Title
Periodicity of Spawning by the Grunion, Leuresthes tenuis, an Atherine Fish

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Periodicity of Spawning by the Grunion, Louresthes tenuis, an Atherine Fish

A thesis submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy in Zoology

by

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Grunion Spawning on Malibu Beach, California
Photograph by Moody Institute of Science

INTRODUCTION

Many people have believed, since time immemorial, that the waxing and waning of the moon exert important effects on the plants and animals of the earth. Thus, it has been handed down for centuries that the full of the moon is the time to sow certain crops, or that likelihood of conception in particular animals is best on one or the other phase of the moon. Many people have noticed that some rhythmic behaviors seem to occur with the same periodicity as do the moon changes.

Most such beliefs now seem to be based only on chance happenings. We do know, however, many examples of animals showing a lunar periodicity in their breeding behavior. This is most clearly apparent in marine animals. Representatives of many phyla tend to spawn on a lunar cycle, or at a certain phase of the moon.

Numerous researches have demonstrated that such cycles exist. Unfortunately, most of these studies have been of too short duration to provide even an indication of the factors that control the periodicity of behavior. It has been demonstrated, in the most thorough investigations, that either the stage of the tide or the amount of moonlight is probably the major controlling influence. In no case, however, has the controlling factor been proven.

One of the outstanding examples of an animal showing a lunar rhythm in its reproductive cycle is furnished by a small silvery fish, the grunion (Leuresthes tenuis). This species, a member of the family Atherinidae, occurs only on the coast of southern California and the adjoining west coast of Baja California.

This small fish has the unique habit of laying its eggs in the moist sand of the beaches, completely out of the water. Spawning occurs only on particular nights during the protracted spawning season, which extends from late February until August or September. In late January, the gonads start to enlarge, and by late February or March the first batch of eggs is matured. The time of maturing is somehow adjusted, so that the first eggs are ready to be spawned just at the time of a high spring tide associated with either the full or the new moon. At intervals of about two weeks throughout her spawning season, each female then ripens and spawns successive batches of eggs. All of her eggs for each fortnightly period are deposited at a single spawning, but there is some variation in the time of ovipositing. Spawning occurs on several nights following the full and new moons, and at no other time. Spawning runs occur only at night, at about the time of high tide, when thousands of these silvery fish may litter the beach. The time of the runs is so definite that predictions can be made with considerable accuracy, not only as to the nights on which spawning will occur, but also as to the time on each night.

The entire spawning act takes place while the fish are out of water. During the run, they swim in with the waves, and then swim against the outflowing water, so that they are left stranded on the beach. The female, when accompanied by one or more males, digs herself, tail first, into the sand to deposit her eggs. When the female is buried about to the pectoral fins, the male curves his body around her and emits his milt into the sand next to her body. The milt flows down around the body of the female and fertilization of the eggs results. The male leaves promptly, and soon thereafter the spent female frees herself from the sand and returns to the sea with the first wave to reach her.

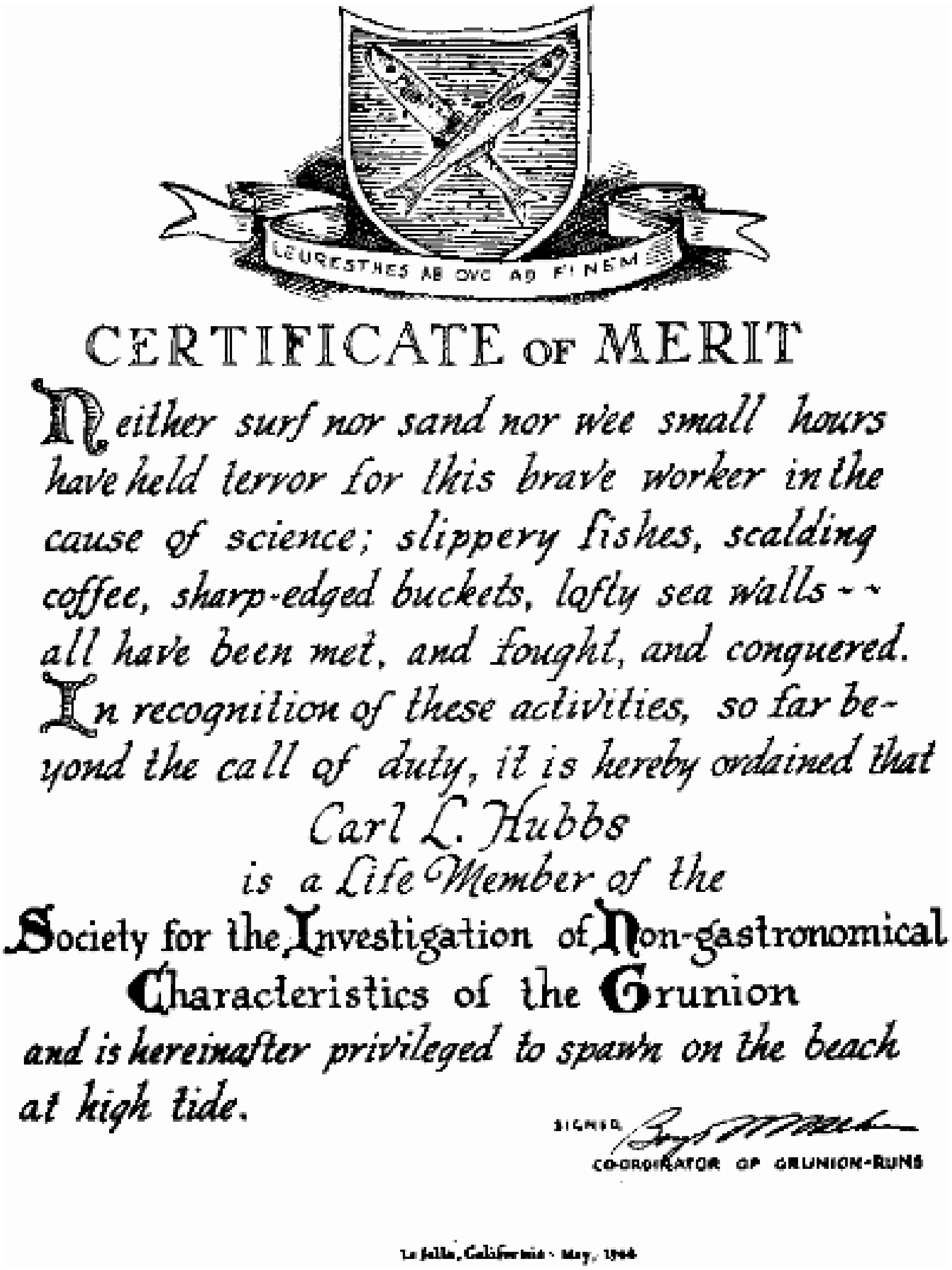
The pods of eggs thus deposited in the upper tidal zone are buried more deeply in the sand as the beach is built up by succeeding series of lower tides. They remain in the damp sand, completely above the wash of the waves, until the next series of high tides about two weeks later erodes the beach and washes the eggs out. When the eggs wash free from the sand they hatch within three or four minutes, and the prolarvae are washed out to sea.

It can be seen from the foregoing resume that the spawning of the grunion is delicately adjusted in many ways to tidal phenomena.

AIM AND SCOPE

The story of the spawning habits of the grunion has been worked out in some detail by Thompson (1919) and Clark (1925). Their data are entirely sufficient to give the general picture. However, there is little in their data which points toward the mechanism by which the timing of the spawning runs of the grunion is controlled. Notably lacking are continuous observations on runs, to determine exactly when they do and do not occur. This information would appear to be essential if the controlling factors and mechanism of timing are to be found. In the present work the results of continuous observations on grunion runs for a period of three years are given. The times of observed runs are correlated with various physical phenomena, in order to suggest which of these phenomena may be important agents in the timing.

Since these observations extended over a period of three years, it is natural that many new details about the general life history of Leuresthes have come to light.



CERTIFICATE OF MERIT

Neither surf nor sand nor wee small hours have held terror for this brave worker in the cause of science; slippery fishes, scalding coffee, sharp-edged buckets, lofty sea walls -- all have been met, and fought, and conquered.

In recognition of these activities, so far beyond the call of duty, it is hereby ordained that

Carl L. Hubbs

is a Life Member of the

Society for the Investigation of Non-gastronomical Characteristics of the Grunion

and is hereinafter privileged to spawn on the beach at high tide.

SIGNED

CO-ORDINATOR OF GRUNION-RUNS

La Jolla, California - May, 1944

Figure 1.

ACKNOWLEDGMENTS

Figure 1 is a copy of the certificate which was presented to all kind people who helped with the field observations on which this work is based. Well over two hundred and fifty certificates have been awarded and I fear that even yet there may be many who have not been thanked. All these people worked at least one evening, and many worked time and time again. Altogether, a total of over three thousand man-hours have been spent by volunteer workers on this problem. There must be few investigations where so many people gave so freely of their time and energy. To all the members of the "Society for the Investigation of Non-gastronomical Characteristics of the Grunion" I give my deepest thanks.

Dr. Carl L. Hubbs first suggested this problem, and has constantly given help on it, not only through criticism and advice, but also by many hours of actual observation and field work. My entire ichthyological training has been under his guidance, which has been a constant source of inspiration.

Mrs. Laura C. Hubbs has been particularly generous in aiding in observations during times of my absence, and has given help wherever and whenever possible during all of the program.

Dr. Frances N. Clark, of the California State Fisheries Laboratory at Terminal Island, has aided materially by advice and in providing help in observation.

Dr. Francis P. Shepard generously made available information on the physical characteristics of Scripps Beach.

The coordinated watch for grunion runs, on many beaches from San Francisco, California, to Bahia San Quintin, Baja California, was participated in by personnel from the following institutions: California Academy of Sciences, Hopkins Marine Station of Stanford University, Santa Barbara College (University of California), University of California at Los Angeles, Hancock Foundation of the University of Southern California, California State Fisheries Laboratory, San Diego State College, and Scripps Institution of Oceanography (University of California).

A program of marking (by fin clipping) was instituted in 1948. Work was done by volunteer workers, mostly from Scripps Institution of Oceanography and San Diego State College. Mr. Merrel A. Taylor and Mr. Andrew C. Olson, Jr. of San Diego College were particularly helpful in organizing crews and assistance. J. L. McHugh, Frederiok H. C. Taylor, Brian P. Boden, John Stackelberg, Carl I. Johnson, A. A. Allanson and Dorothy Allanson of Scripps Institution were also unusually generous with their help during this program and other phases of the problem.

Mr. Eugene LaFond has generously given pictures, as well as information on his observations. Mr. F. Alton Everest of the Moody Institute of Science, has made available many unusually fine pictures of grunion runs. Mr. Lamar Boren has cooperated wholeheartedly in obtaining pictures, and has provided many fine shots.

Mr. Sam Hinton of Scripps deserves special thanks for designing the certificate of merit, and for many nights spent in observations.

PREVIOUS STUDIES

The first notice given to the fascinating story of the spawning runs of the grunion was published by Hubbs (1916). In discussing Leuresthes tenuis he quoted a short letter from Mr. J. S. Joplin, of Santa Ana, describing the spawning of these fish. Mr. Joplin remarked that the fish ran during March, April, and May, on the second, third and fourth nights after the full moon, at full tide. He notes their regularity thus: “I have been observing them for thirty years and the time of their coming is so regular that during that time I have rarely missed them”. Hubbs concludes this description with the statement: “A detailed study of these interesting habits, or a confirmation of them, is highly desirable”. Both the confirmation and detailed study came within a surprisingly short time.

In 1918 Barnhart again called attention to the unusual spawning habits of the grunion. He wrote only a short note describing a run observed at La Jolla, and added little to the story. His notice was the first made by a trained observer, however, and served to spur on the work of others.

It remained for Thompson (1919) to describe the habits of the grunion in detail, and to explain its exquisite adaptations to the tidal cycle. He described the run and the laying of eggs, recorded the times of the runs, and pointed out the advantages and disadvantages of this unique spawning behavior. Thompson believed that the main runs occurred only after the full moon, and that only small runs occurred after the new moon. In this first paper he reported spawning taking place only during March, April, May, and June. In a short note (Thompson 1919b) he later recorded runs in July and August, and thus set the period from March to August as the spawning season for the grunion. Thompson believed the runs to occur only on descending tide series. He did not attempt an explanation of the mechanism of timing.

Frances N. Clark in 1925 delved further into the life history of Leuresthes. She concluded, from an analysis of the state of development of ova in fish collected at various times during the season, that an individual female after starting to spawn continues to breed on each series of high tides throughout its breeding seasons. She concluded that the interval between spawning is about fifteen days. Through the scale method of age analysis, she determined the age at first maturity, the life span, and the growth rate.

From observations made near Long Beach, Clark published in 1926 a list of runs which, although incomplete, constitutes the most complete series published to date. These data upheld her belief in a cycle of about fifteen days. Later (1928c), she recorded grunion spawning on Cabrillo Beach, which had been constructed just one year earlier. She concluded that "homing" is not the rule in grunion.

A review of the life history and spawning of Leuresthes was published by Clark in 1938. In this paper the run-forecasting methods used by the California State Fisheries Laboratory were explained. I published in 1947 a general account of the life history. These two papers were written for popular consumption and included little new information.

MATERIALS, LOCALS AND METHODS

Systematics and Relationships

The grunion, Leuresthes tenuis, was first described by Ayres in 1863, who placed it in the genus Atherinopsis. The type was listed as coming from San Francisco Bay, which is outside the known range at the present time. In 1880 Jordan and Gilbert erected the genus Leuresthes to contain this form. It was classified by Jordan and Hubbs (1919) in the American subfamily Atherinopsinae (of the family Athorinidae). Leuresthes crameri, described by Jordan and Evermann from specimens taken in "Ballenas Bay, Cape Abreojos, Lower California", has been synonymized with Leuresthes tenuis by Osburn and Nichols (1916), Jordan and Hubbs (1919), and Schultz (1948).

Leuresthes is quite distinct from the other atherine fishes occurring within its range. Schultz (1948), following Jordan and Hubbs (1919) and Breder (1936), believed that Hubbsiella sardina, from the Gulf of California, is the most closely related form, perhaps even congeneric. This opinion, with which I agree, is strengthened by new data on the spawning habits of Hubbsiella. Several travelers have told me of the existence of beach spawning fish in the northern part of the Gulf of California. Mrs. Ellen P. Derwin of Oracle, Arizona, has not only written in letters about her observations, but also sent an 8 mm motion-picture film showing fish coming out on the beach at La Libertad, Sonora, Mexico. The pictures are not clear, but do indicate that such a habit exists in fish of the Gulf of California. At my request, Mr. Percy Hussong, of San Felipe, Baja California, collected some beach spawning fish at San Felipe, and these fish were Hubbsiella. Unlike Leuresthes, Hubbsiella evidently spawns during the day as well as at night. As yet, no observations have been made by a scientifically trained observer. Detailed observations on the spawning habits and timing of runs in this species are highly desirable.

Range

The range of the grunion extends from Monterey Bay, California, to southern Baja California. Their southernmost published record is Punta Abreojos, but Scripps Institution parties have collected it as far south as San Juanico and it is possible that the range extends considerably farther south. The known breeding range is from Cayucos, central California, to Punta Abreojos, Baja California.[1] It is probable that the northern limit to the major spawning range is Point Conception, California, and that the southern limit is south of that now known. During the coastwise check made on April 22 and 23, 1947, no runs were observed at Morro Beach or Pismo Beach, San Luis Obispo County, or at Surf in Santa Barbara County. However, Dr. Carl L. Hubbs, W. I. Follett, and party collected grunion running on Morro Beach on the night of July 22, 1948. A total of one hundred and eighty-eight fish were taken. Dr. Hubbs also obtained information on runs from Mr. Donald Glass, California State Fish and Game Warden stationed at Morro Bay. He stated that runs had been reported this year (1948) at Cayucos, and fair runs reported from Morro Beach and Pismo Beach.

1 Information from Dr. Carl L. Hubbs, who was told by native fishermen in this vicinity of large runs there. Dr. Hubbs also collected Leuresthes in large number at Punta Abreojos in January, 1948.

Habitat

Grunion, like most atherines, are top-water fish. They are commonly found within six or eight feet of the water surface. Although evidence is not complete, it is probable that they spend most of the time in this narrow layer. They are taken throughout the year in the shallow gill-nets (two fathoms deep) used to catch topsmelt. Skin divers report seeing them only close to the surface.

I have been able to catch them in quantity in San Diego Bay, during morning, afternoon, and night, in water over twenty feet deep with a floating seine fifty feet long and only eight feet deep. Specimens were taken every time they were thus sought. I have often observed grunion, together with topsmelt, lying at the surface in the kelp beds at night.

The grunion has been taken only close to shore, most often within a mile or two of the coast. So far as is known, they spend their entire life within this area, except for occasional wandering. They are common in the kelp beds, along with the topsmelt. They are also found in larger bays, such as Newport Bay and San Diego Bay.

It seems probable that the grunion populations are relatively static, at least during the spawning season. Lateral movement occurs along the coast, but not in large scale mass migrations such as occur in the herring and sardine.

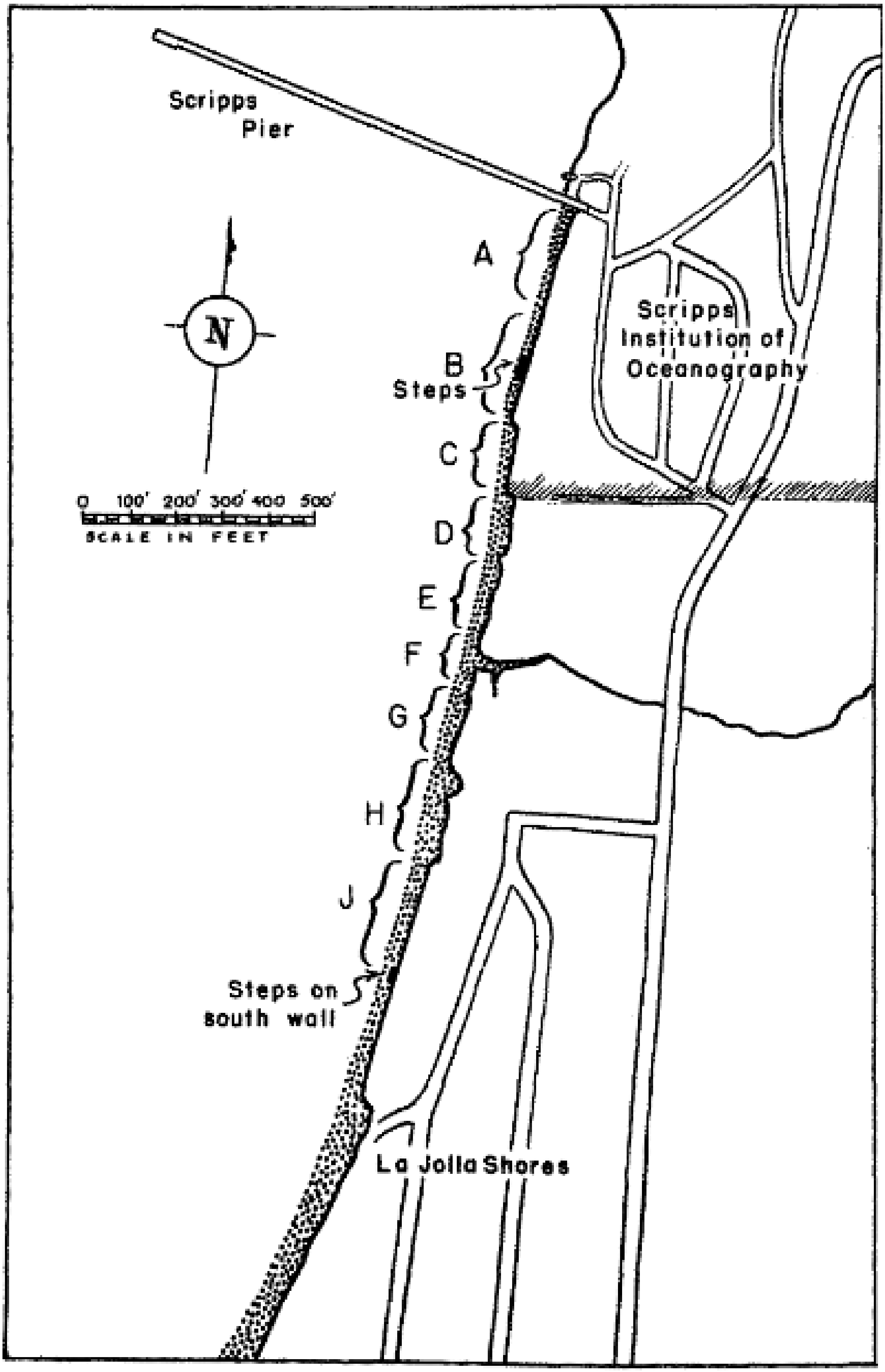


Figure 2. Map of Scripps Beach

Movement between different locations is better described as wandering, and seems to be confined to relatively small groups or individuals, while the greater part of the population stays in one area. This tendency to remain in the same locality is shown by marking experiments performed at La Jolla in 1948 (Walker, MS).

