 0.2	0.124 ± 0.001	0.141 ± 0.001
Pacific Grove (10)	10-18-59	3	*M. c.*	24.4, 15.7 18.2	14.9 ± 0.2	0.120 ± 0.001	0.136 ± 0.001

Table 16

X-ray Fluorescence Determination of the Strontium Content in the Outer Prismatic Layer of *Mytilus* from the Open Coast at Corona del Mar

Date Collected	No. of Specimens	Length of Specimens (mm.)	Estimated Growth Temperature (°C)	Weight % Sr	Mole % $SrCO_3$
7-25-58	4	14.2, 15.0, 13.6, 14.6	18.3 ± 0.5	0.124 ± 0.001	0.141 ± 0.001
2-27-59	4	14.7, 17.9, 17.8, 15.0	15.0 ± 0.2	0.115 ± 0.001	0.131 ± 0.001
4-13-59	3	17.2, 16.3, 15.6	16.1 ± 0.4	0.117 ± 0.001	0.133 ± 0.001
7-24-59	4	17.4, 19.3, 19.5, 15.5	20.3 ± 0.5	0.117 ± 0.001	0.133 ± 0.001
10-29-59	2½	38.-, 23.2, 16.3	19.5 ± 0.4	0.122 ± 0.001	0.138 ± 0.001

Table 17

X-ray Fluorescence Determination of the Strontium Content in the Outer Prismatic Layer of M. edulis edulis from Locations with Reduced Salinity

Location	Date Collected	No. of Specimens	Length of Specimens (mm.)	Collecting Time Salinity ($^{o}/oo$)	Collecting Time Temperature (^{o}C)	Weight % Sr ± σ	Mole % $SrCO_3$ ± σ
Neah Bay (26)	8- 4-58	3	19.8, 18.5 19.9	32.48	15.8	0.126 ± 0.002	0.143 ± 0.002
Port Townsend (27)	8- 5-58	3	17.3, 18.0 17.8	31.73	14.5	0.131 ± 0.003	0.149 ± 0.003
Brinnon (28)	8- 5-58	3	21.2, 20.5 22.2	28.15	23.8	0.126 ± 0.001	0.143 ± 0.001
Twanoh Park (31)	8- 5-58	3	20.0, 20.9 23.5	25.75	25.0	0.126 ± 0.001	0.143 ± 0.001
Potlatch (30)	8- 5-58	3	20.0, 23.5 20.8	18.60	25.0	0.128 ± 0.001	0.145 ± 0.001
Sausalito (12)	7-30-58	2	23.1, 21.7	28.75	16.1	0.115 ± 0.001	0.131 ± 0.001
China Camp (14)	7-30-58	3	16.5, 16.6 16.5	19.96	22.5	0.130 ± 0.001	0.148 ± 0.001

Table 18

X-ray Fluorescence Determination of the Strontium Content of Segments of the Outer Prismatic Layer Parallel to the Growth Lines of M. <u>californianus</u>

Location	Length of Specimens (mm.)	Distance from Posterior End of Sample (mm.)	Weight % Sr ± σ	Mole % $SrCO_3$ ± σ
Corona del Mar (5)	92.0	0- 2	0.114 ± 0.001	0.129 ± 0.001
"	"	9-11	0.116 ± 0.001	0.132 ± 0.001
"	"	19-21	0.118 ± 0.001	0.134 ± 0.001
"	"	29-31	0.121 ± 0.001	0.137 ± 0.001
"	"	39-41	0.127 ± 0.001	0.144 ± 0.001
"	"	44-46	0.120 ± 0.001	0.136 ± 0.001
"	"	49-51	0.123 ± 0.001	0.140 ± 0.001
"	"	54-56	0.127 ± 0.0	0.144 ± 0.0
"	"	59-61	0.125 ± 0.001	0.142 ± 0.001
"	"	69-71	0.118 ± 0.003	0.134 ± 0.003
Pacific Grove (10)	87.-	0- 2	0.115 ± 0.001	0.131 ± 0.001
"	"	5- 6	0.110 ± 0.001	0.125 ± 0.001
"	"	9-11	0.112 ± 0.001	0.127 ± 0.001
"	"	19-21	0.111 ± 0.001	0.126 ± 0.001
"	"	29-31	0.117 ± 0.001	0.133 ± 0.001
"	"	39-41	0.120 ± 0.001	0.136 ± 0.001
"	"	44-46	0.112 ± 0.001	0.127 ± 0.001
"	"	49-51	0.112 ± 0.0	0.127 ± 0.0
"	"	59-61	0.120 ± 0.001	0.136 ± 0.001
"	"	69-72	0.112 ± 0.001	0.127 ± 0.001

