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A RESURGENT POPULATION OF THE CALIFORNIA BAY-MUSSEL (MYTILUS EDULIS DIEGENSIS)[1]

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ONE TEXT FIGURE AND TWO PLATES (TWENTY-THREE FIGURES)

It is well known that wide fluctuations in the populations of the constituent members of a community are of common occurrence. For some of these the causes are known and the course of the waxing and waning of the population can be predicted. Some are cyclical; for others the causal relations are obscure and for some only a single rise or fall has yet been recorded. Such fluctuations have been reported many times among the bivalve mollusks and are presumably as frequent as in any other group of organisms. But there has seldom been observed a more rapid change in population density than has been witnessed recently relative to the bay-mussel on the coast of southern California.

During the past 3 years this mussel, which evidently represents a previously undescribed subspecies, has appeared in unprecedented abundance, not only in the bays and inlets which are its usual habitat but also in suitable situations on the open coast. When recently discovered at the pier of the Scripps Institution of Oceanograhpy at La Jolla, in August, 1943, only one small colony was found and that consisted entirely of young individuals, the largest being less than 50 mm. in length and apparently about 6 months of age. This is considered as evidence of the recent arrival of the colony, because no indi-

[1] Contributions from the Scripps Institution of Oceanography of the University of California, New Series no. 284.

vidual of that subspecies had been reported from the pier since 1927.

Within a few weeks after its recent discovery on the piles this mussel was found in considerable numbers and by the following spring its colonies covered nearly all the available spaces in the lower portion of the intertidal zone, with scattered groups nearly to the bottom, at a depth of about 3 meters below the low-tide level. Other colonies occupied many of the adjacent rocks. Many of the young colonies consisted of hundreds or thousands of individuals associated in compact masses with no spaces for additional growth. This sometimes resulted in the production of several layers of shells, while in other situations many of the competitors for space were eliminated. As many as 163 young mussels 2 to 7 mm. in length have been counted on 1 sq. in. of the piling. This would be at the rate of 23,472 per square foot but not all the space in any square foot was covered, since the young mussels, like other sedentary invertebrates, tend to settle in patches. Of the 163 mentioned, not more than two could have survived to the normal reproductive size without migrating to adjacent areas.

Colonies that had established themselves too high up in the intertidal zone perished during the summer, as did also many of the individuals which seemed to be more favorably situated among the sea-mussels. In the winter of 1944–1945 this subspecies was collected by Dr. Carl L. Hubbs and party at various localities along the coast from Redondo Beach, California, to Estero de Punta Banda, Lower California, including San Pedro, Newport Bay, Oceanside, Pacific Beach, Mission Bay, San Diego Bay and Tia Juana Slough. In the summer of 1945 it was common at many intermediate localities.

The rapidly growing populations of this mussel and the varied configuration assumed by the shells as the population spread to previously unoccupied habitats had attracted attention at Newport Bay at least a year before it was found at La Jolla. By 1944–1945 these mussels had become a nuisance in Newport, Mission and San Diego bays, covering piles, boats, ropes, mooring floats and docks. However, they provided an abundant supply of bait for fishermen. In some protected areas they also formed more or less extensive beds on the surface of sand and mud at a depth of several meters, particularly where there were scattered stones to furnish attachment.

The rapid increase of the population suggested the introduction of some foreign species but comparison with specimens collected in the same region more than a quarter of a century ago seems to confirm the identity of the newcomers with the native or long established form which has hitherto been considered to belong to the widely distributed M. edulis. Consistent differences from typical individuals of that species from the Atlantic coast, however, including shape of shell, shape of lunule, number and shape of lunular teeth, and usually straight, not incurved, ventral side appear to warrant the recognition of this form as a distinct subspecies.[2] The shell is relatively higher and narrower than in the typical M. edulis and somewhat similar to that of M. grayanus Dunker of Japan, but the lunular teeth usually number two to four, instead of only two as is stated by Lamy ('36) to be characteristic of the latter species. The modal number is three.