Area of Investigation

La Jolla

Continuous observations on grunion runs were made at La Jolla during 1946, 1947, for most of the 1948 season, and for part of the 1949 season. During this period watch was kept on a section of beach extending two thousand and thirty feet south from the pier of the Scripps Institution of Oceanography. For convenience this section of beach, in agreement with current local usage, will be referred to as Scripps Beach. A map of this area is shown in Figure 2. Data on this beach have been furnished by Dr. Francis P. Shepard.

Scripps Beach is composed of fine sand (median diameter about one hundred and eighty-three microns), and has a gentle slope. This slope usually varies between two to five percent in the zone of wave-wash at high tide. Occasionally the slope becomes steeper during periods of heavy cutting.

Sea walls back the beach in areas marked A, B, C, and J on the map. The remaining section is backed by low cliffs out into soft silts and alluvial sands of quaternary age. To the north of Scripps Beach is a two-hundred-foot stretch of medium-sand beach, with some large exposed rocks, and north of this is a long rocky area backed by high cliffs. To the south the beach continues as a section called La Jolla Shores Beach, which is about thirty-five hundred feet long and has a slight average slope (about two percent). Originally a bar bordering a lagoon, this beach is now backed by a low artificially filled area.

The high spring tides reach the walls at A, B and C during most of the grunion spawning season. On the higher tide series these parts are often unavailable for spawning. The highest spring tides (those of about six feet and higher) usually reach the cliffs at E, F and G, and the wall at J. In these places, however, spawning areas are usually available. The remainder of the beach almost always provides proper spawning conditions.

The sand level on the beach varies considerably during each season. Early in the season the level is low, and may remain so even during the middle of the spawning season. At times certain areas are swept free of sand, so that the underlying gravel is exposed. This occurred about the middle of each season in the areas E and G. Sand builds up later in the season, and reaches high level during July to September. Shepard and LaFond (1940) discussed the sand movements in this area in detail.

Scripps Beach has many advantages for a study of this kind. As noted by Clark (1928), it has long been known as an area of good grunion runs. The fish here are relatively little disturbed, because the beach is not lighted and is not very readily accessible to the crowds who partake in the sport of grunioning. In addition, much more accurate data on water movements, tides, temperatures and other physical features are available than for any other beach on our coast.

The fact that the beach is backed by seawalls or cliffs for its entire length constituted a definite disadvantage at times of extreme high tides, for then long sections of the beach are not available for observation. This circumstance, however, helped to keep the beach relatively free of grunion hunters.

Other Beaches

Several observations on the time and character of runs at San Diego Bay, California, and at Ensenada, Baja California, were made by myself and Dr. Carl L. Hubbs.

On the nights of April 22 and 23, 1947, a coordinated check was made for grunion runs on beaches from Bodega Bay in Marin County, California, south to Bahia San Quintin, Baja California (a straight-line distance of about six hundred and thirty miles).

In addition to these planned investigations, many incidental observations have been sent to me. Although these reports are seldom detailed enough to be utilized in detailed computations, they indicate occurrence of runs on various beaches and, often, the relative concentration of fish and the times of runs.

Field Observations

Observations were made on all nights when grunion runs were expected, and usually also for one to several nights previous and for one night afterward. This was done in order to be sure that no runs were missed. Watches were also made on all high tides occurring during darkness for one period of twenty days. Observations on each night were continuous for one-half hour before expected time of arrival of the first fish until one-half hour after the last fish was seen. On nights without runs the watch was continued for one-half hour after time of high tide in 1946, but this was extended to one hour in 1947. No regular watch was kept during daylight hours, since there is no authentic record of daylight grunion runs. During hundreds of days of beach studies by the Scripps Institution staff no grunion have been seen on the beach during daylight.

Observations were made by walking up and down the beach in the zone of wave wash. During the first part of observation each night, before fish were seen, a flashlight beam was directed on outflowing waves, to locate any fish in the surf.

The light was flashed parallel to the beach and never shone on the incoming wave. This was done to minimize alarming the fish, which except at the height of heaviest spawning are frightened by the flashing light. Since the fish were also frightened by movement in the water, it was standard practice to move down the beach only between incoming waves and to stand still when the waves washed over the beach and around the observer's feet. After the fish began to stay on the beach, the light was flashed on the sand only after the wave had receded, and for as short a time as possible. At all times great care was taken to disturb the fish as little as possible.

Notes were kept on the numbers of fish seen and the time seen. Table XIV, Appendix, shows a sample of one night's notes. Fish seen in the surf but not on the beach were labeled n.o.b. (not on beach). If no symbol follows the number of fish, the number designates the actual or estimated number seen on the beach. The capital letter following the number indicates the portion of beach where fish were seen. Figure 2 outlines these areas. During the first and last part of a good run, and during light runs, it was possible to record all fish seen. During the heavier part of most runs this was impossible and the number of fish seen was noted only at stated intervals. The number of fish noted was actual count when fish numbered less than ten. For numbers greater than this, estimates were made.

At the end of each series of runs the relative number of fish running each night was estimated on the basis of the numbers of fish as noted in the field notes and as remembered. The estimate was expressed as percent of total number of the fish in the run series running each night, and was called “percentage intensity of runs”. Although in part impressionistic, the percentages are regarded as moderately reliable, because of the great and very obvious differences in numbers of fish.

These estimates of “percentage intensity of runs” were used in computing the midpoint of the run series. Since the runs varied greatly in size and occurred on one to four nights in a series, comparable intervals between runs could not be figured from the raw data. The “run series midpoint” was arrived at by averaging the times of each run (expressed in days and tenths of days), weighted by percentage intensity of each run. This procedure is based on the premise that grunion may be ready to spawn at any time of day, but that this readiness can be expressed only on the high night tide. The distribution of times when fish become ready to spawn probably forms a normal curve. The midpoint of run is a time twelve hours after the time of midpoint of this theoretical curve, because of class groups used.

Accuracy and Completeness of Observations

The accuracy of observations on the timing of grunion runs is limited by several factors. A heavy reliance had to be placed on the observer's estimate of the number of grunion seen. More precise methods were sought, but because of the variable nature of grunion runs no method seemed to achieve the accuracy of the one used.

It is obvious that one observer could not see all that is taking place on a beach about two thousand feet long, even during daylight. Since grunion runs take place at night, the difficulties are magnified. The obvious answer to this difficulty would be to select a smaller portion of beach, which could be watched continuously. That course is precluded, however, because of the variations in condition of the beach, previously discussed, and in strength of runs on different sections of the beach (see section on description of runs).

In 1946 and 1947, to help insure that all runs in each series were observed, observations were usually made on one night previous to and on one night after each run series (Appendix, Tables XV'XVII). When such negative results were obtained, there seems little doubt that all runs of the series were observed. This does not mean that there were no stragglers on these nights or other nights, but because of the careful methods used in observation, it is felt that these must constitute a very small proportion, less than one percent. This is not true of the observations during February and after June of each year, and these cases will be discussed in the section on time of run series.

In 1946 the observations on only two run series, the first series in March and the first series in April, were not accompanied by negative observations at each end. On both series grunion were observed for four nights, and since the numbers observed on the first or last nights were small, it is almost sure that all runs were observed. The observations on the first three series in 1946 are not so reliable as to relative numbers of fish as those following, however. Methods of estimate were not standardized and the error may be considerably larger.

In 1947 it is almost certain that all runs were observed, except, possibly, one in late August. Negative results were not obtained on two run series, late March and early July, but so few fish were seen on the end nights in question that I have no doubt that all runs were recorded.

In 1948 there is considerably more reason to doubt the completeness of observation. It is quite possible that a run occurred on March 11, and on March 30. There is little chance, however, that these runs were heavy ones, and, most probably, if they occurred, they constituted less than five percent of the run series. The observations in April are complete, but again in May incomplete observations were made. There is little chance that there was a run on May 13, since the run on May 12 was relatively light. The run series from May 9 to May 12 is therefore assumed to be complete. Observations were made on only two nights on the second run series in May, however. On the first night of observation, May 25, only about one hundred and fifty fish were observed, so there is almost no doubt that this was the first night of the run series. Mr. F. Alton Everest observed good grunion runs at Malibu Beach, California, on May 25, 26, and 27, and it seems safe to assume from this evidence that runs also occurred at La Jolla.

During June and July, observations at La Jolla were even more incomplete. Probably all runs in early June were observed, but there is some possibility that there was a light run on June 10. There is no complete information for the runs occurring in late June. The entire first run series in July was observed at La Jolla. Observations ceased on July 10 because only six fish were seen on that night. No observations were made after this date.

Even though the observations in 1948 were incomplete in several ways, it is felt that the time of all major runs occurring before the middle of June is known. The general pattern of timing is therefore probably little altered.

The numbers of fish were estimated as those seen in the flashlight's beam. This seemed more accurate than to attempt to estimate number per small quadrat, because of the uneven distribution of the fish on the beach. The length of beam varied with strength of moonlight, and with climatic conditions, but averaged about one hundred and fifty feet. Flashlight batteries were changed every evening, or after having been used about two hours.

Early in the study, estimates of numbers were checked by estimating a group and then counting the fish present. Such checking was possible on groups consisting of numbers up to about one hundred fish. Estimates were accurate to within ten fish in groups up to fifty individuals, and to within twenty in groups numbering between fifty and one hundred. Larger numbers could not be checked by counting. I feel that these estimates are accurate to the nearest hundred up to about three hundred fish. For larger groups only relative numbers were used, such as hundreds or thousands, and these are certainly within the correct order of magnitude. Inexperienced observers, almost without exception, over-estimated numbers grossly, and such estimates were given little attention.

The method of estimating the relative strength of each run within a given run series, as explained under "Field Observations", obviously involves considerable error, but, judging from my experience and that of other observers working with me, it is felt that the error of estimate does not exceed twenty percent.

For the runs during February, July, August and September, the chances for errors in observation were much greater, because of the very small number of fish involved. For this reason the times of these runs have been given less weight in later discussions than the time of runs during March, April, May and June.

Coastwise Check

During the coordinated check on grunion runs, along the coast from north of San Francisco to San Quintin Bay (made on April 22–23, 1947), observers were assigned to most of the beaches where good grunion runs were known to occur, and to possible spawning beaches northward of the known range. Detailed instructions as to time, place, and method of observations were sent to each observer, in an attempt to make the observations as comparable as possible. Methods of observation were the same as described for La Jolla.

Marking

A fin clipping program was instituted in 1948, to determine whether or not individuals actually spawned on every run series during their spawning period, as concluded by Clark (1925). Considerable additional data, particularly in regard to the integrity and size of local populations, were also gained from this work (Walker, MS).

As in the coastwise check, volunteer workers were used. Fin clipping was done at Scripps Beach on two succeeding run series, on April 10 and 11, and on April 26, 1948. Fish were examined for clipped fins during five run series following the first marking and on one run series in 1949. The right pelvic was removed on April 10 and 11, the left pelvic on April 26. This was done by clipping the fin as close to the body as possible with toenail clippers.

The fish to be marked were collected by crews, using ten-foot seines with one-quarter inch mesh. Standing well out in the wave-wash zone, the two seiners held the net parallel to the beach. On the incoming wave the seine was held out of the water, and then dropped as the water started to recede. The fish thus caught were carried in cans to the nearest clipping station. Marked fish were then released well out in the surf. Record was kept of numbers and sex of the fish marked. A total crew of about thirty people was needed on each marking night.

Figure 3. Marking grunion by clipping left pelvic fin, Scripps Beach.

Photograph by Lamar Soren

Figure 4. Netting for marked grunion on Scripps Beach.

Photograph by Lamar Soren

Figure 5. Checking fish for missing pelvic fins on Scripps Beach.

Photograph by Lamar Soren

Returns of the marked grunion were obtained by seining on Scripps Beach in the manner described above. Fish were checked by crews working close to the water in the light of a gasoline lantern, and were then merely thrown out on the wave-washed beach. Very little mortality resulted. All fish checked were enumerated by sex. Those with missing or damaged pelvics were examined later under a microscope (9x magnification), to judge whether a missing or imperfect pelvic had resulted from clipping, natural injury, or natural deformity. If rays appeared to have been cut on a straight line, they were considered to have been clipped, but if the break was irregular, the loss was attributed to natural injury. In a few doubtful cases the base of the fin was dissected to determine if the corresponding girdle was missing, in which event natural loss was indicated.

The clipped pelvic proved to be a very satisfactory mark. It was easily seen, and removal apparently caused no great disability. No clipped fish were held for observation because no suitable tanks were available, so it is not sure whether or not there was a differential mortality. The fish which were recovered, however, were in good condition, and all clipped fine showed regeneration of tissue over the cut surface. For this reason and because return of marked fish was relatively constant, it is believed that there was little if any differential mortality.

Regeneration did not take place if the fin had been clipped at the base. When as a result of the hurried operation more than the basal segment of the rays was left, regeneration did occur. After two months some fins clipped in this manner had regenerated from one-fourth to three-fourths of their original length. For the period of the study in 1948, even these fins were easily identified. It is believed that regeneration of fins did not cause errors in this short term experiment.

TIDAL PECULIARITIES IN THE RANGE OF THE GRUNION

Some knowledge of the major variations and peculiarities of the tidal phenomena in the region inhabited by the grunion is necessary for a full understanding of the time of runs and the adaptations in habits of the grunion to tidal phenomena. Tidal fluctuations on the south Pacific coast of North America follow a rather unusual pattern. There is marked inequality in the heights of the two high and low tides occurring each day. This is shown in Figures 24 and 25, which show tide traces for several days during March and May, 1946. The inequality in high water heights is most pronounced during the periods of high spring tides which occur about the time of each full moon and each new moon during the spring and summer months. In addition, the highest tides of each spring tide series occur during the hours of darkness in the summer. During winter the highest tides occur during daylight hours. Figures 16, 17 and 18 show the varying heights of high tides at La Jolla during spring and summer months. The points representing alternate high tides have been connected by smooth lines, and thus the approximate heights of both high waters occurring each day may be read. Considering the habit of the species, the diurnal inequality in heights of high tides, especially at times of spring tides, would seem to be a basic necessity for the success of spawning of the grunion.

LIFE HISTORY

Spawning Behavior

The story of the spawning act of the grunion is presented in the introduction in about the detail as by Thompson (1919) and Clark (1925). Certain points will now be described in more detail. Throughout the following discussion the term "run" will refer to the coming of the fish onto the beach on any one night. For the runs occurring on successive nights the term "run series" will be used. "Tide series" refers to the succession of tides about twenty-four hours apart. An "ascending tide series" is one in which each following tide is higher. Succeeding tides are lower on a "descending tide series."

Frequency of Spawning by Individual Fish

Clark (1925) indicated that once an individual female grunion starts spawning it continues to spawn periodically on each series of high tides throughout its breeding season. This was determined by studies of the ovaries of grunion taken at various times during the spawning season. She demonstrated that during the spawning season the ovaries contain three classes of eggs. The immature class is of the same size as those found in the ovary during the winter and do not exceed 0.23 mm in diameter. The intermediate class arises from the immature class, and ranges in size from 0.24 to 0.76 mm. Larger eggs are considered as maturing. In January of each year the secondary eggs start to form from the immature group, and by late February some fish were found with eggs at the upper limits of the intermediate class. Later in the spawning season Clark examined samples of females taken at intervals at San Pedro. The fish were classified as to groups of eggs found in the ovary. The results were as given in Table I, taken from Clark (1925).

These data show quite clearly that the same females spawn on succeeding tide series. In addition they indicate that it is probable that females starting to spawn early in March almost surely spawn at least five times during one season, and may spawn more often. Unfortunately there are no data for late May or June. The absence of immature eggs

TABLE I

FEMALE FISH TAKEN AT SAN PEDRO DURING THE SPAWNING SEASON, CLASSIFIED ACCORDING TO THE GROUPS OF EGGS FOUND IN THE OVARY. TAKEN FROM CLARK, 1925.

Date		Immature eggs only		Intermediate eggs also		Maturing eggs also		Total	
1923		No.	%	No.	%	No.	%	No.	%
March	13	9	15	32	51	21	34	62	100
April	8	6	7	26	27	62	66	94	100
April	10	2	11	2	11	15	78	19	100
April	12	0	0	2	6	34	94	36	100
April	14	2	8	3	12	21	80	26	100
April	17	1	3	2	7	27	90	30	100
April	19	0	0	18	72	7	28	25	100
April	21	0	0	26	96	1	4	27	100
April	23	0	0	24	100	0	0	24	100
April	25	0	0	5	21	19	79	24	100
April	28	0	0	1	3	32	97	33	100
May	1	0	0	2	8	22	92	24	100
May	3	0	0	2	5	36	95	38	100
May	5	0	0	49	100	0	0	49	100
May	9	0	0	0	0	31	100	31	100
July	24	34	71	10	21	4	8	48	100
July	26	81	80	15	14	7	6	103	100
August	24	116	100	0	0	0	0	116	100

in any fish during April and early May indicates that all of the fish in the population are spawning or closely approaching spawning condition. The fish starting to spawn early, therefore, must be considered to be spawning during this period.

Clark discussed the possibility that there may be two distinct runs. There is the possibility that spent fish might disappear from the area where collections were made and that other fish migrate into the region of collection. It was pointed out that the presence of a few mature eggs in the lumen of the ovary in the females taken shortly after a run showed that they were freshly spent. These fish also contained eggs in early stages of maturing.

Since this question of repetition of spawning is of great importance in the problem of timing of runs, it was thought wise to make a comparable check in another locality. Fish were collected in San Diego Bay, because here they could be caught by a shore seine between runs, and because the area for movement was somewhat restricted. The ovaries of females were examined and graded without measuring of eggs, in the manner described by Clark. Results of this examination appear in the table on the following page:

TABLE II

FEMALE GRUNION TAKEN AT SAN DIEGO BAY DURING THE SPAWNING SEASON, CLASSIFIED ACCORDING TO THE GROUPS OF EGGS FOUND IN THE OVARY

Date 1948	Immature eggs only No.	%	Intermediate eggs also No.	%	Maturing eggs also No.	%	Total No.	%
April 21	8	13	18	28	38	59	64	100
April 22	8	2	10	2	437	96	455	100
April 25	6	4	11	7	133	89	150	100
April 30	5	3	8	4	179*	94	192	100
May 4	4	5	3	4	72	91	79	100
May 7	1	2	2	3	59	95	62	100
May 23	3	4	3	4	67*	92	73	100

* Freshly spent.

It will be noticed that the percentage of females with eggs in the maturing class is low in the sample taken April 21, 1948. This collection was made at night by seining close to shore, and a high proportion of males and immature females was taken. Later collections were made by setting the seine well off shore, so that a better representation of adult females was secured. The number of females with immature eggs only is higher in these collections than in those reported by Clark. This is probably due to difference in methods of collection.

Clark's fish were taken in a bait-net offshore by a commercial fisherman. In San Diego Bay the net was set only two hundred and fifty feet from the beach, and pulled to shore, fishing all the way. From the results of hauls taken at various distances from shore in San Diego Bay it seems virtually certain that the large females tend to stay further offshore, with the males and immature females close to shore. It is probable that some of the first-year females start spawning only during the last of the spawning season, if at all. Clark indicated all fish to be spawning by the middle of April.

Grunion runs occurred on April 25, 26, and 27, on May 9, 10, 11 and 12, and on May 24, 25 and 26. The conditions of the ovaries fitted the expectations and corroborated the findings of Clark. The collection for the evening of April 25 was made before the run occurred, and no spent fish were found. Thirty-two of the females taken on this date had eggs in the lumen of the ovary, and presumedly would have spawned on this same night. On April 30, the one hundred and seventy-nine females with maturing eggs showed clear signs of having recently spawned. In almost all a few large eggs were found in the lumen of the ovary, and all had enlarged blood vessels in the ovary. The collections on May 4 and May 7 were made between runs, and agree closely with the findings of Clark. The females taken on May 28 were collected just two days after the last run of a series. Here again the ovaries showed clear signs of being recently spent, but a new batch of maturing eggs was already present.