Table 19

X-ray Fluorescence Determination of the Strontium Content of the Nacreous Layer of *Mytilus*

Location	Date Collected	No. of Specimens	Species	Length of Specimens (mm.)	Estimated Growth Temperature (°C)	Weight % Sr ± σ	Mole % $SrCO_3$ ± σ
La Jolla (4)	7-15-58	4	*M. c.*	44.6, 50.3 50.3, 35.-	18.9 ± 0.3	0.141 ± 0.002	0.160 ± 0.002
Corona del Mar (5)	2-25-60	5	*M. e. d.*	35.2, 37.7 37.2, 35.6 38.2	12.6 ± 0.4	0.199 ± 0.002	0.227 ± 0.002
Santa Monica (6)	7-22-58	1	*M. c.*	50.2	18.1 ± 0.3	0.133 ± 0.001	0.151 ± 0.001
"	10-31-59	1	*M. c.*	53.2	19.4 ± 0.2	0.124 ± 0.001	0.141 ± 0.001
Pacific Grove (10)	10-18-59	1	*M. c.*	87.0	14.9 ± 0.2	0.155 ± 0.002	0.177 ± 0.002

Table 20

Structural Type of Fossil Specimens of *M. californianus*

Location	No. of Specimens	Longest Specimen* (mm.)	Shortest Specimen* (mm.)	Range of Structural Type	Standard Deviation	Mean Value (± Probable Error of Mean)
Rosarito Beach	10	70.0	35.0	2-6	1.0	4.4 ± 0.2
Torrey Pines	9	99.6	41.0	2-4	0.9	3.2 ± 0.2
Newport Bay	8	138.0	52.6	1-4	1.0	3.4 ± 0.3
Cayucos	4	90.	60.	7-9	0.7	8.0 ± 0.3

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* Lengths of broken specimens estimated

Table 21

X-ray Fluorescence Determination of the Strontium Content of Segments of the Outer Prismatic Layer Parallel to the Growth Lines of Fossil Specimens of M. californianus

Location	Length of Specimens (mm.)	Distance from Posterior End of Sample (mm.)	Weight % Sr $\pm \sigma$	Mole % $SrCO_3 \pm \sigma$
Rosarito Beach	71.-	0- 2	0.112 ± 0.001	0.127 ± 0.001
"	"	4- 6	0.115 ± 0.001	0.131 ± 0.001
"	"	9-11	0.118 ± 0.001	0.134 ± 0.001
"	"	19-21	0.122 ± 0.001	0.138 ± 0.001
"	"	29-32	0.122 ± 0.0	0.138 ± 0.0
"	"	37-41	0.124 ± 0.002	0.141 ± 0.002
"	"	55-58	0.115 ± 0.001	0.131 ± 0.001
Torrey Pines	84.5	0- 2	0.114 ± 0.0	0.130 ± 0.0
"	"	9-11	0.115 ± 0.001	0.131 ± 0.001
"	"	19-21	0.120 ± 0.0	0.136 ± 0.0
"	"	29-31	0.113 ± 0.0	0.128 ± 0.0
"	"	39-42	0.121 ± 0.001	0.137 ± 0.001
"	"	49-52	0.128 ± 0.001	0.145 ± 0.001
"	"	59-62	0.121 ± 0.001	0.137 ± 0.001
Newport Bay	105.-	0- 2	0.113 ± 0.0	0.128 ± 0.0
"	"	9-11	0.111 ± 0.001	0.126 ± 0.001
"	"	19-21	0.115 ± 0.001	0.131 ± 0.001
"	"	29-31	0.108 ± 0.0	0.123 ± 0.0
"	"	49-51	0.110 ± 0.001	0.125 ± 0.001
"	"	69-71	0.114 ± 0.001	0.130 ± 0.001
"	"	90-93	0.127 ± 0.0	0.144 ± 0.0
Cayucos	82.0	0- 2	0.112 ± 0.0	0.127 ± 0.0
"	"	10-12	0.114 ± 0.001	0.130 ± 0.001