It was tentatively concluded that exceptionally favorable conditions during 1941 to 1945 may have been responsible for the unprecedented multiplication of the native subspecies and the establishment of colonies in new or unusual territories but other possibilities must be considered. First, it is conceivable that a physiological mutation has occurred and that this has resulted in a race of unusually vigorous growth and reproduction. Second, the considerable variability in the shape of the shells (figs. A, 1–23) might suggest an admixture of two different forms, but these variations appear to be a response to different environmental conditions and not necessarily to two or more morphologically distinct genotypes. Individuals from various situations show consistent differ-

[2] For opinions concerning the specific identity of this population the writer is indebted to Dr. Paul Bartsch, Miss Viola Bristol, Dr. Fritz Haas, Dr. L. G. Hertlein, Dr. Myra Keen, and Dr. G. E. MacGinitie.

ences (figs. 17, 18, 20–23). Shells of isolated individuals, particularly those growing at a depth of several meters below the surface are usually higher than average (fig. 17), while those in crowded colonies in the intertidal zone are more slender (figs. 20, 22). But when young individuals which have had their shells modified into these two forms as the result of early environmental influences are grown together for several months their shells tend to become more nearly uniform. Shells from the quiet water of protected bays are much thinner and consequently of considerably less weight than those of the open coast (fig. A).

Hybridization of the native with a foreign species or subspecies has also been suggested as an explanation of the resurgent population. Typical M. edulis is known to have been

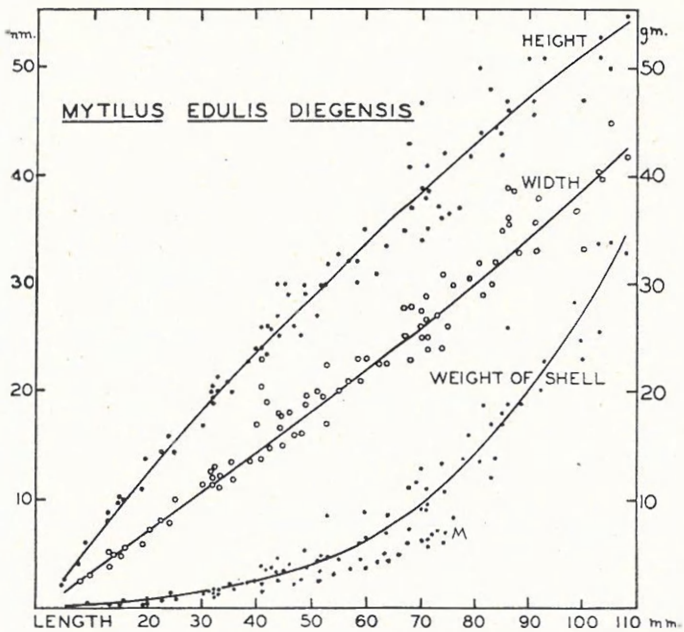

Fig. A Variations in ratios of height and width of shell (in millimeters) and weight (in grams) as compared with length. The graphs show that the height tends to decrease slightly and the width to increase with increase of length. The weights follow the usual exponential curves. The group marked M grew from the under side of a floating dock in quiet water and had much thinner shells than those from more exposed situations.

brought to California on several occasions with shipments of seed oysters from the Atlantic coast. In San Francisco Bay and Puget Sound this form is well established but the writer knows of no satisfactory evidence of its existence on the coast of southern California. However, a distinct subspecies, or species, M. trossulus, is endemic along much of the California coast and northward.

Furthermore there is obviously no way of knowing whether all the individuals responsible for this population were actually endemic at the site of resurgence, for the possibility remains that some or all of them may have been brought to the coast of southern California from a more distant part of the territory occupied by this subspecies. There can be no doubt that this territory extends farther northward along the coast, for the specimen figured by Weymouth ('20) from Humboldt Bay as M. edulis obviously represents this subspecies. It also extends southward along the coast of Lower California. From either of these directions the coastal currents are capable of transporting the free-swimming larvae many miles either north or south, according to the direction of the current. Hence the mature larvae may find places of attachment and develop into adult mussels perhaps 50 to 70 miles from the locality where the eggs were spawned and fertilized. Under favorable conditions a colony may become established. Since some members of the population are in spawning condition through most of the year and at an age of less than 1 year, rapid extension of territory is theoretically possible. If brought by chance to a locality having favorable conditions for growth and reproduction a maximum population may be expected to appear at a considerable distance beyond the usual range of the species. Local conditions however may change so suddenly as to exterminate the entire new colony even more rapidly than it was formed and the range will again be restricted to its usual limits. Under other conditions widely isolated colonies may remain indefinitely. No evidence is available as to whether human agencies may have been partly responsible for the present resurgent population of M. e. diegensis.