A further check resulted from the marking of grunion during two successive run series on the Scripps Beach at La Jolla. Data on numbers of marked fish follow:

Date	No. fish marked			Sex ratio	Fin clipped
1948	♂	♀	Total	♂ - ♀	
April 10, 11	4136	839	4975	4.9-1	Right pelvic
April 26	3709	698	4407	5.3-1	Left pelvic

Collections were made on each run series following the marking, until July 9. At this time checking for returns was discontinued because the runs were so light that only small numbers of fish could be examined. The results of the check for fin clipping are given in Table III.

Thirty-nine male and one female grunion, which were marked on April 10 and April 11, were recovered during the succeeding run series in 1948. The ratio of males to females is extremely close to theoretical expectation, which was 31.5 males to one female. On the nights of May 9, 10, 11 and 12, one hundred and twenty-one male and one female grunion marked on the preceding series were taken. The sex ratio is much higher for these dates than the theoretical expectation, but

TABLE III

RESULTS OF CHECKS IN 1948 AT LA JOLLA FOR GRUNION
MARKED AT LA JOLLA IN APRIL, 1948

Date 1948	Number of fish examined			Returns				Sex Ratio	Expected sex ratio of returns	
				Right clip		Left clip			Right	Left
	♂	♀	Total	♂	♀	♂	♀	♂-♀	♂-♀	♂-♀
April, 26, 27	5,205	804	6,009	39	1	...	1*	6.5-1	31.5-1	....
May, 9-12	14,992	1,699	16,691	63	.	121	1	8.8-1	43.1-1	46.6-1
May, 25	2,467	344	2,811	9	1	29	1	7.2-1	34.9-1	38.2-1
June, 9	2,543	371	2,914	7	.	7	1	6.9-1	33.8-1	36.6-1
June, 24	560	69	629	7	.	2	.	8.1-1	39.7-1	42.9-1
July, 9	229	26	255	.	.	2	.	8.8-1	43.1-1	46.6-1

* This marked female was taken on April 27. It had almost surely been fin-clipped on April 26, for the clip was straight and fresh and the left pelvic was cut only on that night.

the difference is not significant due to the small size of the sample.

Two females were taken in spawning condition on two succeeding run series. This evidence confirms that which is provided by the condition of the ovaries between and during runs, in indicating that female grunion, once they have started to spawn, do spawn on every run series throughout their spawning season. The new evidence shows, even more conclusively, that the males also spawn on each run series.

It may be argued that these fish considered as returns were actually fish with naturally missing pelvics. For the males such an argument would be absurd, because of the large numbers taken, but for the females, this possibility must be considered. It has been shown, from collections made elsewhere, that the incidence of missing pelvic fins with a pelvic girdle still present must be extremely low (Walker, MS). There is very little chance, therefore, that two out of the two thousand five hundred and three females examined would have lost fins from other causes. In addition, the missing fins were examined with great care under a dissecting microscope, at 9x and 18x magnifications. Both fins showed every sign of having been clipped recently. The bases of the rays were cleanly cut straight across, and there was still only a suggestion of regeneration of tissue. There would seem to be almost no chance that the loss of these fins was due to causes other than clipping.

The results from the fin clipping indicate that females spawn at least four times during one season. Both right and left clipped females were taken as late as the fourth run series after being clipped. It seems almost certain, from the evidence of Clark (1925), that many females spawn more often. Fin-clipped males were taken as late as the sixth run series after marking, which shows that they may spawn at least six times during a season. Clark gave no evidence on the number of times an individual male may spawn during one season.

Movement of Fish between Runs

There is little definite information on the movement of fish between runs or between run series. Incomplete personal observations indicate that the fish live in the general area of the kelp beds between run series, and move close to the shore toward spawning beaches at the time of run series. This movement probably starts about a day before the first run of a series. I have usually observed grunion while collecting in the kelp beds with a light. I have no reports on presence or absence of grunion in the kelp bed areas during times of runs, however, since I have then been making observations on beaches.

Some significant data come from night collecting with a light at the end of piers. Many such observations have been made from the end of Scripps Pier. This location lies just outside the breaker zone. Several of these observations were made on run nights, or on nights just preceding runs. Although grunion were sometimes taken there on nights between run series, they were much more plentiful on nights just preceding runs, or on run nights. Andreas Rechnitxer, collecting regularly on Santa Monica Pier, early in 1949 has observed the same tendency (personal communication).

As darkness falls, during the nights of spawning, the fish move so far inshore that they may be seined in the inner part of the surf. They may also be observed in the breakers outside the wave-wash zone as long as an hour before they start to come in with the waves sweeping over the beach. On nights between run series grunion are taken rarely and only as stragglers by seining on open beaches.

Somewhat different habits are exhibited by the grunion in San Diego Bay, where samples were seined between runs and between run series. In collections made during the day the grunion were found to be much further from shore than they were during darkness. Even on nights between run series there was an onshore movement, probably for food. These movements were apparent each night, although the time of high tide varied through twenty-four hours during the period of sampling. Daylight hauls were made on only three occasions, and then were discontinued due to the small samples taken. Good samples were always obtained soon after darkness.

Spawning Beaches

Scripps Beach, described earlier, is a good spawning beach. Other beaches where good runs are known to occur are in the vicinity of Santa Barbara, Malibu, Long Beach, Redondo Beach, Newport, Capistrano area, Oceanside, Del Mar, Ocean Beach, San Diego, Silver Strand, all in southern California, and the beach in the vicinity of Estero de Punta Banda, south-west of Ensenada, Baja California. These are all beaches of fine sand with a gentle slope. Beaches with coarser sand, and with consequently steeper slope, are not generally used, though runs may occur there at times. Gravel beaches are seldom if ever used for spawning although occasionally fish may come out on such areas, or may be stranded there between waves.

Description of the Run

The grunion are in the surf zone, close to shore, on the night of a run. They make their first movements onto the beach about fifteen to thirty minutes before the run (that is, when they begin to stay on the beach). The pioneers, typically few, move in with the waves that sweep over the beach, but they turn and swim out again as the water recedes. The numbers increase until occasional groups of fifteen to twenty-five behave in this manner. This activity is commonly considered by the veteran grunion hunters as scouting. Such movements continue during the whole run, for at no time do all fish in the wave wash strand themselves. It is estimated that about half the fish return with the wave in which they moved onto the beach.

Nearly all of the first fish that stay on the beach are males. At first only single fish come out, but soon groups of two or three lie close together. The numbers gradually increase, until, in a heavy run, thousands may litter the beach in the zone of wave wash. Pictures of such heavy but not maximal runs are shown in the frontispiece and in Figure 6. I have occasionally seen runs at La Jolla where the beach was almost completely covered with fish over an area of about twenty by three hundred feet. John E. Fitch of the California State Fisheries Laboratory, reported seeing a concentration of grunion, approximately five to seven fish deep, which covered an area of about thirty-five by three hundred and fifty feet. This exceptional concentration was seen on the beach north of Newport Pier on April 22, 1947, during the coordinated coastwise check. At Cabrillo Beach, on May 23, 1947, staff members of the California State Fisheries Laboratory saw grunion several layers deep, creating such pressure and activity that large quantities of eggs were extruded on the surface of the sand. During the peak of the spawning season one may often see grunion so thick on the beach that it is impossible to walk in the wave-wash zone without stepping on fish.

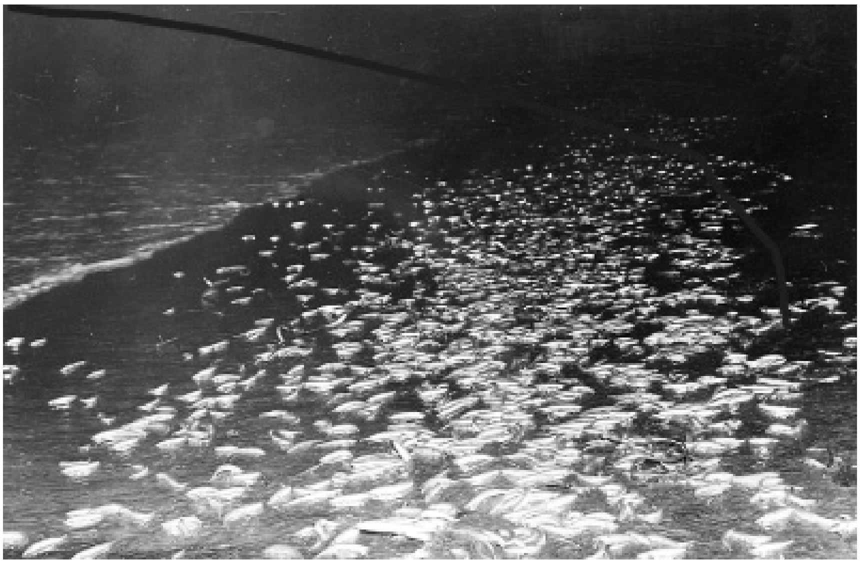


Figure 6. Grunion littering the Scripps Beach at La Jolla. Concentration as heavy as this is not rare, and at times the fish cover the beach so that no sand is visible between them.

Photograph by Lamar Boren

Figure 7. As the wave recedes some fish return with it, while others strand themselves on the beach.

Photograph by Moody Institute of Science

Typically the heaviest part of a run begins about one hour after the first fish stays on the beach and lasts for about one hour. The numbers of fish staying on the beach then gradually decrease, until only scattered pairs or single fish are there. Then, the fish are only in the wave wash, and soon even these disappear. Sometimes the runs and abruptly. It is truly amazing to see hundreds of fish on the beach, and then five minutes later to be unable to find any.

Although the runs generally follow the pattern just described, there are many variations in the pattern and, often, abrupt fluctuations in behavior within one run. Short surges and drops in numbers often occur in any part of a run. Some nights there may be several very heavy surges, between which very few fish are out of the water. Some idea of this variation may be seen in the graphs on time of runs (Figures 20 and 21).

Many of the fluotuations in numbers of grunion on the beach are attributable to variations in the height and period of the waves. Fluctuations in the wave pattern are common on our beaches, because the waves typically come from different sources. The trains of waves of slightly different periods alternately interfere with the reinforce each other in such a way that series of higher waves alternate with periods of relative calm. The grunion definitely favor the higher waves and seldom utilize very low ones. When the high waves come in pairs or groups, it is usually the second wave that brings in most fish. At times the fish strand themselves far beyond the reach of the lower waves, and remain exposed for several minutes. Waves nearly in phase that produce much turbulence as the backwash of one meets the inwash of the next, seldom are used by the grunion in the movement onto the spawning area. The type of wave that is effective in surf boarding and "body surfing" is the type that most often brings in large numbers of grunion. Such waves have a large forward component of energy.

During exceptionally heavy runs the fish may cover the beach in almost uniform abundance, but usually there are separate areas of concentration, with few fish in the intervening stretches, even where conditions seem to be uniform. At times hundreds or even thousands of fish are exposed on one section of a beach, while one hundred feet away there are only single fish or scattered pairs. The seemingly favored areas often change during a single run. For these reasons it is impossible to obtain a true view of a run by remaining in one area of a beach.

Although at times there is no apparent reason for such places of continued concentration, some beach conditions can be recognized as affecting the numbers of fish congregating there. Fish tend to gather in low spots where incoming waves converge, probably because the fish are carried there by the flow of water. Areas covered with kelp or other debris are usually avoided, as are the harder sand sections of the beach and the areas where gravel is exposed.

In the nearly landlocked San Diego Bay the picture is much the same, except as it is modified by the small wave-wash zone. Here the beaches are washed merely by low wind waves and by the wakes of passing vessels. The slope of the beach is moderately steep. For these reasons the wave-wash zone, to which the spawning is restricted, is usually only one to four feet wide. One flip sends the fish back into the water, and sometimes the fish may spawn with their tails in the water.

Description of the Spawning Act

The female swims in with the incoming wave, accompanied by one or more males. These fish swim vigorously, especially as the water recedes, so that they strand themselves on the beach. They tend to concentrate most heavily in the upper ten feet of the wave-wash zone. The female starts to dig in while there is still some water left on the beach, less often as soon as the water has receded.

When digging in, the female arches her back so that her head is held high, at an angle of about forty-five degrees with the sand. At the same time she vibrates the caudal portion rapidly sideways, causing the posterior half or third of her body to sink into the semifluid, water-filled sand. Usually the female attains this position by the time the water has run off the beach. Since the fish are oriented against the flow of the receding wave, the female almost always starts to dig in with her tail pointed toward the water. This first part of the process is difficult to observe, as it usually takes place when there is still water on the beach and lasts only a few seconds.

When her tail is buried, the female causes her body to sink further into the sand by a twisting motion. Most of the movement is now a revolving on the long axis, rather than the rapid sidewise movement previously used. This usually continues until her body has sunk into the sand almost or quite to the level of the pectoral fins. Often, however, she may become buried to her gills or eyes, sometimes concealed completely. In hard sand, on the other hand, where digging is difficult, she may become buried little beyond the genital opening, so that eggs are scarcely buried.

When the sand is particularly hard, only a small portion of her body, about the vent, may be covered. Figure 8 illustrates several stages in the digging-in process.

The body of the female is not straight under the sand, but instead forms an arc. The caudal region is flexed almost at right angles to the axis of the exposed parts, and is curved, so that the caudal fin points toward the surface of

Figure 8. A most unusual picture, showing several stages in the spawning process. The female at the bottom of the picture has just buried her tail and is preparing to lift the anterior part of her body to dig in farther. A male lies just behind her. The females in the upper and lower right, accompanied by males, are still digging in. The female, buried up to her head, lying between them, remains in the spawning position. The males which have already emitted their milt about her are now flopping toward the water to the left of the picture.

Photograph by Moody Institute of Science

Figure 9. The female grunion buries herself in the sand, and the male, lying half coiled around her, emits his milt near her body. The blurred male to the left of the female has also spawned, and is just flipping away. The water which has gathered in the depression formed by the female, is cloudy with milt.

Photograph by Lamar Boren

Figure 10. While one male is coiled tightly around the body of the female, another male tries to get into position to spawn. Milt may be seen on the sand just back of the female's head.

Photograph by Lamar Boren

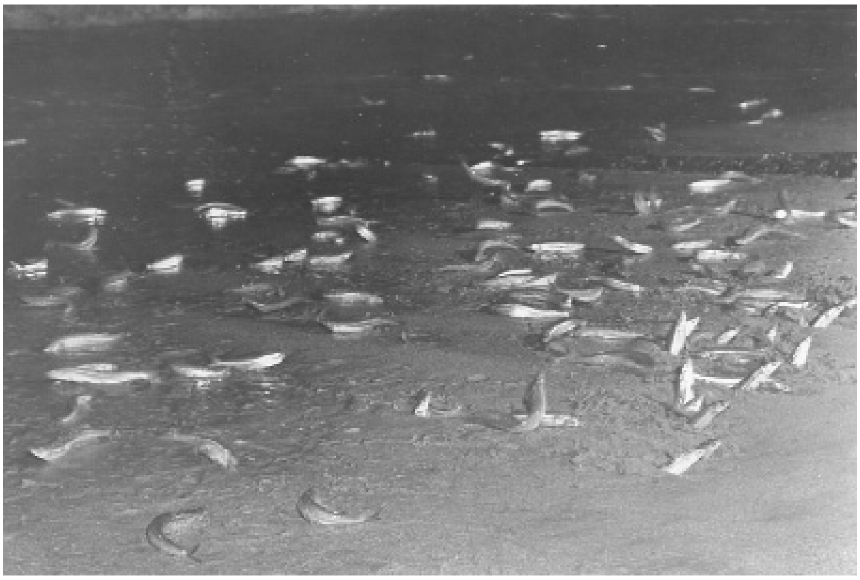


Figure 11. An unusually heavy concentration of spawning females on Malibu Beach. Most of them have completed spawning and are almost free of the sand. The males have moved down the beach toward the water. Notice their tracks in the sand.

Photograph by Moody Institute of Science

Figure 12. A heavy spawning concentration at Malibu Beach, California. In the upper part of the picture note the females dug into the sand.

Photograph by Moody Institute of Science

the sand. These points were determined by quickly digging the sand away from one side of females buried in soft sand. The axis of her head makes an angle varying from about fifty to ninety degrees with the surface of the beach.

In very hard fine sand on parts of the beach near Ensenada, on April 23, 1947, Dr. Carl L. Bubbs observed hollow, curved molds, from which females had wriggled. These molds retained the curved form assumed by the female in ovi-positing, and contained eggs.

The male or males lie close to the body of the female while she is digging in, but not always in contact. As soon as the egg-laying position is attained, or slightly earlier, the male curves his body around the female, and emits his milt onto the sand close to her body (see Figures 6, 7, and 8). He flips away as soon as he has emitted his milt, and works his way rapidly toward the water (Figures 8 and 9).

The female emits her eggs about two inches under the surface of the sand (Thompson, 1919). This is accompanied by slight twisting of her body, and a tensing of the body. The pectoral fins are usually expanded fully, and flutter slightly. At the same time the female utters a series of very faint squeaks, which can be heard only when the listener's ear almost touches the fish. When a female is held in the hand and made to spawn by applying pressure on her belly, the anal fin moves in a series of waves as the eggs are emitted. It seems probable that this movement also takes place during natural spawning. It may aid in the formation of the egg pod and in the fertilization of the eggs.

The movements of the female probably works the milt down around her body to the eggs. I have dug up many pods of eggs from the sand, and have never found one without fertile eggs. Quite the contrary, the fertility observed is above ninety-five percent. Mr. Alton Everest, of the Koody Institute of Science, reports similar observations.

After her eggs have been deposited, the female bends slowly from side to side until she frees herself from the sand. Obviously exhausted, she lies on the sand waiting for a wave to take her back to the sea, or takes a few feeble flops toward the water. This is in contrast to the swift return of the males to the sea. The female completes her spawning at one session, retaining at most a few mature eggs to be resorbed. Thompson (1919) found the number of eggs in five pods to vary from 1,479 to 2,705, with an average of 2,200.

The number of males attending one female varies widely. When few fish are running only one male, sometimes two, accompany each female. During heavier runs, the ratio of mating males to females tends to increase and sometimes a female is surrounded by a writhing mass of males (Figure 13). As many as eight males have been counted actually mating

Figure 13. Many males may cluster around a spawning female. These squirming masses were photographed on Malibu Beach, California. There are ten spawning females in this picture.
Photograph by Moody Institute of Science

or attempting to mate with one female, and although counts were not always possible, it is believed that as many as twelve to fifteen may attempt to mate with a single female.

Thompson (1919) said, “The affair is, however, not a real pairing, for frequently there are four or five males surrounding one female, and in one case two females were seen to mate with one male which lay between them. In fact the mating is accomplished in a casual way, the fish happening to come to rest in the same slight hollow, or in a small group as the swirl of the water left them. Nor do males and females always find each other, for females turgid with eggs may be picked up in numbers after the waves, energetically pursuing their course back into the water. There are certainly, however, the best of reasons to consider the pairing, or mating, as necessary before spawning can occur, for in observing six runs of fish not a single female was caught in the act of burying herself which did not have, or had not had, a male near her.”

My observations disagree with Thompson’s in one small point. As stated before, the female usually comes on the beach accompanied by one or more males. In the few actual observations that could be made on individual fish, the ripe female found alone on the beach, and not digging in, had been separated from the males, or had been unsuccessful in digging in. That some sort of pairing takes place before the fish come on the beach is especially apparent on nights of very light runs. At these times fewer than one hundred fish may be observed in an evening, and yet a very high percentage of the fish observed are spawning. On such a night the chances of a male and a female coming close to each other on the beach by chance are extremely remote. During three years only one female has been observed spawning on the beach with no males near. This fish had not even dug in, and was arched on the sand emitting her eggs on the surface.

Development and Hatching of Eggs

The eggs, which are clear orange in color and average 1.80 mm in diameter (average of one hundred original measurements of fertilized eggs), are laid in compact bunches under the surface of the sand. The relation of the sand movements to these pods of eggs was clearly described by Thompson (1919). He pointed out that as the tide rises the beach is eroded, and as the water recedes the beach is built up. Sand is picked up by each incoming wave and carried inshore where some is deposited in the highest area reached by the wave. The outflowing wave, gaining momentum, again picks up sand and carries it out. Thus there is an area of deposition at the higher levels reached by waves and an area of erosion, and since they most often spawn on descending tides and descending tide series, the eggs are usually covered with more sand than they were at the time of deposition. Here they stay with the embryos developing rapidly. The development of the eggs and character of the early larval stages have been described by David (1939).