Table 21 (con't.)

Location	Length of Specimens (mm.)	Distance from Posterior End of Sample (mm.)	Weight % Sr $\pm \sigma$	Mole % $SrCO_3 \pm \sigma$
Cayucos	82.0	14-16	0.114 ± 0.001	0.130 ± 0.001
"	"	19-21	0.113 ± 0.001	0.128 ± 0.001
"	"	31-33	0.113 ± 0.0	0.128 ± 0.0
"	"	46-48	0.113 ± 0.001	0.128 ± 0.001
"	"	56-60	0.128 ± 0.0	0.145 ± 0.0

Table 22

Mineralogy of Fossil Specimens of *Mytilus* from the Pacific Coast of North America

Location	Species	Length of Specimens (mm.)	% Aragonite
Rosarito Beach	*M. c.*	45.-	19.0
Torrey Pines	*M. c.*	99.6	27.2
Newport Bay	*M. c.*	89.1	27.9
San Francisco	*M. e. e.*	8.8, 10.7, 8.6, 8.6	20.9

Table 23

Oxygen and Carbon Isotopic Analysis of Portions of the Outer Prismatic Layer of Fossil Specimens of *Mytilus*

Location	Species	Mole % $SrCO_3$	$SrCO_3$ Temperature* ($^\circ C$)	δO^{18} ($^\circ/oo$)	δC^{13} ($^\circ/oo$)	O isotope Temperature** ($^\circ C$)	δO^{18} of Water*** ($^\circ/oo$)
Rosarito Beach	*M. c.*	0.134 ± 0.001	15.0	1.2	-.1	11.5	+0.8
Torrey Pines	*M. c.*	0.137 ± 0.001	15.0	.4	.3	15.0	0.0
Newport Bay	*M. c.*	0.127 ± 0.001	13.0	-.7	-.6	19.5	-1.4
Cayucos	*M. c.*	0.130 ± 0.0	13.5	.8	-.2	13.0	+0.1
San Francisco	*M. e. e.*	0.127 ± 0.001	11.5	.1	-.6	16.0	-1.1

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* Temperature of deposition based on $SrCO_3$ content