It was mentioned in a preceding paragraph that the rapid growth and multiplication of this subspecies had attracted attention at Newport Bay as early as 1941, more than a year before it was found at La Jolla, only 60 miles distant. It was also noted that the colony when first found at La Jolla in 1943 consisted exclusively of young individuals, indicative of a recent arrival. Furthermore no large colonies or large individuals had been reported in recent years from either Mission or San Diego bays previous to 1943, although they were common in 1944 and abundant in 1945. The evidence therefore indicates that Newport Bay may have been the original site of this resurgent population as early as 1941, followed by dispersal both northward and southward.

The mechanism for the rapid transportation of the free-swimming larvae along the coast of southern California is provided by the ocean currents which generally flow southward in the spring at a rate averaging 4 to 5 miles a day and northward in autumn at a somewhat lower rate. Spawning by the mussel occurs at both seasons, but more abundantly in the spring. Hence young larvae from eggs spawned and fertilized in Newport Bay in the spring could be carried the 60 miles to La Jolla in time for attachment to the piles or other objects at the end of their free-swimming period. Other colonies would doubtless be established at intermediate localities. Within less than a year La Jolla would itself become a source of dispersal.

The numerous varieties of M. edulis listed by Lamy ('36) are of world-wide distribution on seacoasts in both north and south temperate zones. The species is reported from the Pliocene or Pleistocene at San Diego and elsewhere on the California coast and this may, perhaps, have been the ancestral stock, or one of the stocks, from which the present population has been descended. San Diego was included in the range of M. edulis in Cooper's 1894 list but that species is not mentioned among the mollusks of that locality collected by Kelsey ('07). The records of the San Diego Natural History Museum however prove that it was present on the Marine

Ways in San Diego Harbor in September, 1907. It would be interesting to know whether that colony represented a new introduction or the multiplication of a sparse population previously overlooked. The distribution of M. edulis on the Pacific coast is given by Dall ('21) as Arctic Ocean to Cerros (Cedros) Island, Lower California.

But the question still remains as to whether the present population actually does represent merely the multiplication of an endemic or long established subspecies to unprecedented numbers and its concurrent extension to previously unoccupied territory. Such an explanation seems to be most nearly in harmony with the evidence at present available. The fortuitous union of two physiologically diverse but compatible races of this subspecies may have yielded a stock of unusual vigor. Such an event accompanied by exceptionally favorable environmental conditions may, perhaps, have been the principal contributing conditions.

Wide fluctuations in the populations of pelecypods are evidently as common as in any other group of animals. On the coasts of Europe and on the Atlantic coast of North America the rapid waxing and waning of local populations of Mytilus edulis have been reported by Field ('22), White ('37), Loosanoff ('43) and others. In 1930 Prof. G. E. MacGinitie witnessed an unusual resurgence of what was presumably M. edulis diegensis in Monterey Bay. He estimated that a single boat 45 feet long must have had about 4 tons of mussels attached to its exterior. That resurgence is reported to have been terminated by an increased population of Cryptothallus magnus which devoured the young mussels.

Such fluctuations in abundance are of frequent occurrence in cultivated oysters and commercial species of clams and scallops. For some of these the decreased population or complete disappearance can be explained by overfishing or a change in the environmental conditions. The bay-scallop, Pecten irradians, diminished in numbers and eventually disappeared from many localities on the Atlantic coast with the disappearance of the eel-grass on which the young scallops find suitable places for temporary attachment. Scarcity of food, storms, with associated heavy surf, floods of fresh water, ice, excessive cold during periods of low tide, abnormal temperature during the spawning season or during some portion of larval life, parasitic infections and predaceous enemies are among the conditions which may lead to the partial or total destruction of a susceptible population over a considerable extent of territory. The period during which the young pelecypod is finding attachment to some solid object is especially hazardous. The converse of these conditions may lead to the rapid resurgence of the population and subsequent extension of territory. Because of the instability of the environmental conditions, associated with the variable chances of receiving a continuous supply of young individuals, the littoral marine community is subject to extensive alterations from year to year and even in many cases from month to month, as MacGinitie ('39) has so clearly explained. The possibilities of favorable or unfavorable physiological mutations and of the establishment of hybrid vigor resulting from the chance crossing of different genetic strains may also be considered as of some importance in population changes.