In about seven days after fertilization, at either room temperature or the temperature of the sand where the eggs develop, the eggs are ready to hatch. They remain unhatched in the sand, however, until washed out by the next series of high spring tides. As the beach is eroded, the eggs are washed free from the sand, and then hatch within three or four minutes. The larvae are washed out to sea where further development takes place. These points were determined by Thompson (1919) and have been confirmed by others, including myself. The actual stimulus to hatching was not stated by Thompson, but his discussion seems to infer that the freeing of the eggs from the sand causes them to hatch.

An original unrepeated experiment indicates that agitation while the eggs are being washed from the sand is the actual stimulus for hatching. Two samples of about five hundred artificially fertilized grunion eggs were placed in two battery jars. Sea water to a depth of seven inches was added, and aeration provided. The aeration was sufficient to provide circulation, but did not cause movement of the eggs. At the end of two weeks a sample of eggs was taken from one of the jars by pipette and placed in a beaker of sea water, agitated for a minute, and then checked for number of hatching larvae. Eight minutes after agitation the unhatched eggs were examined and the number of eggs and larvae was recorded. Samples from the same container were taken at intervals of two to four days thereafter until no more live eggs remained. The eggs in the other container were left undisturbed until near the end of the trial, when they were tested for ability to hatch. Results are shown in the table below.

TABLE IV

RELATION OF AGITATION TO HATCHING OF GRUNION EGGS

The eggs were fertilized on March 15

Date (1948)	Days after fertil-ization	After agitation			Control jar (No agitation)
		Eggs hatching	Live eggs not hatching	Dead eggs	
March 29	14	13	31	0	0
April 2	18	56	16	0	0
April 4	22	45	2	10	0
April 8	26	32	4	84	0
April 10	28	21	3	many	0

Fungus began attacking the eggs on about April 3 and by April 10, when the experiment ended, only the twenty-four good eggs shown in the table were left in the test jar. A sample of twenty-seven good eggs was removed from the control jar on this date, and twenty-one of these hatched after agitation. Six fish also hatched in the control jar after this sample was taken, probably due to movement caused by the taking of the sample. Development time was evidently slowed down during this work by low water temperature, which varied from 15.5° to 17.0° C.

These results indicate that agitation not only accelerates hatching, but is necessary for hatching of grunion eggs. In normal hatching this agitation is provided by the action of the waves. The eggs are protected from premature agitation by the cushion of sand surrounding them.

The experiment recounted above, as well as one run by J. L. Roberts and A. M. Dowell at the University of California at Los Angeles in April, 1949, indicates that at temperatures of 15.5° to 17.0° most of the eggs are not yet ready to hatch two weeks after fertilization. In the second run no eggs could be hatched by agitation until after the fifteenth day. Obviously the rate of embryonic development bears a normal relation to temperature, rather than being independent of temperature as the intraovarian development seems to be. These relationships call for more critical study.

Size Groups of Larval and Juvenile Grunion Resulting from Periodic Spawning

Size-frequency groups resulting from successive spawnings have frequently been analyzed in fishes and the size-frequency method has long been utilized in life-history investigations. Such groups ordinarily represent annual spawnings, but any periodic spawning with intervening rest periods should produce distinct size-frequency groups, which will remain distinct until varying growth rates or differential survival cause the groupings to coalesce. It was recognized early in this study that larval and juvenile grunion should group about evenly separated length modes, each corresponding to a single run series. Demonstration of such size-groups would confirm the peculiar life-history pattern of the species and would indicate that there is no extensive spawning, if any, between the run series.

On a number of nights through the period of this study large numbers of larval and juvenile atherines were dip-netted under bright light at the end of Scripps Pier to test the occurrence and sharpness of size-frequency groups that could be correlated with the preceding run series. Only one series — the most complete and the most striking — is herein discussed in detail and graphed (Table V and Figure 14). This one, however, as well as the others that have been tabulated, amply confirms the inference that such size groups should occur in the young-of-the-year of Leuresthes tenuis. The sample, comprising two hundred and fifty-five specimens, was taken on July 12, 1947. It is clear that the few 5–6 mm prolarvae had just hatched, unusually early, from the spawning of July 5–7 — presumably because that spawning was at an exceptionally low tidal height, during a series of very low spring tides, and because there followed a series of very high springs, the early tides of which were high enough to wash out the eggs spawned only a week previously (Figure 14). The four very distinct modes that follow obviously represent the spawnings of June 20–22, June 5–8, May 21–23, and May 6–9. Differences between the adjacent groups in average size may be due to differences in average age, dependent on irregularities in the tide cycle; the second and third main size-groups are most closely approximated in both size and age. Earlier spawnings were represented by few fish in the July 12 collection because most extant fish of this size were swimming at lower water levels or farther offshore.

In another such collection of larvae and juveniles some nearly missing size-frequency groups appear to have stemmed from spawn which was assumed to have been destroyed by storms that followed the corresponding run series.

The distinctness of the modes in the July 12 collection permits approximate age and growth computations for the young fish (Table V). The average daily growth increment for the first two months of life, slightly exceeding 0.5 mm, was computed on the assumptions that the prolarva measures 5.0 mm on hatching and that hatching took place on the tides thought from an examination of the tidal data (Figure 17) to have been high enough to have washed out and hence to have caused the hatching of the eggs. This estimate compares rather closely with those for other species of fish of roughly the same order of size. A somewhat smaller daily increment, about 0.4 mm, was determined by Hubbs (1921) for the smaller, fresh-water atherine, Labidesthes sicculus, over a comparable period of life.

Size-frequency analysis can be employed to determine whether or not the very young of other species have resulted from periodic spawnings. The whitebait larvae of Galaxias attenuatus in New Zealand should show a frequency distribution like that of Leuresthos young, for the spawning periods of the two species bear the same relation to the lunar periods. No evidence has been obtained to suggest that the other species of Atherinidae in California spawn periodically. No definite multimodal curves have been obtained in analyzing the size frequencies of the very young of either Atherinopsis californiensis, the jackamelt, or Atherinops affinis, the topsmelt. The one analysis here presented (Figure 15), based on eight hundred and eighty-six very young jacksmelt, is definitely unimodal.

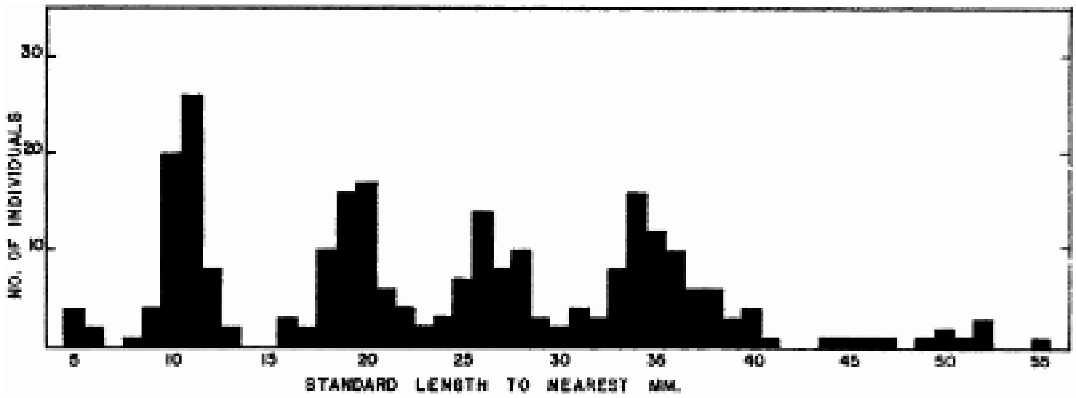


Figure 14. Size frequencies of 255 larval and juvenile grunion taken with a fine-meshed dip-net at Scripps Pier, La Jolla on July 12, 1947.

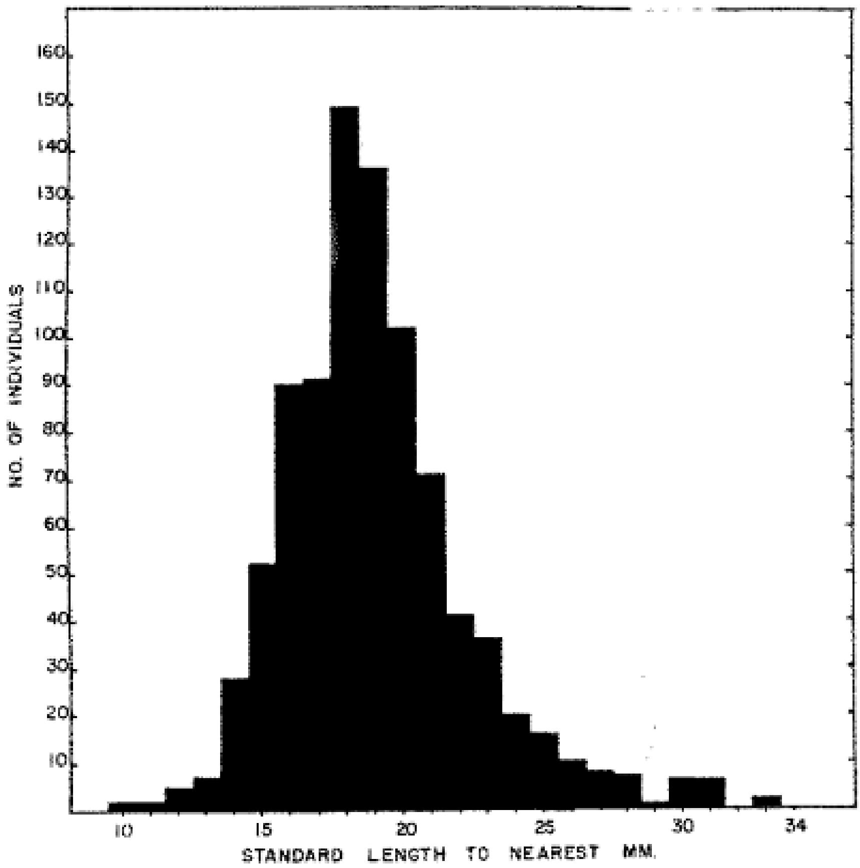


Figure 15. Size frequencies of 886 very young jacksmelt Atherinopsis californiensis, collected with a fine-meshed seine by Carl L. Hubbs and party in Laguna Coyote, Bahia de Ballenas, Baja California, on February 14–15, 1948.

TABLE V

AGE AND GROWTH ESTIMATES FROM SIZE-FREQUENCY ANALYSIS OF LARVAL AND JUVENILE GRUNION IN COLLECTION OF APRIL 12, 1947

	Four main size-groups			
	1	2	3	4
Size range, standard length, mm	8-13	16-23	23-31	31-41
Average standard length, mm	10.7	19.4	26.8	35.4
Average age, since spawning days	20	35	50	65
Average age (estimated) since hatching days	11	28	41	56
Average growth since hatching, mm	5.7	14.4	21.8	30.4
Average growth per day, mm	.48	.52	.53	.53
Difference in average size, mm	8.7	7.4	8.8	
Difference in average age, days	17	14	15	

Mortality of Eggs and Prolarvae

Incidental observations and information gathered during this study confirm Thompson's (1919) conclusion that the greatest mortality in the eggs is from physical factors, rather than from predators. No attempt was made to study the fate of the eggs in the sand, however, and the actual amount of predation is unknown. Thompson found a histerid beetle, Saprinus sulcifrons, “very often in the midst of the eggs,” and considered it the most serious predator. He also found the larvae of two species of flies in two different pods.

Certain shore birds should be added to this short list of known grunion predators. G. E. McGinitie reports (personal communication, 1948) seeing large numbers of Marbled Godwits feeding on grunion eggs in the beaches near Karkchoff Laboratory, Corona del Mar, California. John E. Fitch observed Marbled Godwits and Hudsonian Curlews probing in the sand for and eating grunion eggs on April 1, 1949, at La Jolla. The birds were first noticed because they were throwing their heads back, evidently to swallow, after withdrawing their beaks from the sand. These actions were observed for some minutes. When the area was examined, many large probe holes about 20 to 30 mm in diameter were found. Around the tops of these holes were numerous grunion eggs. Western Gulla were engaged in picking up these loose eggs.

Although there is some predation on the eggs, physical factors must destroy much greater numbers. It becomes evident, on examining the graphs showing the occurrence of runs in relation to tide height (Figures 15–17), that during the early part of the season grunion sometimes spawn on ascending tide series. In most such runs the eggs will be washed out by the higher tide of the succeeding night. These eggs which are washed out would have almost no chance for survival. If left on the surface of the beach they would be completely dessicated. If washed out to sea they would be subject to heavy predation scouring by wave-carried sand in the surf zone, and, being demersal, might well be covered by detritus if carried outside the wave zone. Even if the eggs did survive long enough to become fully developed, there would be no agency to agitate them at the proper time, therefore no stimulus for hatching.

At times it is probable that all the eggs laid during a complete run series are destroyed in this way. Thus on the runs occurring on March 4, 5, 6 and 7, 1946, all of the eggs would have been washed out by higher tides occurring on the next nights or by the higher series following by only six days. In fact, the high daylight tide occurring on March 5 is higher than the night tide of March 4. The eggs deposited on the nights of February 22 and 23, 1947, were certainly washed out by succeeding higher night tides, and, again, the daylight tide following the first run was higher than the night tide. Most of the eggs from the runs of March 22, 23 and 24, 1947, were probably freed by tides on succeeding nights. In 1948 the runs on March 11 and 12, and on April 25 and 26 were on ascending tide series, and in all probability most of the eggs were washed free by the tides following twenty-four hours later.

Eggs may also be washed out too early by succeeding tide series. This is most apt to happen late in the spawning session. Many, if not all, eggs deposited June 18, 1946, were probably washed out by the high night tide of June 24, just six days later. Only a very small percentage, if any, of these eggs would have been ready to hatch. This is also true of the run on August 15, 1946. The few eggs deposited September 13 and 14, 1946, would have been washed out by the higher series of day tides occurring at that time.

The eggs deposited during the runs of June 7, June 8, July 7, August 4 and August 5, 1947, and also those of May 27 and July 10, 1948, probably suffered high mortality because of being freed too early by the succeeding tide series.

The proportion of runs occurring at times probably unfavorable for complete development of eggs was eighteen percent in 1946, twenty-six percent in 1947, and nineteen percent of the observed runs in 1948. The percentage of eggs during a season must be much lower than these figures, since most of the runs occurring at unfavorable times are very light. Only a small percentage of the total breeding population spawns litter in February or early March, or during July, August and September, and most of the unfavorable runs occurred during these parts of the year. In addition, the number of fish spawning on an unfavorable night is often small compared to the number spawning on the rest of that run series.

There is no way to estimate directly the mortality of the larvae as they hatch in the zone of wave wash. At times, however, it must be very high. Tremendous numbers of newly hatched larvae must be destroyed during storms in this area of surging water and sand. Indirectly, as indicated above, size frequency data on very young grunion may indicate great or perhaps even a total loss of the eggs or larvae from one or more run series.

Mortality of Adults during Spawning

Apparently there is no sound confirmation of the natural inference that a high mortality accompanies spawning by a fish that leaves the water to lay its eggs. Actually losses are comparatively slight while the fish are on the beach. On a normally sloping beach, fish rarely die by being stranded. During three years of observation on Scripps Beach no uninjured grunion have been found stranded on the beach after a run. On occasional very high tides the waves beat against the sea wall with great force. Twice, injured fish have been found in this area, obviously hurt by being dashed against the wall. The percentage of such injuries was estimated to be much less than one percent of the fish in this particular vicinity, however, and at the same time fish were running by the thousands on other parts of the beach.

The greatest mortality probably occurs on beaches which have a back slope. Such low spots back of the beach ridge commonly occur on a few beaches, and always occur where a lagoon backs the beach. In such areas many grunion may be trapped when larger waves during exceptionally high tides cause them to be washed over the ridge into the low area. Mr. A. A. Allanson reported seeing hundreds trapped in this fashion on the beach at San Miguol, Baja California, on April 22, 1947. Grunion have also been seen trapped behind a bar or beach ridge on Wind-and-Sea Beach, La Jolla, and, on several occasions, by Mr. Buy Flemming at Doheny State Park, south of Capistrano Beach, California.

Grunion may also be trapped behind large bunches of kelp washed in on the beach. Frederick H. Stoye reported seeing hundreds caught in this manner on the beach at Del Mar, California, on the night of April 22, 1947. I picked up one thousand two hundred and eighty-six dead grunion from a one hundred yard stretch of beach north of the Crystal Pier, Pacific Beach, California, on the morning of May 11, 1947, after I had heard that they had been stranded here behind kelp during a very heavy grunion run on the preceding night. Many reports of seeing such casualties at times when kelp was heavy on the beach have been received.

Dr. Carl L. Hubbs reported what certainly must be a rare cause of mortality. On Estero Beach, near Ensenada, Baja California, many grunion were found buried by cave-ins from the sand cliff backing the beach. A very high tide had eroded the bank, causing the miniature land slides that buried the spawning grunion.

There seems to be little predation on shore, except from man. Near heavily populated areas large numbers of grunion are taken for food and sport. This take is now (1949) illegal during April and May, but the law is seldom enforced, and many grunion are taken during the closed season.

Reports have been received on only two other predators, but neither can be considered serious. Skunks, which often forage on the beach near Scripps, have been observed by John Stackleberg taking grunion in small numbers. He once had a cat that usually attended grunion runs. This cat sometimes went into the water to take grunion and would often catch eight or ten in an evening.

ANALYSIS OF TIME OF SPAWNING

The time relations in the spawning of the grunion involve the spawning season, the run series and the runs.

Spawning Season

The major spawning season certainly falls within the previously assigned period, but the extreme limits are now extended. Some spawning may occur in late February and in some years may continue until middle September.

Thompson (1919) considered the spawning season of the grunion as beginning in March and extending through June. Later (1919a) he reported small runs occurring on July 15 and 16 and August 14. Clark (1925) indicated the same limits and further showed that during the latter half of April and the first part of May nearly all grunion were spawning.

It is probable that no grunion spawn until late February and it is possible that at times no runs occur until early March. In both 1947 and 1948 small runs of grunion occurred in late February (Tables XVI and XVIII, Appendix). No observations were made during February in 1946. Watch for spawning fish was also made on February 11 and 12 in 1948, but none were seen.

The runs may continue through August and even into September. Grunion were observed on the beach at the expected time for a run on August 29, 1946, and again on September 13 and 14, 1946. In 1947, however, none were found after August 5, although watch was kept on appropriate tides on August 17, 18, 19 and 20 and on September 1, 2 and 3. No observations were made late in the season in 1948. The runs in early August in both 1946 and 1947 were very light, and it is probably unusual for fish to spawn later.

In the three years of investigation good runs were observed at La Jolla from early March until late June. The heaviest runs occurred during April and May, when apparently almost all individuals in the population spawned.

The start of the spawning season corresponds closely with warming of the ocean and with increase in daylength.

Run Series

The data on the runs during 1946 and 1947, and in 1948 before the middle of June, are believed to be complete enough to warrant drawing conclusions as to timing that are more definite than those reached by previous workers.

The ideas of both Thompson and Clark were based on observations of relatively few runs. No attempt was made by either to watch all runs during a season, or all runs in the run series which they observed.

Thompson (1919) first considered that the grunion ran only on the descending tide series following the full moon. In a footnote he noted that a light run had occurred on a tide series following the new moon. He felt, however, that the runs following the new moon were light as compared to those associated with the full moon. He concluded that runs come only after the highest tide of a series.

Clark (1925) showed that runs of equal intensity follow the full and the new moons. She also believed that grunion run only after the highest tide of a series has been reached. From studies of the ovaries, she concluded that as soon as one batch of eggs is spawned out, another batch begins to develop, matures, and is spawned out about two weeks later. She wrote, "the interval between spawnings is apparently fifteen days instead of two weeks. This condition results in the fishes spawning on later and lower tides during the higher tide series of high tides than on the lower series of high tides."

The many observations made during 1946, 1947 and 1948 are summarized in the Appendix (Tables XV–XVII). Here are presented all times of observations, times of observed runs, time of high tide on nights when watches were maintained, and the percentage intensity of runs.

The occurrence of grunion runs bears a definite but varying relation to the heights of high night tides (Figures 16–18). It is at once obvious, upon referring to the charts, that the grunion exhibits an amazingly clear-cut lunar rhythm in its spawning cycle. Reduction is entirely restricted to sharp peaks that occur with great regularity shortly after the moon phases.