** Temperature of deposition based on δO^{18} considering δO^{18} of water = 0

*** δO^{18} of water considering the $SrCO_3$ temperature to be the actual temperature of deposition

APPENDIX II

PHOTOGRAPHIC PLATES

Facing p. 215

PLATE I

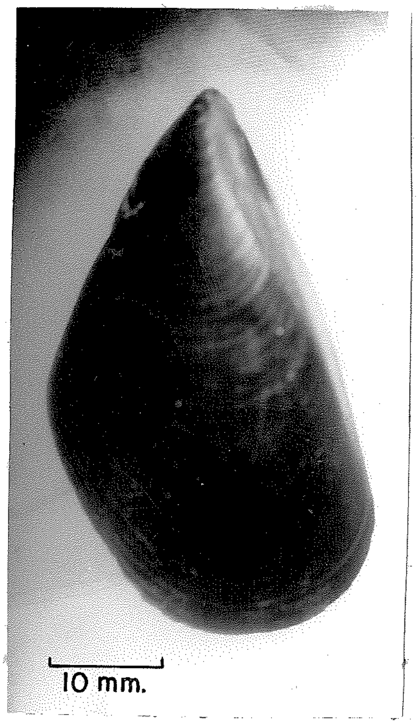
a. - *Mytilus californianus*

b. - *M. edulis edulis*

c. - *M. edulis diegensis*

a

b



c

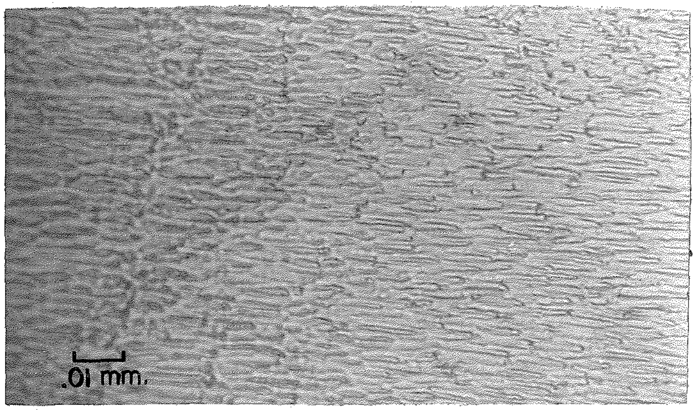
PLATE II

a. - Thin section showing the outer prismatic layer and periostracum of M. californianus. The periostracum bends around the posterior end of the shell. The faint lines which recline slightly to the left are crystal boundaries. In places, these lines can be seen to diverge in a fan-shaped pattern. The faint, nearly horizontal lines are growth lines. The dark band showing in both the periostracum and outer prismatic layer in this photograph are not characteristic.

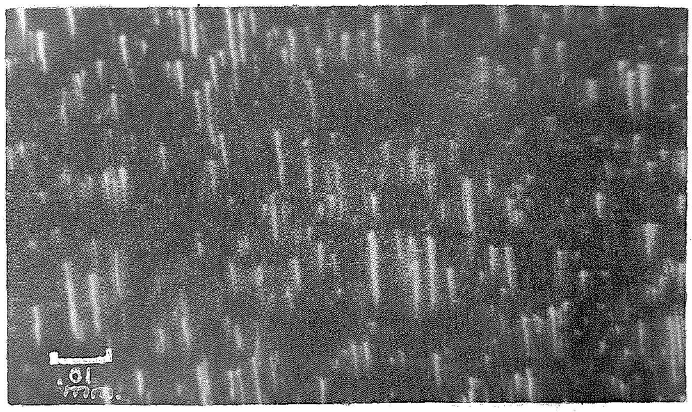
b. - Peel showing calcite crystals of the outer prismatic layer. The plane of the section is nearly but not quite parallel to the long axes of the crystals. This peel contains actual crystals as well as crystal impressions.

c. - Peel containing calcite crystals of the outer prismatic layer (crossed Nicols).

a



b



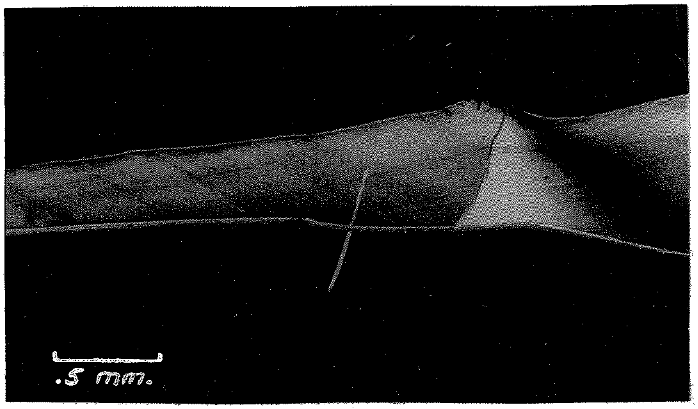
c

PLATE III

a. - Outer prismatic layer of M. edulis diegensis (crossed Nicols). The anterior end is toward the left. The lines reclining toward the left in the left half of this photograph are the crystal boundaries showing the normal orientation found in this species. The right side of the photograph shows a very pronounced crystal fan. The irregularity at the top of the section suggests that this fan formed at a point where the shell was damaged as it was being deposited. The nearly horizontal lines are growth lines. The light band at the bottom of the section is the thin edge of the nacreous layer.