Previous to the present resurgent population, the only occurrence of the bay-mussel on the pier at the Scripps Institution known to the writer was in 1926–1927. The report by Coe ('32) on the growth of organisms on experimental blocks indicates that it was at that time commonly associated on the piles with M. californianus. The species was then identified as M. edulis and the accuracy of this identification was confirmed by Dr. Paul Bartsch of the U. S. National Museum. No statement was made as to whether it was also found on the nearby rocks but small colonies were known to be living in San Diego Bay, only 15 miles distant. It now seems highly probable that all those colonies consisted of the subspecies described in this paper.

The much weaker byssus of the bay-mussel renders individuals of that species less resistant than those of the sea-mussel, M. californianus, to the pounding of the heavy surf to which the open coast is subject in stormy weather. As a consequence of that condition and perhaps because of other reasons the usual habitat of the bay-mussel is mainly restricted to bays and sloughs. On the protected sides of breakwaters and islands along the Pacific coast the bay-mussel is generally the dominant species of Mytilus, while on the exposed side the sea-mussel is the chief representative of the genus. Only a small fraction of 1% of the young mussels which were attached to the pier of the Scripps Institution in the summer of 1944 survived until the following spring. Nevertheless these relatively few survivors were able to supply a new crop of young in the summer of 1945 not less numerous than that of the preceding year.

With the exception of Mytilus californianus, which has maintained a dense and apparently constant population in the intertidal zone for the past quarter century, all the common species of pelecypods on the pier at the Scripps Institution have been subject to wide fluctuations in numbers from year to year. Even within the past 8 years periods of relatively great abundance have alternated with periods of scarcity or, perhaps, disappearance. Such has been the history of Chlamys latiaurata, Ostrea lurida, Septifer bifurcatus, and Saxicava arctica, as well as of Mytilus adamsianus stearnsii and its associated Lasaea cistula and L. subviridis. If complete disappearance from the piles were to occur for a season, repopulation from the nearby rocky shores or from more distant localities would presumably occur promptly or eventually.

For some species of pelecypods an irregular periodicity has been observed in which the population seems to disappear locally for a number of years, to reappear later in almost incredible numbers. For other species only a single resurgence has yet been reported. Not infrequently the increased population spreads to situations unfavorable for survival and is rapidly reduced in numbers or exterminated. An interesting account of the annual fluctuation in the abundance of winter. The most extensive setting took place during June in both 1944 and 1945. Very little setting resulted from the autumn spawnings in either year.

The increment in size and relative proportions of the shells of typical individuals are shown in figures 1–14. Under favorable conditions the maximum increase in length occurs during the second and third months after the completion of the free-swimming stages, and the rate decreases thereafter. It is only about half as great in winter as it is in summer. The average maximum rate for the entire year during each of the first 12 months after attachment was found to be approximately 7, 10, 10, 9, 8, 7, 6, 5, 4, 4, 3 and 3 mm. respectively. Consequently the length of the shell at the end of each successive month of life is about 7, 17, 27, 36, 44, 51, 57, 62, 66, 70, 73 and 76 mm. A maximum length of 82 mm. at the age of 1 year was observed.

An average increment of about 2 mm. per month or a total of 20 to 24 mm. may be expected for the second year, bringing the length at the age of 2 years to 96 to 104 mm. The largest individual seen by the writer was estimated to be about 3 years old and measured 108 mm. in length (fig. 19). This was collected by Dr. Bradley T. Scheer in Newport Harbor. The writer is also indebted to Dr. Scheer for several hundred shells of various sizes collected from eight different situations in that harbor and vicinity, together with the record of the finding of nine individuals between 70 and 80 mm. long which had grown on a boat within 1 year after the boat had been painted. It may be noted that this is the same size as was obtained in the experimental boxes at La Jolla.

The increment of each age group during each month of the year and the correlations found between growth rates, temperature and food supply have already been reported (Coe, '45). Organic particles and organisms small enough for intracellular digestion, including diatoms, flagellates, animal and plant reproductive cells, as well as the detritus resulting from the disintegration of any kind of plant or animal cell, are the principal sources of nutrition. Dinoflagellates and other cells covered with cellulose are often ingested in large numbers but usually pass through the digestive canal without apparent change, many of them remaining viable and capable of forming vigorous colonies when cultured in sterile media.