The belief that grunion spawn only on descending tide series is also shown to be in error. In fact, two of the runs in the first series observed in this investigation occurred on ascending tide series. In 1946 these runs (March 4 and 5 and April 2) took place on tides which were followed the next night by higher tides. In 1947 the runs on February 22 and 23 and on March 22, 23 and 24 took place before the highest tide of the series was reached. During the February, 1947, runs the following daylight tides were higher than the tides on which the fish spawned, and the tides following in the same series were higher than the run tides for a period of two weeks following. Runs on March 11, 12 and 13, and on April 9 and 10, 1948, also occurred on ascending tide series.

The fact that run series are indicated as including three or four runs during the major part of the spawning season, and only one or two at the first and last part of the season, does not signify a difference in timing. Runs were recorded only when fish could be seen on the beach. Early and late in the season, the percentage of the population that spawns is very much smaller than in the main spawning period. Therefore, even though a few fish may run on three or four nights during the light early and late runs, the chances of seeing them are small, despite careful observation. This may be clearly seen in the summary of observations table for 1946 (Appendix, Table XV). The run series for late July consists of a single run on July 31, when only three fish were seen. When so few fish are running that only three can be observed, there is good chance that other runs of the same intensity might take place and be missed by the observer; still lighter runs would almost certainly be missed.

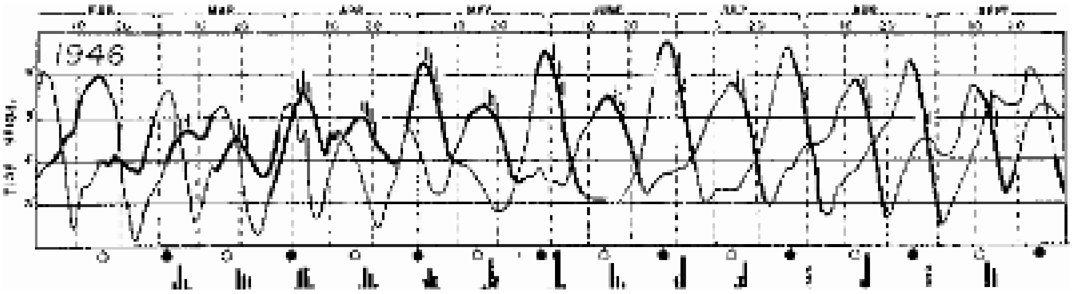


Figure 16. Grunion runs observed at La Jolla in 1946, plotted in relation to variations in observed high-tide heights at La Jolla.

The heights of high tides only have been plotted. The high tides about twenty-four hours and forty minutes apart have been connected by smooth lines, darkened for the night tides. The two tides of each day yield the two series of curves. Data for time and height of tides are from records of the tide-recording machine maintained for the Coast and Geodetic Survey on Scripps Pier. It is possible to read the approximate heights of the high tides and to see the relation to them of the times of runs, which are indicated by the short vertical lines above the curves. The moon phases are plotted at the bottom of each graph, by solid circles to indicate the new moons and open circles to indicate the full moons. The histograms at the bottom portray the percentage intensity of runs. No attempt is made here to show the numbers of fish relative to the total spawning population. The data on runs were obtained only from observations on Scripps Beach, La Jolla, except for three runs in May and June 1948, which were observed at Malibu Beach, California, by Mr. F. Alton Everest of the Moody Institute of Science.

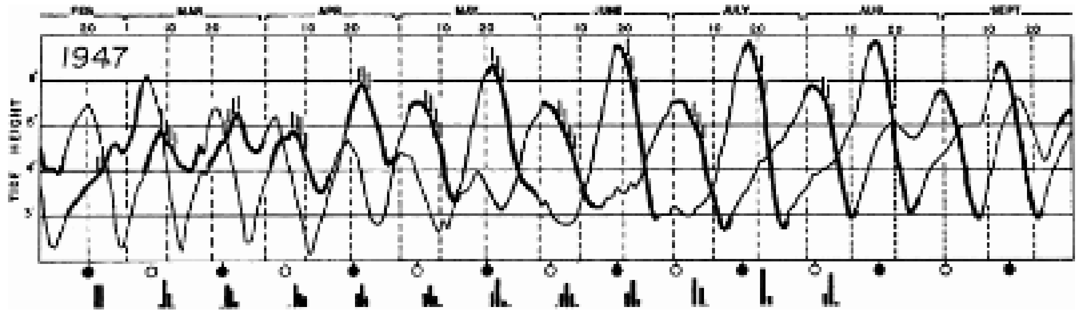


Figure 17. Grunion runs observed at La Jolla in 1947, plotted in relation to variations in observed high-tide heights. See Figure 16 for explanation of symbols.

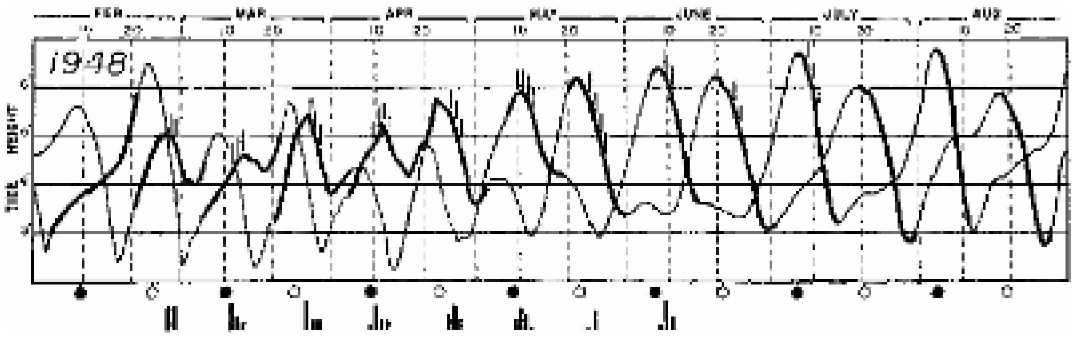


Figure 18. Grunion runs observed at La Jolla in 1948, plotted in relation to variations in observed high-tide heights. See Figure 16 for explanation of symbols.

It is probable that during these times fish are seen only on nights which correspond to the heavy run nights during March, April, May and June.

Possible Controlling Factors

Since the number of observed runs in a run series varies from three to four during most of the spawning season, and may be only one or two at times, it is difficult to analyze the precise times of run series, in relation to each other and to associated natural phenomena. For a ready comparison of the times of each run series, the run series midpoint has been computed (see Methods, p. 20). This midpoint represents the mean time of runs of a series, and is computed to the nearest tenth of a day. Since the grunion may express the urge to spawn only once every twenty-four hours, this point does not denote the mean of the time fish are first ready to spawn. This point would be approximately twelve hours earlier. The calculated midpoints are given in the Appendix (Table XXII). Data for the very small runs during February and after the second run in June (and in 1948 after the first run of June) are not sufficiently complete or accurate to warrant use in the following discussion of timing.

The factor or factors that control the times when grunion spawn have never been determined, though the approximate relation of the time of run series to the spring tides has become well established. Thompson (1919) hold that runs occur only on descending tide series, soon after the highest tide, and apparently inferred that the relative heights of high tide might control the timing. Clark (1925) also believed that the times of runs and run series were tide-controlled.

Korringa (1947), basing his conclusions entirely on the findings of Thompson and Clark, stated: "I believe that here too rhythmical variations in water pressure bring about a synchronization of egg-development and the sequence of neaps and springs."

The run series have a definite time pattern that is best shown by comparing the intervals between their midpoints (Tables VI–VII). Long and short intervals alternate. This pattern was not very clear in 1946, but became progressively clearer in 1947 and 1948. During these years the shorter intervals almost always fell during the period in which the moon was passing from full phase to new.

The establishment of this pattern provides leads in the search for the factors that control the time when run series occur. We must assume that such a factor or factors will have a periodicity closely corresponding with that of spawning by the grunion. Although there is the possibility that many factors may act simultaneously, it seems probable that so uniform a pattern is primarily controlled by a single factor.

It seems highly improbable that internal rhythms are alone or even primarily involved. Even though involved they would probably need to be inaugurated or kept in phase (or both) by external stimuli. The alternation of long and short intervals between run series points towards control by external stimuli. Furthermore, changes in the intervals between run series are too closely correlated with changes in the intervals between certain physical phenomena, as shown below, to render plausible any idea that interval rhythms are alone involved.

The observed pattern of spawning times corresponds very closely to the lunar cycle and hence to the time pattern of various phenomena that are dependent upon the movements of the moon. The relationship is particularly obvious when we compare the pattern of intervals between midpoints of run series (Tables VI–VII) with the corresponding intervals between new and full moon phases (Tables VIII–IX). In 1946, when the intervals from full moon to new and from new moon to full were more nearly equal than they were in the two subsequent years, the concurrent intervals between spawnings were relatively uniform. In 1947 and 1948, as the intervals between successive lunar phases became increasingly discordant, the fluctuations in the intervals between successive runs also increased. The times of run series also correspond

TABLE VI

INTERVALS IN DAYS AND TENTHS OF DAYS BETWEEN MIDPOINTS OF ADJACENT MAJOR RUN SERIES

Midpoint Dates of Adjacent Run Series	Interval in Days	Change in Moon Phase*
1946		
March 6.0 - March 20.8	14.8	N - F
March 20.8 - April 4.5	14.7	F - N
April 4.5 - April 19.5	15.0	N - F
April 19.5 - May 4.1	14.6	F - N
May 4.1 - May 19.2	15.1	N - F
May 19.2 - June 3.1	14.9	F - N
June 3.1 - June 17.5	14.4	N - F
1947		
March 10.2 - March 24.6	14.4	F - N
March 24.6 - April 8.7	15.1	N - F
April 8.7 - April 22.8	14.1	F - N
April 22.8 - May 7.9	15.1	N - F
May 7.9 - May 22.8	14.9	F - N
May 22.8 - June 7.0	15.2	N - F
June 7.0 - June 21.8	14.8	F - N
1948		
March 12.6 - March 28.6	16.0	N - F
March 28.6 - April 11.5	13.9	F - N
April 11.5 - April 26.9	15.4	N - F
April 26.9 - May 11.2	14.3	F - N
May 11.2 - May 26.8	15.6	N - F
May 26.8 - June 10.2	14.4	F - N

* N = New moon; F = Full moon.

TABLE VII

ANALYSIS OF INTERVALS IN DAYS BETWEEN MIDPOINTS OF MAJOR RUN SERIES

Based on data in Table VI

Intervals	1946	1947	1948
Intervals, full to new moon runs	14.6 - 14.8 Ave., 14.73	14.1 - 14.9 Ave., 14.55	13.9 - 14.4 Ave., 14.20
Intervals, new to full moon runs	14.4 - 15.1 Ave., 14.83	15.1 - 15.2 Ave., 15.13	15.4 - 16.0 Ave., 15.67
All intervals	14.4 - 15.1 Ave., 14.79	14.1 - 15.2 Ave., 14.80	13.9 - 16.0 Ave., 14.92
Difference between shortest and longest intervals	0.7	1.1	2.1
Average difference between adjacent intervals	0.37	0.60	1.46

TABLE VIII

INTERVALS BETWEEN TIME OF NEW AND FULL MOON
1946, 1947 and 1948

	Change in Phase	Dates of Moon Phase	Interval
1946	N - F	March 3.4 - March 17.4	14.0
	F - N	March 17.4 - April 1.8	15.4
	N - F	April 1.8 - April 16.1	14.3
	F - N	April 16.1 - May 1.2	15.1
	N - F	May 1.2 - May 15.7	14.5
	F - N	May 15.7 - May 30.5	14.8
	N - F	May 30.5 - June 14.4	14.9
1947	F - N	March 6.8 - March 22.3	15.5
	N - F	March 22.3 - April 5.3	14.0
	F - N	April 5.3 - April 20.8	15.5
	N - F	April 20.8 - May 4.8	14.0
	F - N	May 4.8 - May 20.2	15.4
	N - F	May 20.2 - June 3.4	14.2
	F - N	June 3.4 - June 18.5	15.1
1948	N - F	March 10.5 - March 24.7	14.2
	F - N	March 24.7 - April 9.2	15.5
	N - F	April 9.2 - April 23.2	14.0
	F - N	April 23.2 - May 8.7	15.5
	N - F	May 8.7 - May 22.6	13.9
	F - N	May 22.6 - June 7.2	15.6

TABLE IX

ANALYSIS OF INTERVALS IN DAYS BETWEEN NEW AND FULL MOON PHASES

Based on data in Table VIII

Intervals	1946	1947	1948
Intervals, full to new moon	14.8 - 15.4 Ave., 15.10	15.1 - 15.5 Ave., 15.38	15.5 - 15.6 Ave., 15.53
Intervals, new to full moon	14.0 - 14.9 Ave., 14.43	14.0 - 14.2 Ave., 14.07	13.9 - 14.2 Ave., 14.03
All intervals	14.0 - 15.4 Ave., 14.71	14.0 - 15.5 Ave., 14.81	13.9 - 15.6 Ave., 14.78
Difference between shortest and longest intervals	1.4	1.5	1.7
Average difference between adjacent intervals	.72	1.47	1.52

to the times of spring tides (Figures 16–18), which of course are chiefly controlled by the position of the moon. No phenomena other than those associated with the moon are known to have a similar time pattern.

Thompson (1919) and Clark (1925) believed the times of run series to be tide controlled, but did not specify how. Korringa (1947) on the basis of their findings, concluded that the factor was the change in water pressure due to fluctuations of the tide. It has already been shown, however, that there is considerable variation in the relative heights of the tides on which run series occur, and that runs occasionally take place on ascending rather than on descending series of tides, particularly during the early part of the spawning season. In 1948 the time in days between the highest (or first highest) of the associated night tides and the run series midpoint varied as follows: 2.7, -1.3, 1.7, -1.3, 4.1, 1.4, 5.0, 2.4. Similarly varying estimates results from the data for 1946 and 1947. The intervals between run series and the next preceding tide series (about two weeks previous) vary as widely, and the results are similarly inconsistent if comparisons are made to time of lowest tides or time of greatest tidal amplitude.

There are additional reasons for doubting tide control. A consideration of the conceivable agencies through which tidal phenomena might act reveals none which plausibly can be regarded as effective. The chance that the factor is changing water pressure seems remote, since, as pointed out previously, the grunion is essentially a top-water fish, whose orientation as to depth seems to be with the water surface only. A pelagic, top-water fish is not apt to detect changes in water pressure due to tidal movements. Recognition of actual tide heights or of changes therein seems out of the question, since there are no accurate reference points for relative tide height in the surf zone off most sandy beaches. Variations in height of surf or sound of surf correlated with tide height are not well marked, if they exist, and are overshadowed by variations due to storm and calm. The chance that such factors are effective seems to be precluded also by the fact that grunion run at the same time on surf-swept beaches as they do in bays where no surf zone exists.

Marked anomalies in the temperature of coastal waters seem to be correlated with tides (Leipper, personal communication), but these anomalies are neither consistently nor regularly correlated with the spring tides on which the fish spawn. One might argue that substances leached from the upper beach, reached only by spring tides, might stimulate the fish, but rainstorms and intervening periods of high and low surf must also leach out such substances, but do not cause irregularities in the spawning sequence.

Other variable phenomena primarily due to the moon's movements are variations in lunar radia ion and the changes in the acceleration of gravity due to the moon and the sun. The possibility of light being the controlling factor seems remote, since runs occur after both full and new moon phases, when conditions as to light are at opposite extremes. The possibility that both increasing and decreasing intensities or duration of moonlight might act to produce this pattern is remote, since the patterns do not match. There is also no recognizable effect from changing cloud conditions, which range from continuous heavy cloud cover during some run series to completely clear skies for others.

The total changes in acceleration of the earth's gravity due to the movements of the moon and sun are approximately .0002 cm/sec.2 (Sverdrup, et al., 1946). This is less than the change in acceleration of gravity produced by a change in elevation of one meter. It seems impossible that this fluctuation could operate on a fish which constantly changes depth through a range of six to eight feet. The pattern of variation in acceleration of gravity, however, is very close to that of the moon at the time of spring tides, and even this possible factor should not be summarily or completely disregarded.

Detailed comparison of the data on intervals between run series midpoints (Table VI–VII) and between corresponding moon phases (Tables VIII–IX) shows not only that the patterns were closely comparable for each year, but also that they varied through the three years of observation in a like manner. As already noted, the pattern of alternately long and short intervals became increasingly evident. The patterns, however, were not in phase, for the intervals between run series were short when the intervals between moon phases were long. Consequently, the intervals between midpoints of runs are negatively correlated with the intervals between concurrent moon phases, but are positively correlated with the preceding interval between moon phases (Table XII).

The intervals of a few days between the first preceding moon phase and the run series midpoint vary considerably more than do the intervals of about 2.5 weeks between the second preceding moon phase and the midpoint, both in total range of variation and in difference between successive intervals (Tables X–XI).

When all moon phases are considered, therefore, there is a better correlation between the second preceding moon phase and the midpoint than there is between the first preceding moon phase and the midpoint. When the new and full moon phases are considered separately, however, there is little difference in the variations between the two periods.

TABLE X

INTERVALS BETWEEN MIDPOINT OF EACH MAJOR RUN SERIES
AND FIRST TWO PRECEDING MOON PHASES

Moon Phase	Date of Moon Phase		Next Run Series (midpoint)		Interval from First Preceding Moon Phase	Interval from Second Preceding Moon Phase
	1946					
Full	Feb.	15.8	....		...	....
New	March	3.4	March	6.0	2.6	18.2
Full	March	17.4	March	20.8	3.4	17.4
New	April	1.8	April	4.5	2.7	18.1
Full	April	16.1	April	19.5	3.4	17.7
New	May	1.2	May	4.1	2.9	18.0
Full	May	15.7	May	19.2	3.5	18.0
New	May	30.5	June	3.1	3.6	18.4
Full	June	14.4	June	17.5	3.1	18.0
	1947					
New	Feb.	20.7	....		...	....
Full	March	6.8	March	10.2	3.4	17.5
New	March	22.3	March	24.6	2.3	17.8
Full	April	5.3	April	8.7	3.4	17.4
New	April	20.8	April	22.8	2.0	17.5
Full	May	4.8	May	7.9	3.1	17.1
New	May	20.2	May	22.8	2.6	18.0
Full	June	3.4	June	7.0	3.6	17.8
New	June	18.5	June	21.8	3.3	18.4

TABLE X (Continued)

INTERVALS BETWEEN MIDPOINT OF EACH MAJOR RUN SERIES
AND FIRST TWO PRECEDING MOON PHASES

Moon Phase	Date of Moon Phase	Next Run Series (midpoint)	Interval from First Preceding Moon Phase	Interval from Second Preceding Moon Phase
	1948			
Full	Feb. 24.3	....	...	....
New	March 10.5	March 12.6	2.1	18.3
Full	March 24.7	March 28.6	3.9	18.1
New	April 9.2	April 11.5	2.3	17.8
Full	April 23.2	April 26.9	3.7	17.7
New	May 8.7	May 11.2	2.5	17.8
Full	May 22.6	May 26.8	4.2	18.1
New	June 7.2	June 10.2	3.0	18.6

TABLE XI

ANALYSIS OF INTERVALS BETWEEN MIDPOINT OF EACH MAJOR RUN SERIES AND FIRST TWO PRECEDING MOON PHASES

Based on data in Table X

Intervals	1946	1947	1948
Interval from first preceding moon phase			
All data	2.6 - 3.6 Ave., 3.15	2.0 - 3.6 Ave., 2.96	2.1 - 4.2 Ave., 3.10
From full moon (F)	3.1 - 3.5 Ave., 3.35	3.1 - 3.6 Ave., 3.37	3.7 - 4.2 Ave., 3.93
From new moon (N)	2.6 - 3.6 Ave., 2.95	2.0 - 3.3 Ave., 2.55	2.1 - 3.0 Ave., 2.47
Difference between average intervals (F - N)	0.40	0.82	1.46
Difference between adjacent intervals	0.1 - 0.8 Ave., 0.65	0.3 - 1.4 Ave., 0.91	1.2 - 1.8 Ave., 1.48
Interval from second preceding moon phase			
All data	17.4 - 18.4 Ave., 17.95	17.1 - 18.4 Ave., 17.69	17.7 - 18.6 Ave., 18.06
From full moon (F)	17.4 - 18.0 Ave., 17.77	17.1 - 17.8 Ave., 17.45	17.7 - 18.1 Ave., 17.97
From new moon (N)	18.0 - 18.4 Ave., 18.17	17.5 - 18.4 Ave., 17.93	17.6 - 18.6 Ave., 18.13
Difference between average intervals (F - N)	0.40	0.48	0.20
Difference between successive intervals	0.0 - 0.8 Ave., 0.50	0.1 - 0.9 Ave., 0.41	0.1 - 0.5 Ave., 0.25

TABLE XII

INTERVAL BETWEEN MIDPOINT OF RUN SERIES CORRELATED WITH AVERAGE CORRESPONDING INTERVAL BETWEEN MOON PHASES

Average Interval between Moon Phases

Interval between Run Series	Concurrent Period	One Period Earlier
13.9 - 14.1 (2)*	15.5	14.1
14.2 - 14.4 (4)	15.4	14.2
14.5 - 14.7 (2)	15.3	14.1
14.8 - 15.0 (5)	14.7	14.8
15.1 - 15.3 (3)	14.2	15.4
15.4 - 15.6 (2)	13.9	15.5
15.7 - 16.0 (1)	14.2	15.2

* Number of cases indicated in parenthesis.