b. - Transverse thin section of M. californianus (crossed Nicols). The lighter, top part of the section is the outer prismatic layer. The darker zone at the bottom of the section is the nacreous layer. The other lines which are parallel to the layer boundary are growth lines. The top of the section is irregularly worn.

c. - Peel showing the inner surface of nacreous layer. The zigzag lines crossing the photograph are formed by the overlapping of the lamellae of crystals. The individual "bumps" on the lamellae are individual aragonite crystals. The hazy polygonal outline between lines are probably also individual crystals.



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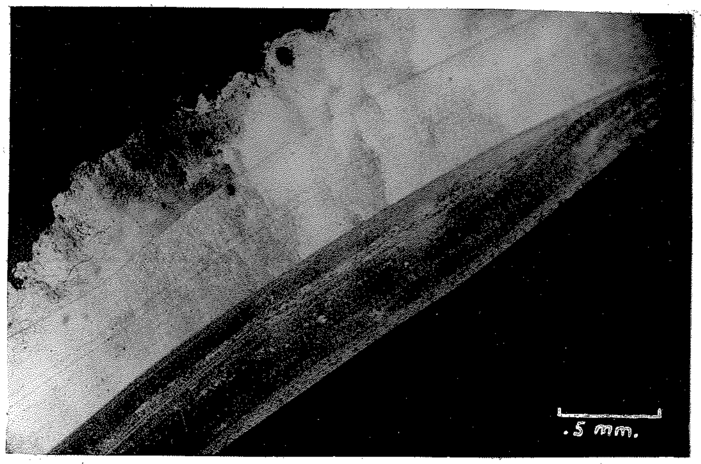

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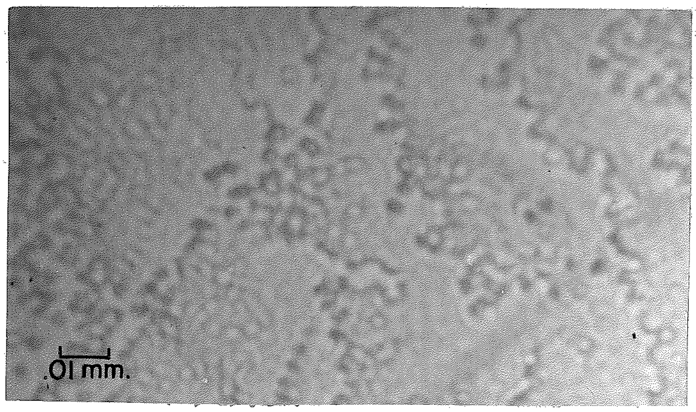
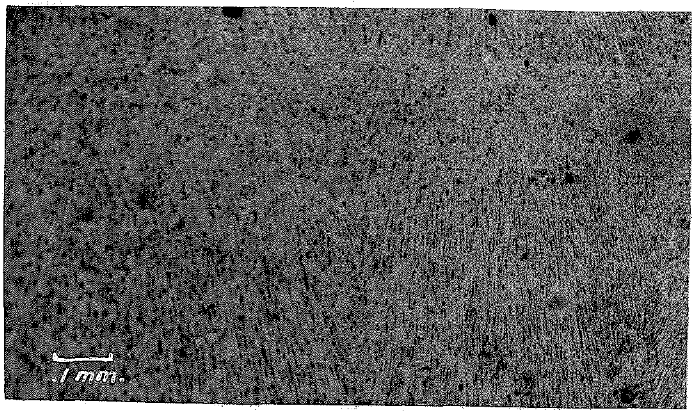


c

PLATE IV

a. - Peel showing the inner prismatic layer of *M. californianus*. The small, nearly vertical bars are individual calcite crystals. They diverge in their characteristic fan-shaped arrangement in this photograph. The horizontal band of fine texture crossing a quarter inch below the top is a "color band" which appears to be characteristic of summer deposition. The crystal fans appear to be interrupted by this zone and then continue below it.