In this subspecies the shell is narrower than that of the typical M. edulis as the result of more nearly flat valves. There is also a greater relative height as compared with length, resulting in wider angle at anterior end; shells less than 30 mm. in length average five-eighths to two-thirds as high as long (figs. 1–7) but the relative height decreases with increasing length until the height may be less than half the length (figs. A, 14, 19). The proportions of the shell vary in conformity with habitat; shells of isolated individuals in deeper water are usually higher than average (fig. 17); those in crowded colonies in the intertidal zone are more slender (figs. 20, 22); relative width increases slightly with increasing length (fig. A); weight of shell is much greater when exposed to surf than in calmer waters (fig. A). An occasional shell is fan-shaped, with a relatively sharp beak, due to the incurving of the anterior ventral margin.

DIAGNOSIS OF MYTILUS EDULIS DIEGENSIS

Shells average much higher and narrower than in typical M. edulis; usually smooth, with delicate, closely placed growth rings (figs. 1–23); color usually glossy black, often with brown anterior third; occasionally brown or horn-colored; prismatic layer varies from gray to violet; internal surface bluish with black border and usually black muscle scars, shading gradually to whitish toward anterior end. Lunule narrow, usually with three cornucopia-shaped ridges and two to four teeth, the modal number being three; rarely one or obsolete or as many as five or six; teeth average fewer and are usually more widely separated and more regularly conical than in typical M. edulis; minute supplementary denticles occasionally present. The number of teeth is not always identical on the two valves. Examination of the teeth on 216 valves showed a variation of 0 to 6, with a mean of 2.94. On ninety-three valves of typical M. edulis, kindly supplied by Dr. Victor Loosanoff from Milford, Connecticut, the lunules were much broader than in M. e. diegensis, and consisted usually of four or more ridges, the teeth numbering from 0 to 13, with a mode of 4 and a mean of 4.1.

Gills vary from light brown to dark violet; foot brown or black, often with median yellow stripe. Maximum size observed: length 108 mm., height 55 mm., width 42 mm., weight of shell 34 gm. (fig. A).

Known distribution, northern California to coast of Lower California; generally in bays and sloughs, less frequently on the open coast. Type locality, La Jolla, San Diego, California. Holotype (fig. 12) and paratypes in U. S. National Museum; paratypes in Chicago Natural History Museum, San Diego Natural History Museum and California Academy of Sciences.

The shells of large individuals, exceeding 80 mm. in length, of this subspecies often resemble those of M. galloprovincialis Lamarck of the Mediterranean and other European seas in having the posterior half of the dorsal edge nearly parallel with the ventral edge (figs. 14, 19). M. trossulus, or M. edulis trossulus, Gould, also found on the California coast, but more generally northward, is usually smaller, more bluish and even more nearly cylindrical than typical M. edulis, although with many intergradations.

SUMMARY

The California bay-mussel, Mytilus edulis diegensis, which is described as a new subspecies, has appeared on the coast of southern California during the past 3 years in unprecedented numbers and over a widely extended territory. It is concluded that this represents a localized resurgent population of the endemic or long established subspecies which ranges from northern California to Lower California. It is now abundant both in bays and inlets and in favorable situations on the open coast.

This exuberant population consists of a race of unusual vigor as indicated by the rapid growth of its constituent indi-

viduals to a larger size than is usual in that subspecies, by the high rate of multiplication and by the establishment of new and flourishing colonies at distant localities and in situations unfavorable for long survival. It is uncertain whether all the individuals responsible for this population originated at the place of resurgence or whether some or all of them may have been brought from some other part of the range as free-swimming larvae transported by the coastal ocean currents. These currents are capable of transporting the larvae for a distance of 70 miles or more, either north or south, according to the season, during the free-swimming period.

The fortuitous union of two physiologically diverse but compatible genetic strains, together with exceptionally favorable environmental conditions may, perhaps, have been the principal contributing agencies in the origin of this vigorous resurgent population. Having become established, its spread has been rapid. Examples of similar populations of other pelecypods on the Pacific coast are reported.

Cultures of this new subspecies in experimental boxes immersed in the sea for more than 2 years have demonstrated an exceptionally rapid rate of growth under favorable conditions. Young individuals reached a maximum length of 82 mm. at the age of 1 year and a length of 96 to 104 mm. at the age of 2 years. Thereafter the growth rate was very slow. Maximum length observed 108 mm.

These cultures also demonstrated that the shells of young individuals which have assumed different configurations because of early environmental influences tend to become more nearly uniform when grown under identical conditions.

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PLATE 1

EXPLANATION OF FIGURES

Mytilus edulis diegensis n. subsp.