The particularly close correlation between the midpoints of run series and the second preceding moons recalls the findings of Clark (1925) on the initial time in the final maturation of the eggs. She found that the rapid final growth started in all mature females at about the time of spawning. Although she concluded that when one batch of eggs was spawned out another immediately started maturing, her own data indicate that the maturing class was already developing before the actual spawning. Thus on April 19, 1923, ova of the maturing class size were present, though spawning was not completed. Again on May 3, 1923, the maturing class had become evident, though spawning had not yet started. On May 5, 1923, some ova already measured 1.09 mm, which is 0.31 mm over the limits of the intermediate class. It therefore seems probable that the maturation of the succeeding batch of eggs started several days before actual spawning of the matured group. The initiation of the process, therefore, coincides closely with the moon phases.

All available evidence indicates that, once started, the growth of the eggs continues until the ova that are about to be spawned are released into the lumen of the ovary. None of the many collections that have been made, other than those made during a run series or on the day preceding the first run of a series, have contained females with eggs in the lumen.

The number of days required for the development of the eggs, from about the time of the preceding moon phase until the spawning period, is at least approximately constant.

Though other explanations are not excluded, the foregoing evidence leads to the hypothesis that the time when the females run is dependent on an approximately constant period of maturation of eggs, initiated by some factor effective at or very close to the time of the second moon phase before the run.

The males spawn on the same cycle, presumably as the result of a similar pattern of gonadal development governed by the same stimuli. No detailed study of the males has been made, but it has been observed that the testis undergoes gross changes similar to those undergone by the ovary. The testis shrinks after spawning and the contents become too viscous to be extruded readily on pressure. Development is gradual during the interval between run series and the milt does not become really fluid until the day preceding the first run of the next series.

Since grunion spawn during a season of sharply rising temperatures, the assumption that time of spawning is dependent on an approximately invariable period of maturation of the gametes calls for the further inference that this period is independent of temperature. There is no significant difference in intervals between runs through the spawning season, even though the temperature may vary from an average of 12.78° C in February to 21.21° C in August (Table XIII).

If the development is approximately constant through the range of temperatures observed, there must be some temperature compensating mechanism to equalize the changes in metabolic rate normally produced by variations in temperature. There are indications that such mechanisms exist in at least some cold-blooded animals, for some invertebrates (Melvin, 1928; Edwards and Irving, 1943; Sayle, 1928) and some fish (Fry, 1947) have been shown to have a relatively constant metabolic rate over rather wide ranges in temperature. Brown and Webb (1948) found that the twenty-four hour rhythm in the fiddler crab Uea persists between the temperatures of 6° C to 20° C, even though the animal is kept in darkness. Furthermore, some closely related species and even some populations of the same species have similar rates of general or special activities, despite the widely different environmental temperatures (Spârck, 1936; Thorson, personal communication).

The hypothesis advanced above is consistent with the observed intervals between moon phases and spawning. If we take values approximating those obtained for the 1948 season, when the alternation of long and short intervals was rather extreme, and graph schematically (Figure 19), the various

TABLE XIII

SEASONAL RISE IN SURFACE TEMPERATURE AT SCRIPPS PIER AND STABILITY OF INTERVALS BETWEEN MIDPOINTS OF ALTERNATE RUN SERIES ON ADJACENT BEACH

Monthly Average of Daily Temperature

Year	Feb.	March	April	May	June	July	August
1946	12.78	13.63	16.17	17.63	19.62	20.39	21.21
1947	13.86	14.87	15.76	17.99	19.15	19.29	20.01
1948	13.19	13.41	14.80	16.91	17.26	18.47	19.86
Average	13.29	14.03	15.58	17.51	18.77	19.38	20.36

Interval between Midpoints of Alternate Run Series*

Year	Feb.	March	April	May	June	July	August
1946	....	29.5	29.6	30.0	29.8	29.2?	29.0?
1947	....	29.5	29.2	30.1	29.4	29.4?	....
1948	....	29.9	29.7	30.0	....	....	....
Average	....	29.6	29.5	30.0	29.6	29.3?	29.0?

* Each interval is listed under the month that includes all or the major part of the interval.

rather complicated time relationships can be clarified.

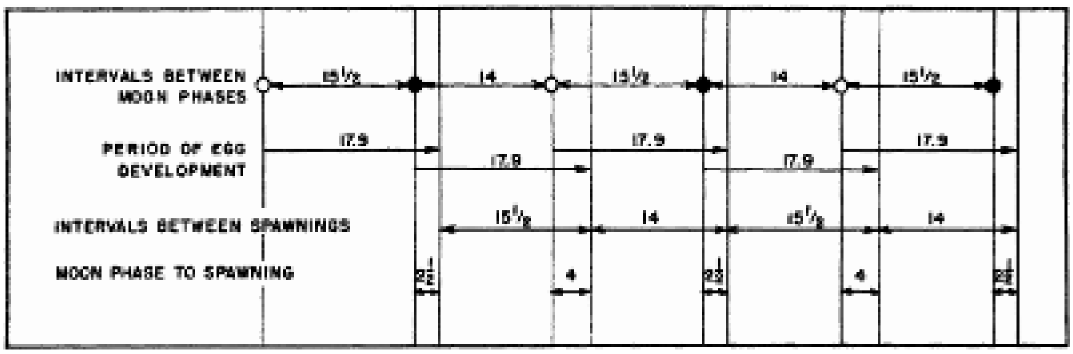


Figure 19. Scheme representing the time relations that are basic to the hypothesis that the spawning times of the grunion depend on the initiation of egg (or sperm) development at the time of the moon phases and on a constant period of development.

The moon intervals are set alternatingly at 15.5 days and 14, days, in a pattern similar to the actual. The several intervals are indicated by arrows, with the number of days specified. Assuming a constant period of egg and sperm development of 17.9 days, dating from the initiation at the time of the second preceding moon phase, either full or now, the time of the runs is theoretically determined and plotted (17.9 days is the mean of all the observed values). The resulting intervals between runs are then seen to be alternately 14 and 15.5 days and the longer of these intervals are seen to be concurrent with the shorter intervals between moon phases, again in agreement with observation (Table XII). Another set of alternately long and short intervals results, namely between run series midpoints and the first preceding moon phase, and these also approach the observed values for 1948 (Table X). These intervals are shown by the short arrows at the bottom of Figure 19.

The observed interval between the second preceding moon phase and spawning (Table XI) shows some slight variations that may be significant and that may eventually lead to a more definite indication of the controlling factors. When the second preceding moon was full, the average interval in the three years varied from 17.45 to 17.97 and averaged 17.73 days; when it was new, the average interval ranged from 17.93 to 18.17 with a mean of 18.08 days. The difference is .25 day. The average differences between successive intervals (.25 to .5 day in each year) may exceed the error of estimate.

All of the many other possible controlling mechanisms thus far conceived involve even more doubts and complexities than the one offered above. Postulating that an internal rhythm initiates the final maturation of the gonads involves the same problem of temperature regulation discussed above, as well as other difficulties. If spawning is the initiating factor, long and short periods of development would alternate and the time when such seasonal cycle starts would be left unexplained. If a single factor should both initiate the gonadal development and determine the time of development, alternately long and short intervals again would result, but such a condition seems improbable.

Runs

Thompson (1919) concluded from his observations that grunion runs start at about the time of high tide and last for about one hour. He was not specific as to the start of the run, but he did indicate that isolated pairs and scattered fish come in before and long after the larger schools. We may conclude, therefore, that the time listed by Thompson for grunion runs included only the time when a relatively large number of fish were on the beach. His timings are listed below:

TIMES OF GRUNION RUNS OBSERVED BY THOMPSON
From Thompson (1919)

Tide beginning on	Run beginning	Run ending	Time of High Tide
April 13, 1919	10:30 p. m.	11:40 p. m.	10:15 p. m.
May 16, 1919	9:15 p. m.	10:00 p. m.	9:25 p. m.
May 17, 1919	10:00 p. m.	11:00 p. m.	9:54 p. m.
May 18, 1919	10:20 p. m.	12:01 a. m.	10:25 p. m.

Thompson noted, “The data given in this table are, however, somewhat unreliable. The runs were not at all continuous, and were found to be made up of various small runs, some of which came in on but parts of the beach, making it extremely difficult to be sure that all were observed." Clark (1925, 1938) also indicated that the runs last for about an hour, starting at about the turn of the tide.

Mr. J. B. Joplin (quoted in Hubbs, 1916) stated that the run usually lasts three hours or longer. Barnhart (1918) wrote, "The nightly run begins within a few minutes of the time when the tide is at its highest point and lasts for several hours."

Although runs were considered by me to last as long as any fish remained on the beach between waves, the most significant time seems to be the period when the heaviest part of each run occurs. Using these times for comparison, many of the very light, short runs may be considered, since their entire extent probably corresponds with the heavier parts of the major runs.

There is a very close correlation between the times of high night tides and the time of runs, not only at La Jolla (Figures 20–21 and 24–25) but also at other localities (Figures 22–23). The relationship, however, is not strictly a straight-line correlation. During the early part of the season, the runs are clearly shown by the La Jolla date to be in relation to tide time than they are during May and June. There

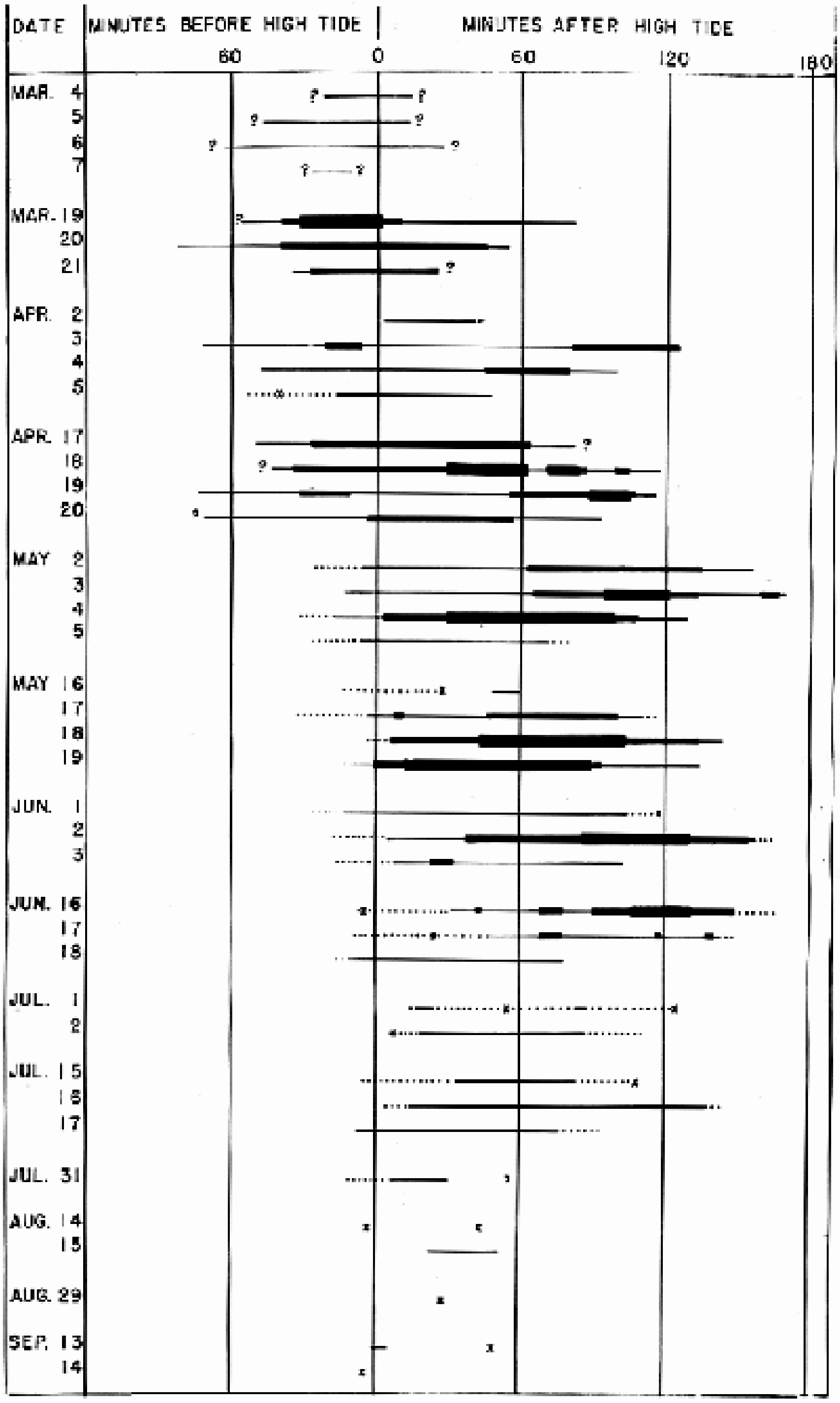


Figure 20. Times of grunion runs at La Jolla in 1946, plotted in relation to time of high night tide. Explanation of symbols used in figures 20–23: Time of runs are indicated by lines or crosses opposite dates of occurrence in Figures 20–21, and opposite locality in Figures 22–23. Thickness of lines represent the approximate estimates of the numbers of fish.

Dotted lines - fish in waves but not remaining on beach

Thin lines - 1–19 fish per minute

Medium lines - 20–99 fish per minute

Thick lines - 100 or more fish per minute

x = single fish

? = observations started after start of run, or ended before end of run

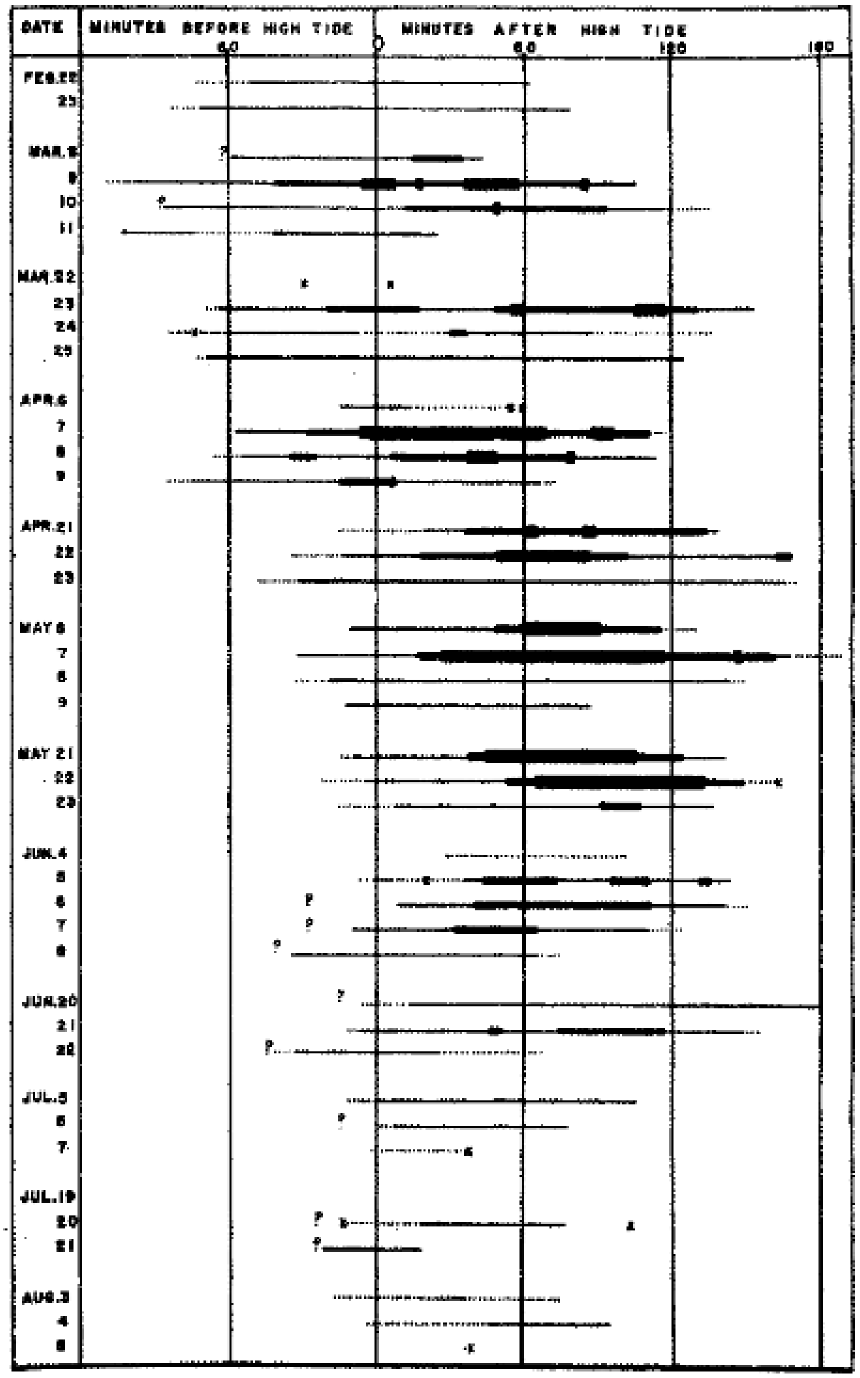


Figure 21. Time of grunion runs at La Jolla in 1947, plotted in relation to time of high night tide. See Figure 20 for explanation of symbols.

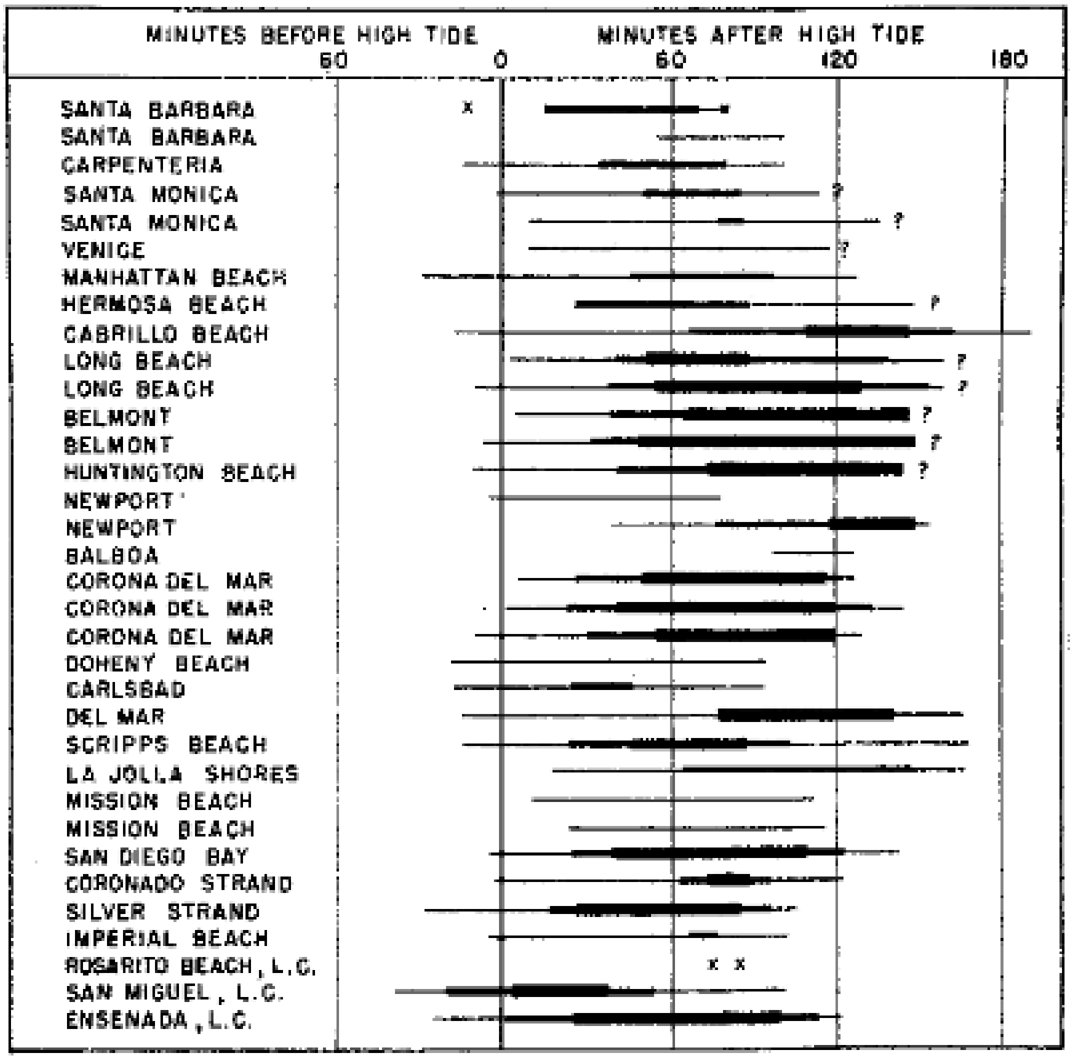


Figure 22. Time of grunion runs on various beaches in southern California and Baja California (L. C.), on the night of April 22, 1947, listed from north to south.
See Figure 20 for explanation of symbols.