b. - Peel of the inner surface of the inner prismatic layer. Due to the irregular nature of this surface, part of this photograph is out of focus. The polygonal outlines in the rectangle are the cross-sectional boundaries of individual crystals. The light areas probably represent the organic framework and the darker areas the actual calcite. Crystal outlines can be seen less clearly in other portions of the photograph.



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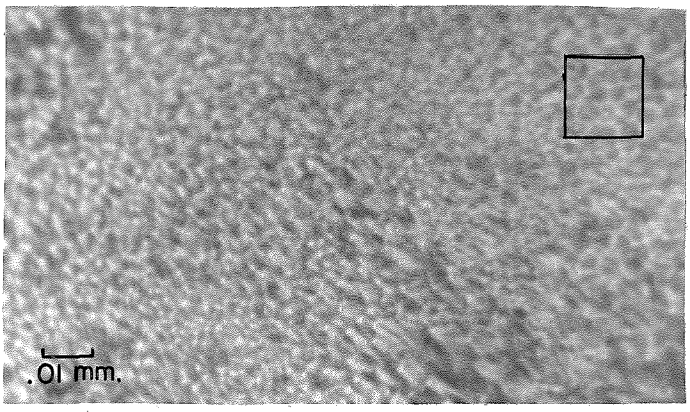


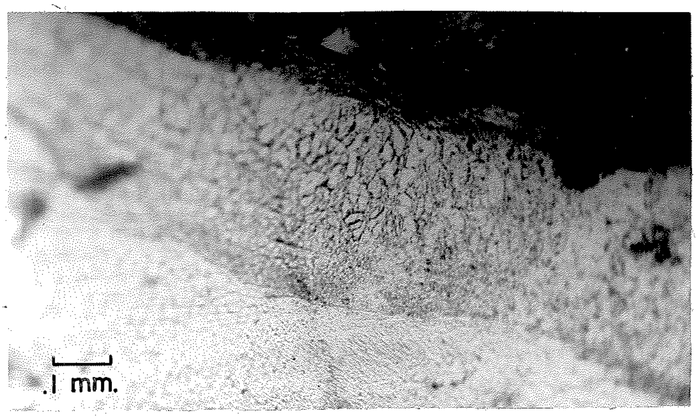
b

Facing p. 219-

PLATE V

a. - Peel showing the blocky aragonite layer. This layer appears to form only under the muscle attachments. The area below this layer in the photograph is the inner prismatic layer. Small tongues of the blocky layer can be seen to extend into the inner prismatic layer at several points in this section, particularly in the poorly focused area at the right.

b. - Peel showing intertonguing of nacreous and inner prismatic layer in *M. californianus*. The anterior end of the shell is to the left. The nacreous tongue presumably formed during the summer.