Figures 1–13 Rate of growth and change in proportions of shell with advancing age; grown in experimental boxes at La Jolla, California; from recently attached young taken from Scripps Inst. pier. Nearly natural size of shells of average proportions.

1–3 Age 2–4 weeks.
4–6 Age 5–8 weeks.
7 Age 3 months.
8 Age 4 months.
9 Age 5 months.
10 Age 6 months.
11 Age 7 months.
12 Age 1 year. Holotype.
13 Age 15 months.
14 Estimated age 2 years; from Newport Bay.

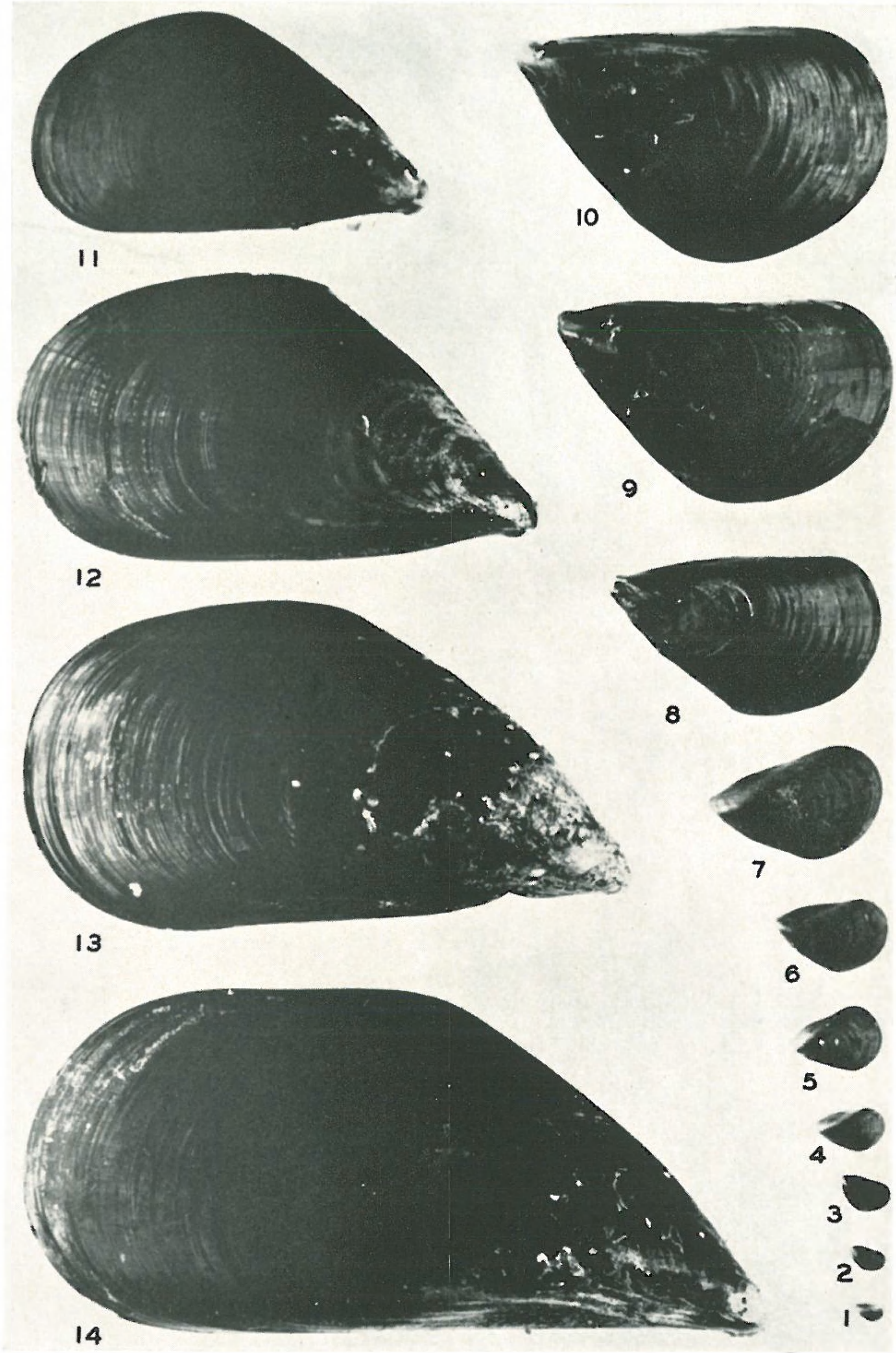
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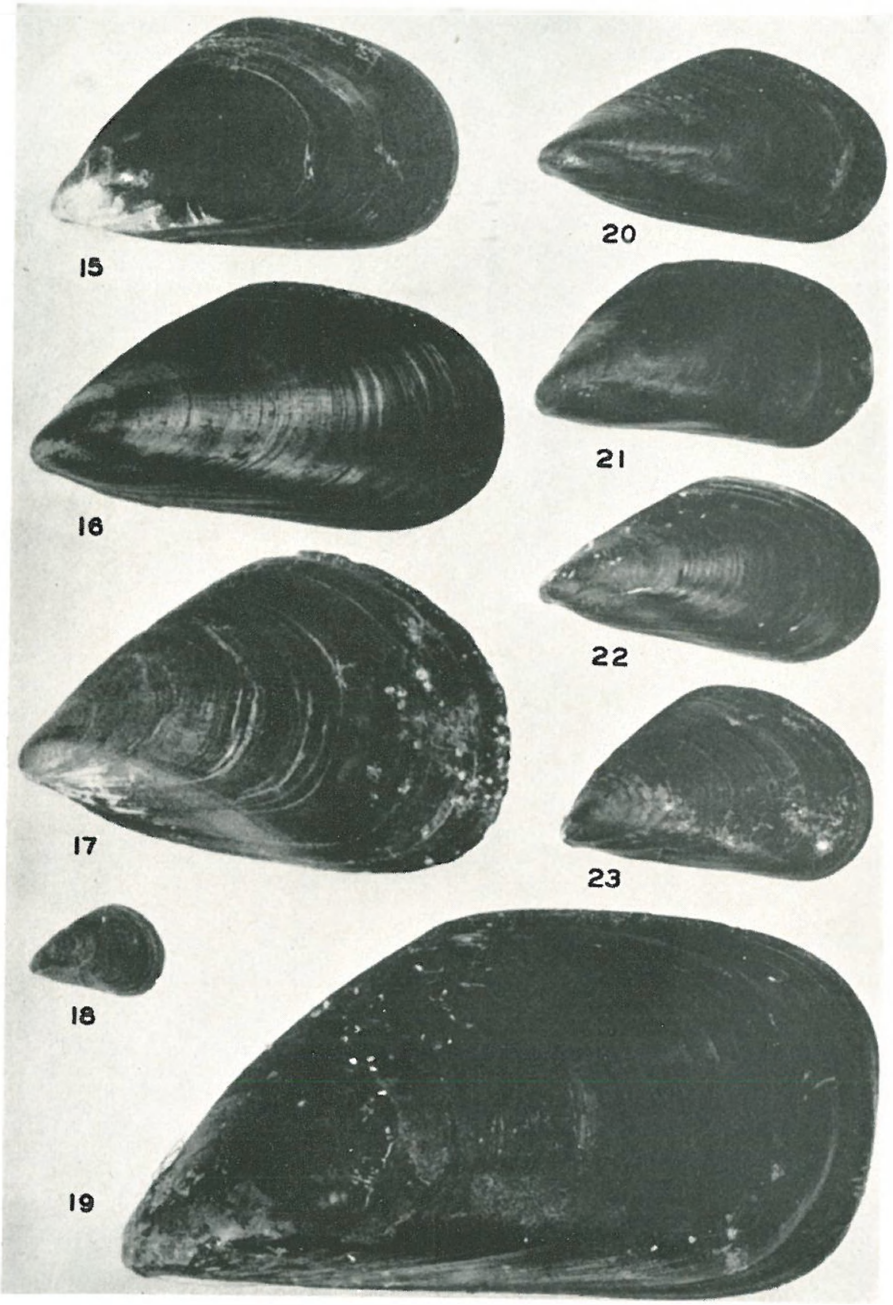
PLATE 2

EXPLANATION OF FIGURES

Mytilus edulis diegensis n. subsp.

Variations in shape of shells. Nearly natural size.

15 Tia Juana Slough.
16 Mission Bay.
17 Unusually high form; Scripps Inst. pier; after 8 months in culture box.
18 Scripps Inst. pier.
19 Newport Bay; estimated age 3 years.
20 Intertidal zone; Scripps Inst. pier.
21 San Diego Bay; collected before 1920.
22 Slender form; intertidal zone; Scripps Inst. pier.
23 High form; 3 meters below low water level; Scripps Inst. pier.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