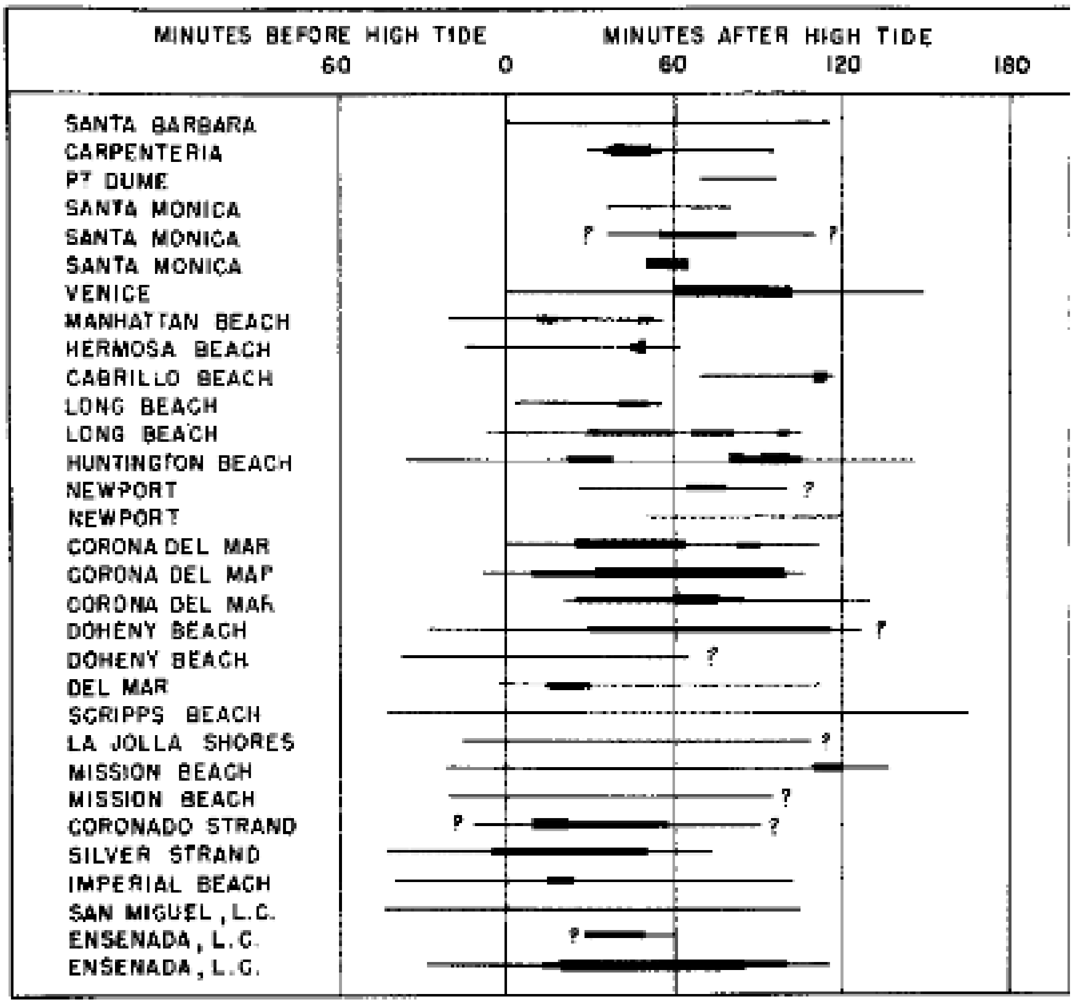


Figure 23. Time of grunion runs on various beaches in southern California and Baja California (L. C.), on the night of April 23, 1947, listed from north to south.
See Figure 20 for explanation of symbols.

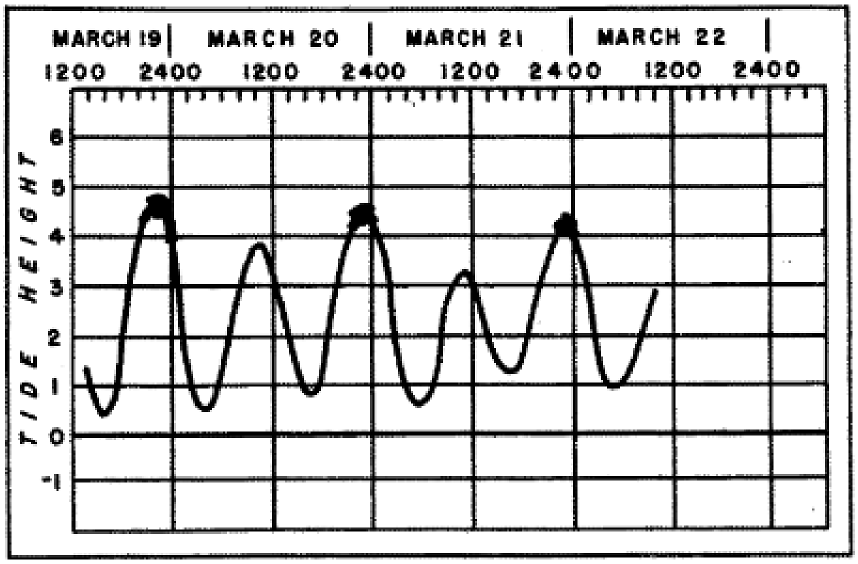


Figure 24. Times of runs in reference to tidal height early in season (in March, 1946). These runs occur at the peak of the high tide. Times of runs are indicated by the medium-broad lines and times of heavy part of run by the breadest line.

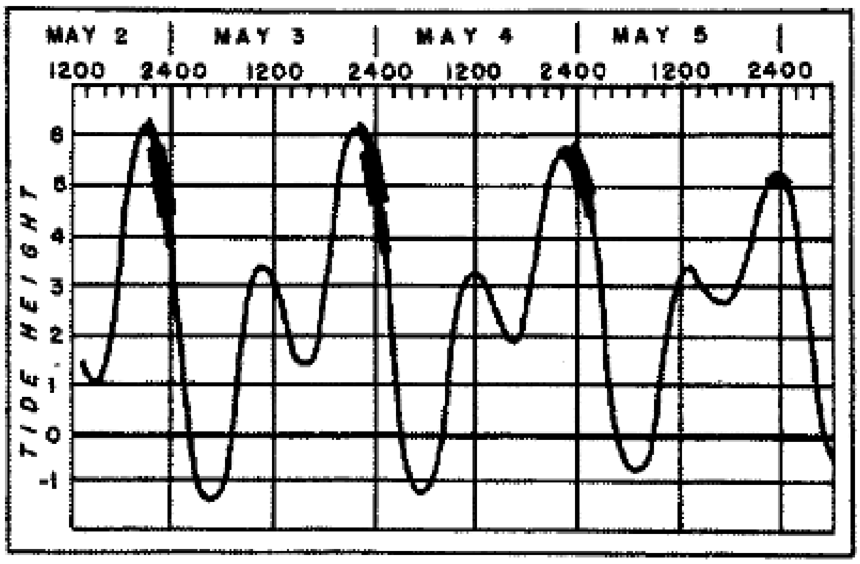


Figure 25. Times of runs in reference to tidal height later in the season (in May, 1946). Like most runs these occur after the peak of the tide. Times of run indicated as of Figure 24.

is some indication that runs again occur earlier during the later part of the season.

Possible Controlling Factors

As has been shown, the timing of grunion runs seems to be associated in some way with the timing of tides. Other phenomena which might show or do show cyclic changes have been considered. When compared with the time of sunset or darkness, the time of runs becomes progressively later during a run series. Times of moonrise and moonset vary greatly from time of runs. The lunitidal interval varies rather widely at times, and since the time of runs corresponds very closely to time of high night tide, the pattern of changes in acceleration of gravity does not match.

Although the times of runs correspond closely to time of high night tide, the seasonal variation indicates that another factor must operate, either together with time of tide or separately. But no factor is known which shows such a time pattern.

Evidence (discussed above) that seems to outrule various other conceivable factors determining the days when grunion run (that is, the time of the run series) applies equally well to the determination of the hours when grunion run on any given night.

Geographical Consistency in Time Pattern

Although minor variations undoubtedly occur, the data given above and in this section indicate that the stimulus to spawn operates at about the same time relative to tide time throughout the area of observation. The results of the investigations at La Jolla, therefore, are believed to be applicable to this entire area and probably to the whole range of the species.

Any controlling factor that is not definitely, closely and rather directly connected with the moon seems to be outruled only by the precise pattern of spawning at any one locality but also by the striking uniformity of pattern throughout the range of the species (south at least to Ensenada, Baja California). A large volume of data indicates such precision and uniformity of pattern. The most concrete and extensive indication of uniformity stems from the coastwise check of April 22 and 23, 1947 (Figures 22–23). On many beaches from Santa Barbara, California, to Ensenada, Baja California, including some in bays, the grunion ran at about the same time in reference to tide and the run of April 22 was consistently the heavier. Variations between distant beaches were not greater than those between beaches close together, for instance those from Del Nar to La Jolla Shores on April 22. For about three hundred miles up and down the coast the grunion started to run at about the same tide time and followed a very similar schedule. The greatest inconsistency involved the run at one beach (San Niguel) in Baja California, where the heavy run started about one-half hour earlier and reached a peak perhaps an hour earlier than it did on most beaches. In general the grunion at the more southerly localities seem to have run slightly earlier than those on the northern beaches, but the difference is hardly significant (the possibility of small latitudinal differences is not excluded, however, and should be further studied over a wide north-south range, providing a marked difference between tide time and sun time, in the hope of obtaining new leads as to the stimulating agency).

The agreements in spawning series and in spawning runs over a long distance far overshadow the disagreements and many of the observed discrepancies may be attributed to errors in base data or in observation. The time of high tide could not be accurately determined for many beaches because of the distance from reference points. The most experienced of observers may misjudge times of runs because of irregularities. On the coastwise check of April 22–23, 1947, the observations varied in reliability, despite efforts to secure uniformity.

Runs observed as far north as Morro Beach, San Luis Obispo County, central California, and as far south as Estero

Beach, near Ensenada, Baja California, coincide in dates and approximately in hours with those occurring in southern California. No known runs at any locality have been greatly out of phase with those at other localities (Tables XVI–XIX). Especially noteworthy is the agreement to the day in the spawning of Leuresthes tenuis in California and of its Gulf of California relative, Hubbsiella sardina. The observed consistency would seem to eliminate from consideration such stimuli as wave height and substances leached from upper beaches.

Evolution of the Spawning Pattern

As Thompson (1919) emphasized, the spawning pattern of the grunion is marvelously adjusted to the tidal cycles that prevail through its geographical range and through its spawning season. In other places and at other times of the year the spawn, even though deposited in the same way, would be destined to destruction. Where and when the day tides are the higher, eggs spawned the previous night would be washed out and, no doubt, would be largely or entirely lost. Where spring tides are so high, as in the Gulf of California, that the beach at the highest tide levels dries out, the eggs laid just after the turn of the highest tides could not survive (Hubsiella sardina, the Gulf form, seems to spawn at midtide levels). Beaches bathed by but one tide in twenty-four hours, or by two tides of equal height, and those much subject to heavy storms, would be much less favorable for grunion spawning. There are probably few places and times, other than the range of the grunion and its spawning season, that would provide the physical conditions to which the spawning pattern of the species is so perfectly adapted.

The main adaptational features of grunion spawning, involving several precise time relations, have been so thoroughly presented by Thompson (1919) as to require only brief review, confirmation and, in some details, a little reservation. Within its range and spawning season, tidal heights and sand transport are ordinarily such as to secure a safe and satisfactory retreat for the developing eggs. The grunion spawn on the spring-tide series, so that the eggs usually remain undisturbed until the next series, when they are ready to hatch. On each run they spawn at night, usually soon after the turn of the high tide, when and where the sand cover is increased to a propitious degree. Through the main part of the run the tides are higher at night than by day. The details of egg laying and other spawning behavior are well adapted and the grunion has, as it must have, great resistance to stranding. The development of the fertilized eggs is adjusted to the peculiar time relations. A special rapid hatching mechanism exists (enzymatic?). The development of the eggs seems to cover exactly the number of days required to keep the fish in proper phase with the tide. The adjustments are many and precise, but only to the special tide and beach conditions that are encountered.

The many and precise adaptations are so well adjusted to the conditions along the coast from central California to middle Baja California as to indicate not only the evolution of the special habits in this region but also the long perpetuation of the local tidal phenomena.

How the habits evolved is conjectural, but we can imagine that the ancestral grunion first spawned in the water of the beach zone, probably with some burying of the eggs. They may have spawned much as the surf smelt Hypomesus pretiousus now does. Individuals or stocks that spawned their eggs at the water's edge might have afforded their offspring a slight advantage. As one adaptation led to another, the adjustment finally attained the present perfection.

As soon as the evolving grunion developed its habit of coming on the beach and burying the eggs in the sand, selection for periodic spawning no doubt became very rigid. Thompson (1919) demonstrated how the grunion tends to utilize for egg deposition the area of sand deposition at the highest levels of the wave-wash zone. He also pointed out that the habit of spawning on descending tides of descending tide series places the eggs where they will not be washed out by tides on succeeding nights. Eggs laid on ascending tides or ascending tide series would almost certainly be flushed out before development could be completed (Figures 16–18). The developmental period necessary for hatching is about seven days, but the eggs that remain in the sand as long as four weeks still hatch successfully when washed free (Thompson, 1919). Thus for only a few hours during a few tides of each series are the conditions such as to give the eggs then deposited a good chance for complete development and hatching. Selection for individuals tending to deposit their eggs at proper times must be very rigid, since eggs deposited at other times would be washed out too soon. Such eggs would probably not produce larvae, not only because of predation but also because of peculiarities in the hatching mechanism previously discussed (page 59). Only those fish adapted to spawn at proper times could reproduce themselves.

The concentration of spawning at the times when chances of egg survival are greatest has no doubt resulted from the rigorous selection. Probably more than ninety-five per cent of the spawning take place during the period when the tide conditions are favorable. The few fish that ineffectually spawn on very unfavorable tides, early and late in the season, do so on the time scale that evolved to the high precision required, to secure maximal survival during the height of the spawning.

Methods of Prediction

The regularity of the spawning pattern and its close correlation with various phenomena associated with the lunar movements make possible prediction of the time when grunion will run. On several bases forecasts of approximate reliability can be made. The method heretofore employed by the State Division of Fish and Game, on the empirical basis preposed by Clark (1938), provides estimates in good agreement with observations for some years but not for other years. When the lunar intervals are very irregular, as they were in 1948, that method fails to forecast many runs that do occur and predicts others that did not materialize. Clark's method calls for three runs each series, starting one night after the date of the highest tide of the spring-tide series, in March, April and May, and starting two nights after the date of the highest tide during the remainder of the season.

The more precise data on grunion runs now available make possible forecasts that prove much more reliable. The runs can be predicted rather accurately by using the data presented in Figures 19–21, the information given previously on the spawning season, and the tide and moon predictions. Midpoints of run series are found by projecting the average interval (17.9 days) from the time of full or new moon phases during and just prior to the spawning season. Time of moon phase to the nearest tenth of day should be used. From the midpoints thus derived the dates of individuals runs may be predicted. Runs normally occur during the last tenth of a day, and runs may be expected on the day, the last tenth of which most closely approximates the midpoint, and on the preceding day and the following day. If the midpoint falls about midway between two evenings, runs should be predicted for these two nights, with smaller runs on the nights before and after.

The time of run on any particular night may be forecast from the relationships of run times to tide times shown in Figures 20–21. Runs start about one hour before time of high night tide in February, March and April, and about at the time of high night tide during the rest of the season. Duration of runs averages about 2.5 hours from March through May and about two hours in June and July. Times of runs in February and August vary widely. Because few fish spawn at these times, these runs are of little general interest.

Since the best runs of the series usually occur closest to the theoretical midpoint, the relative intensity of runs may also be forecast.

Forecasts for runs in 1949 were made in this manner, and reports from fishermen and other observers indicate that runs occurred on all nights predicted between the middle of March and the middle of May. Only one run was reported on a night when a run was not predicted, and on this night fewer than a dozen fish were seen. No reports of observations were received for the periods earlier and later than those mentioned above.

It is probable that small runs did occur on some nights not reported, since series often extend over four nights. Usually one of these runs is very light, however, and it is believed that all heavier runs were forecast.

More precise predictions could be made by including the slight variations in timing between new and full moon phases (Table XI). It is not known, however, what the pattern of these minor variations will be in those years when the lunar pattern changes. Hence, it is felt that attempts at further precision are unwarranted at this time.

OTHER ANIMALS HAVING SIMILAR SPAWNING HABITS

Several other animals show a breeding periodicity similar to that of the grunion, but, with the possible exception of Galaxias attenuatus, none so far studied seems to show as close a relationship to the time of moon phases. The sharp peaks of reproductive activity by Leuresthes, alternating with complete cessation, are also rarely found in other animals.

Although few patterns of lunar periodicity so far studied seem directly comparable to that of the grunion, a rapid review of the better studied examples is warranted. Since Korringa has recently published (1947) a detailed review of these phenomena, examples only of certain patterns will be mentioned here. There are three general types of reproduction with a lunar cycle. In one type breeding covers a protracted period, with two maxima each lunar month. In another, there is one spawning maximum in each lunar month for several months. In the third type only one or two spawning maxima occur each year, on a definite lunar period.

Those animals showing single annual maxima, or a single maximum in each lunar month, have a quite different breeding pattern than does Louresthes. Among these types are the famous Palolo worms (Woodworth, 1906; Clark and Hess, 1942).

Of more interest in the present discussion are those animals which have two breeding maxima each lunar period. The pattern of the breeding cycle in Ostrea edulis, studied in great detail by Korrings (1947) is characterized by him as follows: "Breeding period mid-June till late in August. Maxima in spawning at both full and new moon spring tides. Expulsion of larvae sight days later, at any time of the day; major maximum in swarming between June 26 and July 10, ten days after full or new moon." He concluded that variation in water pressure, due to the spring and neap tides, caused rhythmic and synchronous gonadal development, and that spawning occurred when the sex products were matured.

Fage and Legendre (1923, 1927) clearly demonstrated that Platynercis dumerilii, a polychaete worm, spawns on a semilunar rhythm. Several other polychaetes (Odontosyllis phosphorea (Potts, 1913), Kereis japonica (Izuka, 1908), Amphitrite ornata (Scott, 1909), Spiroruis borealis (Garbarini, 1933) have two breeding maxima per lunar period. Littorina neritoides (Lysaght, 1941), a gastropod, has spawning maxima at both spring tides.

All animals mentioned above breed with a definite lunar periodicity but, unlike the grunion, do not cease their breeding activity completely between the periods of maximum spawning. Because of the method used, namely the sampling of larvas or eggs, it is more difficult to fix exact times of spawning, and hence to compare these times with possible controlling factors. The variations in breeding activity, however, do follow the tidal rhythm closely.

Several fishes other than the grunion spawn in semilunar rhythm. Enchelyopus cimbrus, for example, has been shown by qualitative sampling of the floating eggs to have definite maxima of breeding activity at both spring tides (Battle, 1930). There is, however, no complete cessation of reproductive activity between maxima. Battle concluded that the tides are probably the chief factor in timing.