a

b

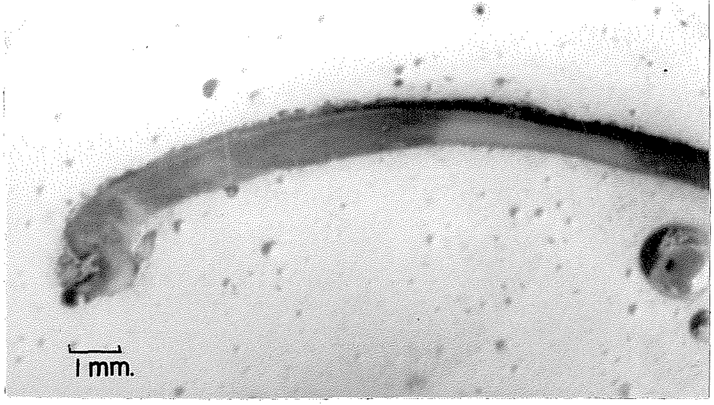
Facing p. 220

PLATE VI

a. - Longitudinal polished section of *M. edulis diegensis*. Staining of this section is not well shown by the photograph. The thin layer at the top is the outer prismatic layer. Most of the remainder of the section is the nacreous layer. The light material in the extreme anterior end is beak calcite.

b. - Longitudinal polished section of *M. edulis edulis*. The outer prismatic and nacreous layers are clearly visible in this section. The entire beak area is composed of calcite. A wedge of this calcite extends forward from the beak for a short distance.

c. - Interior of a valve of *M. californianus* showing the inner prismatic layer. The mottled area nearest the beak is the inner prismatic layer. The smooth white and the shiny area are the nacreous layer. The outermost rim in the posterior portion of the shell is the outer prismatic layer.



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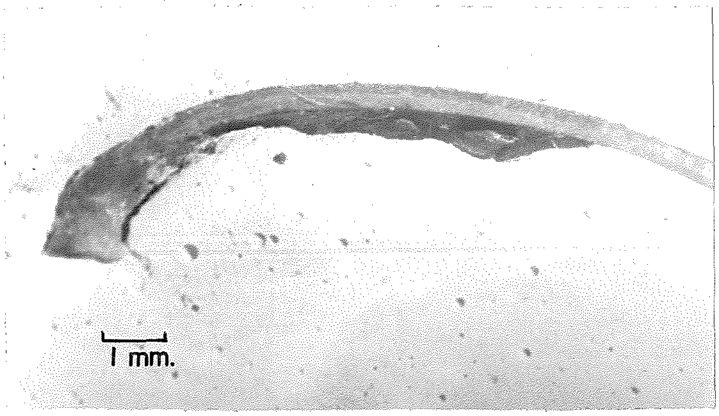
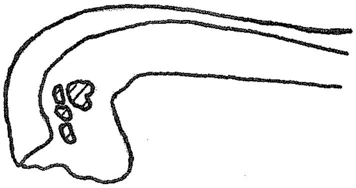


b

c

PLATE VII and VIII

Photographs and drawings of sections showing shell structural types. The drawings on the left were traced from the photographs to more clearly show relationships between the layers. The lined areas are beak calcite and the inner prismatic layer. The numbers between the drawings and photographs are structural types. See the text for a description of the structural types.



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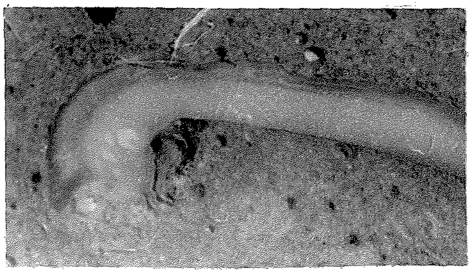

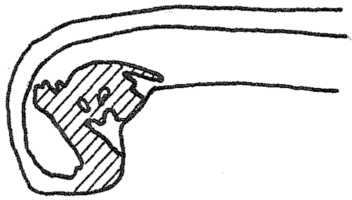

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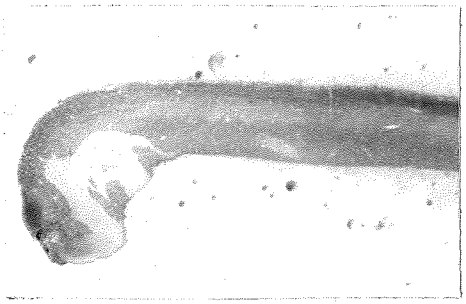

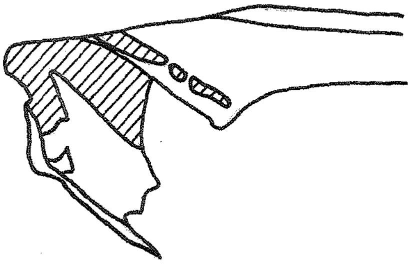

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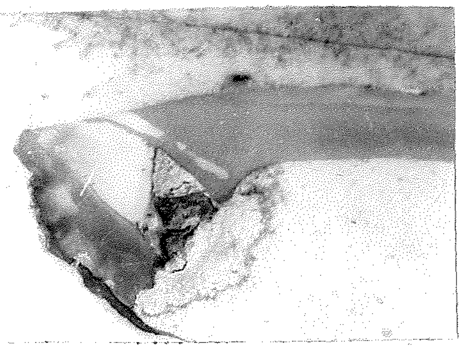

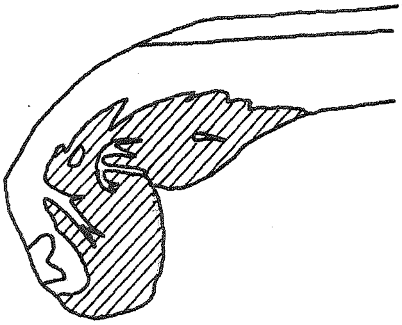

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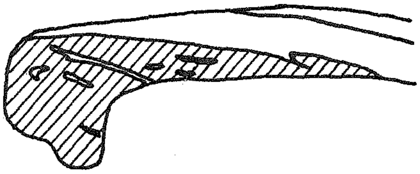

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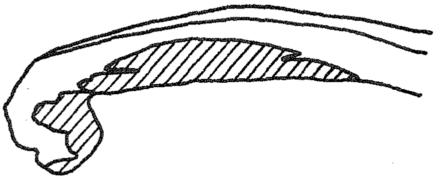

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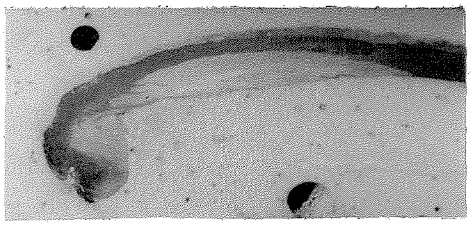

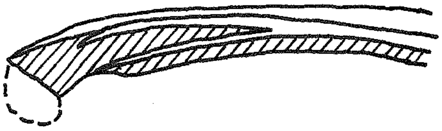

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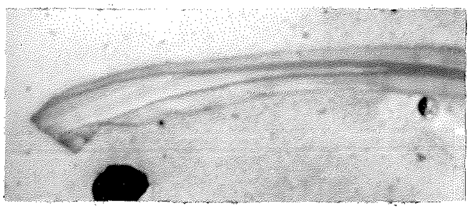

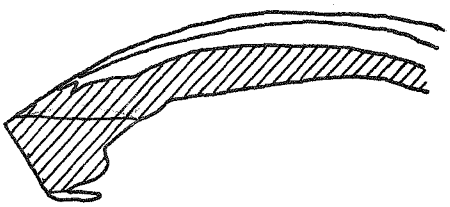

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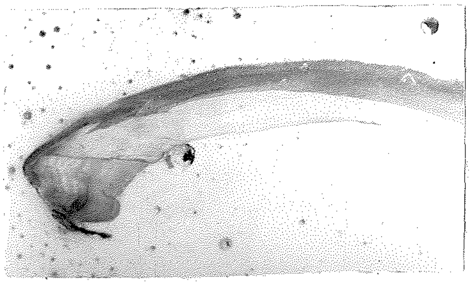

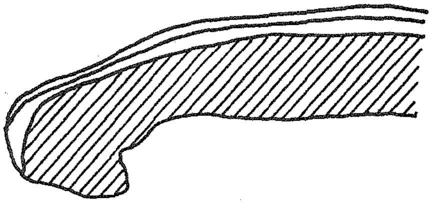

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