Several travellers from California as well as local residents have reported seeing “grunion” or “pejereyes” coming out on the beaches of the upper part of the Gulf of California, by day and at night. In Angeles Bay, Baja California, Mr. L. W. Walker now them during the day, and shot several to eat. In 1947, at my request, Mr. Percy Hussong of San Felipe, Baja California, sent a small sample of fish taken on the beach at San Felipe at night. These fish were described as behaving in a manner similar to spawning grunion. Confirming previous inferences, they proved to be Hubbsiella sardina, a close relative and the Gulf representative of Leuresthes tenuis.

Mrs. Lewis T. Derwin, of Oracle, Arizona, has observed fish running on the beach during daylight at La Libertad, Sonora, Mexico. Her short description (letter, 1948) of the fish agrees with Hubbsiella. Mrs. Derwin also sent a short motion picture film showing fish on the beach. The pictures are not clear, but fish can be seen being left on the beach by waves. Recently (1949) Mrs. Derwin wrote of again seeing daytime runs of fish at La Libertad, and included dates of observed runs. Runs occurred on March 17 at 5 p. m. and March 18 at 4 p. m., and again at 2 p. m. April 1, 1949. It is not clear whether or not observations were made on other days. The moon was full on March 14, and new on March 29. The fish ran on the same days as the grunion did in California.

It is hoped that more information on this fish will be available soon.

The most outstanding parallel adaptation in breeding habits is exhibited by Galaxies attenustus, an unrelated small fish found in New Zealand and Australia (and also in Chile if G. maculatus is a synonym). Its spawning habits are summarized by Hefford (1931a, pages 22 and 23) as follows:

> These observations were carried out by Captain Hayes on the Manawatu River between about three and a half and eight miles from its mouth, on a visit made about the middle of March, 1930, and on subsequent visits. The main facts which he brought to light are as follows: The ripe fish migrate to the tidal water in shoals, arriving at the time of spring tides. These migrations were observed to take place in the Manawatu River this year in March (once) April (twice) and May (twice). There was evidence to support the supposition that a spawning had also taken place in February. For spawning the shoal approached the very margin of the river at the time of high water. The minute eggs are deposited among rushes, grass, or other vegetation which affords concealment for the spawning fishes and cover for the eggs which adhere in masses on the ground about the bases of the stems of rushes or grasses. Spawning did not take place till the highest of the spring tides had passed. The ova were thus left "high and dry" when the tide receded, and, since they were deposited as near the water's edge as the fish could get and the tides which followed were of diminishing height, there could be no further contact with the water until the next spring tides occurred. The spawn is thus assured complete protection from any aquatic enemy for practically the whole of the incubation period. When the eggs are once more submerged on the next spring tide reaching them, hatching takes place and the larvae are carried down by the ebb tide. At the time when the eggs were hatching out considerable quantities of the larvae were taken by two-netting in the estuary just above the bar. It has been demonstrated that if the spring tides succeeding

the one on which spawning took place are not so high and therefore do not reach the zone where the spawn is deposited, the embryos remain unharmed while hatching is deferred. The period between spawning and hatching may thus be about fourteen days, or it may be extended to as much as forty-eight days. This provision by which the parent fish deposit their spawn at places which are only covered with water at the highest tides practically ensured immunity from enemies under the original natural conditions which held previous to the colonization of New Zealand. Under present-day conditions, however, adverse factors come into play which were not contemplated, so to speak, in the original natural state of affairs. In the locality investigated it was found that horses, cattle, and even human beings, by trampling over the ground on which the whitebait eggs were deposited in hundreds of thousands, wrought a considerable amount of destruction. A full account of these observations and other points connected with the natural history of the whitebait will appear in a later report.

Unfortunately the later report has never materialized.

Later Hefford (1931b) published the results of Captain Hayes continuous observations on the times of spawning by Galaxias attenuatus in the Manawatu River, New Zealand. Runs were reported as follows:

	Moonphase	Date of Moonphase	Dates of Runs
1930			
	Full	March 15	March 17-18
	Full	April 13	April 13-15
	New	April 29	April 29-30
	Full	May 13	May 13-15
	New	May 28	May 29-30

(Continued)

	Moonphase	Date of Moonphase	Dates of Runs
1931			
	Full	Jan. 5	Jan. 8-10
	Full	Feb. 3	Feb. 6-8
	Full	March 4	March 7-9
	Full	April 3	April 5-7
	New	April 18	April 19-20
	Full	May 2	May 4-6
	New	May 18	May 19-20

Hefford also wrote, "It will be noticed that in relation to the dates of full moon or new moon (or the theoretical dates of the highest tide consequent upon these phases) spawning activities in 1931 were later than in 1930. This is ascribed to the fact that the spring tides of 1931 were higher than average, presumably owing to meteorological conditions."

A more detailed report on the habits of this fish is most desirable, especially in respect to a study of the times of runs. The absence of runs following the new moon phases during January, February and March is most puzzling. In 1934 Hefford reported a spawning of Galaxias attenuatus in a nontidal river on a freshet. This indicates that relative height of water amy be the controlling factor in time of runs.

Although exhibiting no lunar periodicity, the breeding habits of the surf-smelt Hypomesus pretiosus are similar in some other respects to those of the grunion (Loosanoff, 1937; Schaeffer, 1936; Thompson, 1936). The surf-smelt is adapted to spawning in the wave swept zone of the beach, on high tides, as is the grunion. Unlike the grunion, Hypomesus spawns in the rapidly flowing water, and does not come out on the beach. The zone of wave-wash on fine gravel beaches is utilized to provide clean gravel areas for the deposition of adhesive eggs. The descending tide then causes a thin film of sand and smaller pebbles to be deposited over the eggs, partially protecting them from dessication. Thus we have here another adaptation in breeding habits to the action of waves on beaches.

VALUE AND CONSERVATION OF ORUNION

The new data and interpretations on the spawning habits and on the relative stability of the local populations have a bearing on the conservation and management of this very interesting fish, which supports a rather large and very attractive sport fishery (Figure 26) and provides a tourist attraction of no mean proportions. For this reason, in particular, the grunion is a valuable resource, though it enters only incidentally

Figure 26. A scene on Scripps Beach during a good grunion run. On the nights of poor runs there are sometimes more grunion hunters than grunion.

and in small and not accurately recorded amounts into the commercial fishery. Small quantities are locally used as bait, for grunion, either whole or cut, has been found to be very attractive to bottom fish. The grunion is an excellent panfish and very considerable but unmeasured numbers contribute to the local food supply. The educational as well as the recreational and food value of the species is well recognized. The conservation and perpetuation of the grunion supply are therefore of considerable importance.

In the early years of "grunion hunting" large quantities were often gathered for such purposes as chicken feed or were merely piled on the beach to die. Use of nets was started. Depletion on much frequented beaches became evident (Clark, 1926). As a consequence a law was passed in 1927 to establish a closed season, making it unlawful to take grunion in April, May or June. The sport fishing has also been restricted to the hands. These measures have probably had a beneficial effect, though they have very seldom been enforced. Probably the saner attitude that now prevails toward the utilization of natural resources has been even more effective in preventing an excessive drain on the stock, despite the enormous growth of population of southern California and the great increase in the popularity of grunion fishing.

Early in the present investigation it appeared that the closed season of April, May and June eliminated most of the grunion from legal availability. Runs in February are very small and those in March are still too early to be very attractive for beach parties. In July the runs taper off and those in August and occasionally September are too light to be of much significance. Respect for the law and compliance with it were discouraged. In view of these circumstances, the law was revised in 1947 to allow fishing in June, a month of good runs. If other limitations of the catch could be enacted and adequately enforced it might be more reasonable and desirable to eliminate the closed season entirely. Until such time, however, the closed season of April and May would appear to be needed.

Restriction on the catch per person certainly is essential, in view of the great numbers of people who participate in the fishery, and in view of the great vulnerability of the species. During the good runs almost all grunion come on the beaches where they are readily catchable, even by hand. Since the local grunion populations have been indicated by the marking experiment at La Jolla to be highly restricted and independent, much frequented areas are likely to suffer depletion, from which recovery may be very slow.

The current method of restricting the catch by outlawing all gear other than the hands has been at least moderately effective and should be continued and enforced, to withhold the occasional “game hog”. whether this one restriction will remain adequate is very doubtful, in view of the increasing pressure. There are nights on which one can gather many hundreds of grunion by hand. Some still do so, out of sheer enthusiasm or to feed pets or to fertilize gardens. It seems desirable to limit each night’s catch per person to the number likely to be eaten by one family, perhaps fifty fish, and the number in possession to, say, one hundred. Even though complete enforcement would be impossible, such a provision would undoubtedly be effective as an influence on public opinion. Spot checking and enforcement would not appear prohibitive.

Should still further restriction be called for, the use of lights might be outlawed, for lights tend to frighten the fish off the beach and on most nights many can be seen and caught without lights.

Education on reasonable catches and on limited use of lights, as well as on adherence to the state regulations, should be encouraged. The importance of the resource warrants its wise utilization and perpetuation.

SUMMARY AND CONCLUSIONS

Observations were made on all grunion runs occurring at La Jolla in 1946 and 1947, and on most runs occurring there in 1948. A simultaneous check by cooperating agencies on runs was made on two nights in April 1947. In 1948 a grunion marking experiment was conducted at La Jolla, and collections of grunion from San Diego Bay were made and examined. In addition, reports of observations at other localities have been gathered and utilized. During these years grunion eggs were also hatched many times in the laboratory. The principal conclusions arising from those investigations are listed below:

1. Both females and males, once they have begun to spawn, spawn on every successive run series during their breeding season. Evidence of this, gained from marking studies, confirms the findings of Clark (1925), who based her conclusions on studies of the ovaries.
2. Eggs of grunion will not hatch unless agitated.
3. The periodic hatching of grunion results in several distinct length-frequency modes in samples of larvae and young. Age and growth estimates made from those modes indicate that the average growth per day during the first two months of life is about 0.5 mm.

4. It is indicated that greatest mortality in grunion eggs is due to eggs being laid on unfavorable tides, when the eggs will be washed out before development is complete.
5. Natural mortality of adults during spawning is very low, almost nonexistent under usual conditions.
6. The major spawning season extends from early March through June, but some spawning usually occurs from late February to the middle of August, and occasionally may extend into September.
7. The grunion spawn in a definite but complex pattern, with changes from month to month and from year to year in close correlation with variations in lunar cycles. From 1946 to 1943 the intervals between runs as well as between moon phases became increasingly discordant in a pattern of alternately long and short intervals. The long intervals between spawning were concurrent with the short intervals between moon phases.
8. The times of grunion run series are probably not controlled by tides as heretofore believed, since the fluctuations in tides differ markedly from the pattern of grunion runs.
9. The times of run series are most closely and consistently correlated with the time of full or new

moon phase occurring about 2.5 weeks earlier. The interval between first preceding moon phase and spawning varies widely in some years, with an alternation of long and short periods.

10. The most plausible hypothesis agreeing well with observed differences in such intervals, is that the time of spawning is dependent on an approximately constant period of final maturation of the gametes, which is initiated by some factor effective at or very close to the time of the second preceding full or new moon phase.
11. The period of final development of the sex products appears to be independent of temperature.
12. Times of runs on a given night are correlated closely with the time of high tide, over a long coastal distance, but early in season runs occur earlier in relation to tide time than they do later.
13. Times of run series are also consistent throughout the range of the grunion.
14. Natural selection must have been very rigid in the evolution of the new very precisely adapted spawning habits.
15. Forecasts of runs can now be made with high precision, by estimating midpoints of run series at

17.9 days after each full or new moon phase during the spawning season.

16. The lunar periodicity of spawning by the grunion is outstandingly precise. Habits similar in many ways appear to characterize a related atherine, Hubbsiella sardina. The only other known closely parallel lunar periodicity of spawning among fishes characterizes Galaxias attenuatus.
17. The grunion is a valuable resource calling for wise utilization and conservation.
18. The natural pattern of timing is now well enough known to warrant the experimental approach to determine possible control factors.

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APPENDIX

EXPLANATION OF HEADINGS, SYMBOLS AND SPECIAL ABBREVIATIONS USED IN SUMMARIES OF OBSERVATIONS

?	Exact time not noted
c	Fish on beach when observation started or when observation stopped before usual termination time (one-half hour after last fish was seen).
L. C.	Baja (Lower) California
n.o.b.	Not on beach -- means fish observed in wave wash.
Obs.	Observation
Obs. Inc.	Observations incomplete
x	Less than one percent

Numbers in "Remarks" column refer to numbers of fish seen on nights when run was light.

TABLE XIV

SAMPLE FIELD NOTES

Date: 19 May 1947 Sky: Clear

Tide time: 2202; Height: 5.6 Surf low

Time	Remarks
2100	Started obs.
2149	1 n.o.b., H
2151	1, G
2153	2, D
2158	20 since last obs.; D-H
2205	8 to 20 per min. since last obs.; J-G
2210	15 to 35 per min. since last obs.; G-D
2211	30, C
2214	200, spawning, A
2230	Several hundred, A; 2-5 per min. B-C, since last obs.
2236	Continuing
2237	25, B
2238	100, B
2245	200-300, A since last obs., now off beach (Grunion hunter scaring them)
2249	0, A
2255	Several hundred, A
2259	Three to four schools of 30-50 fish each, C
2330	100-300 per 50 yds. of beach since last obs., A-J; run now thinning to scattered schools of 15-20 fish

TABLE XIV (Continued)

SAMPLE FIELD NOTES

Date: 19 May 1947 Sky: Clear

Tide time: 2202; Height: 5.6 Surf low

Time	Remarks
2335	About two per minute since last obs., now 1, G - all fish noted hereafter
2338	3, 15 n.o.b. since last obs., G-C
2339	20 (spawning), A
2341	1 n.o.b., C
2348	5, A
2350	15, A (spawning)
2352	3, A
2353	4, A
2359	1, A
2400	3 n.o.b., A
0002	7, A
0007	1, A
0010	1, C
0011	1, D
0015	1, C
0016	4 n.o.b., C
0045	Stopped obs., no fish A-J

Note - Letters in Remarks column refer to lettered areas in Figure 2.

Spawning noted only when first observed and when observed near end of run.

TABLE XV

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1946

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
March	4	2156	2145	2145*	2220*	2315	15	B. W. Walker	Obs. Inc.
	5	2227	2140	2140*	2245*	2300	58	B. W. Walker	Obs. Inc.
	6	2306	2200	2200*	?	2340	25	E. Kampa, E. LaFond	Obs. Inc.
	7	2346	2200	?	?	2335	2	E. Kampa	Obs. Inc. 5
March	16		2000	....	....	2200	..	B. W. Walker	
	17		2030	....	....	2215		B. W. Walker	
	18		2100	....	....	2230		B. W. Walker	
	19	2204	2108	2108*	2325	2400	45	B. W. Walker	
	20	2227	2100	2105	2320	2330	30	B. W. Walker	
	21	2255	2130	2220	?	2320	25	B. W. Walker	
	22		2200	....	....	2400	..	B. W. Walker	
April	2	2117	2015	2119	2156	2245	2	B. W. Walker	
	3	2151	2030	2039	2358	0028	45	B. W. Walker	
	4	2229	1940	2141	0008	0045	50	B. W. Walker	
	5	2313	2145	2255	2359	0025	3	B. W. Walker	
	6	0005	2315	....	....	0035	..	B. W. Walker	
April	15	2037	1945	....	....	2110	..	B. W. Walker	
	16	2059	1947	....	....	2145	..	B. W. Walker	3 n.o.b.
	17	2119	2000	2029	2240	2310	5	E. Kampa, C. McMillan	
	18	2141	2056	2058*	2338	0010	50	B. W. Walker	
	19	2203	2050	2050*	2358	0040	35	B. W. Walker	
	20	2232	2115	2120*	0004	0047	10	B. W. Walker	
	21	2310	2200	....	....	2400	..	B. W. Walker	

TABLE XV (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1946

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
April	29	1938	1900	....	....	2010	..	B. W. Walker	
	30	2021	1915	....	....	2043	..	B. W. Walker	
May	1	2045	2000	....	....	2118	..	B. W. Walker	
	2	2124	1948	2117	2358	0040	23	B. W. Walker	
	3	2205	2046	2151	0054	0130	45	B. W. Walker	
	4	2252	2150	2221	0110	0122	30	B. W. Walker	
	5	2344	2233	2336	0046	0128	2	B. W. Walker	100+
	6	0055	0006	....	....	0125	..	B. W. Walker	
	7	0228	0200	....	....	0253	..	B. W. Walker	
	8	0401	0351	....	....	0457	..	B. W. Walker	
	9	0520	0452	....	....	0552	..	B. W. Walker	
May	12	1909	1900	....	....	1952	..	B. W. Walker	
	13	1935	1904	....	....	1959	..	B. W. Walker	
	14	1957	1922	....	....	2033	..	B. W. Walker	
	15	2021	1954	....	....	2052	..	B. W. Walker	
	16	2042	2025	2108	2141	2230	x	B. W. Walker	10 + 20
	17	2105	2000	2102	2255	2400	5	B. W. Walker	(n.o.b.
	18	2129	2000	2135	0025	0045	70	B. W. Walker, Earl Hubbs	
	19	2202	2100	2151	0015	0045	25	B. W. Walker	
	20	2240	2200	....	....	2313	..	B. W. Walker	
May	30	2022	1945	....	....	2047	..	B. W. Walker	
	31	2102	2042	....	....	2200	..	B. W. Walker	
June	1	2148	2057	2135	2332	0012	2	B. W. Walker	100 +

TABLE XV (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1946

Date		High Tide	Times of Start Obs.	Times of First Fish	Times of Last Fish	Times of End Obs.	% Run Series	Observer	Remarks
June	2	2236	2145	2241	0113	0137	90	B. W. Walker	
	3	2332	2244	2339	0115	0143	8	B. W. Walker	
	4	0033	0004	....	....	0057	..	B. W. Walker	
June	14	2016	1945	....	....	2045	..	B. W. Walker	
	15	2041	2000	....	....	2145	..	B. W. Walker	
	16	2114	2045	2146	2342	0030	60	B. W. Walker	
	17	2149	2100	2212	0006	0050	30	C. McMillan	
	18	2230	2200	2219	2348	0020	10	B. W. Walker	100+
	19	2323	2245	....	....	2350	..	B. W. Walker	
	20	0031	2330	....	....	0055	..	B. W. Walker	
June	28	2006	1930	....	....	2045	..	B. W. Walker	
	29	2052	2030	....	....	2143	..	B. W. Walker	
	30	2137	2100	....	....	2244	..	B. W. Walker	
July	1	2225	2215	2242	0001	0055	25	B. W. Walker	15
	2	2313	2300	2357	0040	0150	75	B. W. Walker	47
	3	0012	2200	....	....	0025	..	B. W. Walker, C. L. Hubbs	
July	14	2032	2030	....	....	2145	..	B. W. Walker	
	15	2109	2045	2153	2257	2328	10	B. W. Walker, C. L. Hubbs, L. C. Hubbs	17
	16	2142	2120	2155	0001	0040	30	B. W. Walker	54
	17	2225	2210	2217	2342	0030	60	B. W. Walker	87
	18	2316	2215	....	....	0130	..	B. W. Walker, C. L. Hubbs	

TABLE XV (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1946

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
July	30	2210	2145	....	....	2305	..	C. L. Hubbs, L. C. Hubbs	
	31	2255	2228	2305	2350	0025	100	C. L. Hubbs, L. C. Hubbs, B. Boden	3
August	1	2344	2322	....	....	0047	..	C. L. Hubbs	
August	13	2059	2057	....	....	2201	..	C. L. Hubbs, L. C. Hubbs, Earl Hubbs	
	14	2138	2125	2135	2220	2238	20	L. C. Hubbs, Earl Hubbs	2
	15	2219	2224	2240	2310	2335	80	L. C. Hubbs, Earl Hubbs	10
	16	2308	2248	....	....	2400	..	L. C. Hubbs, Earl Hubbs	
August	28	2154	2150	....	....	2300	..	B. W. Walker	
	29	2235	2210	2303	2303	2340	100	B. W. Walker	1
	30	2315	2250	....	....	2345	..	B. W. Walker	
Sept.	12	2132	2120	....	....	2225	..	L. C. Hubbs, Clark Hubbs	
	13	2216	2203	2215	2305	2335	60	L. C. Hubbs, Clark Hubbs	5
	14	2306	2250	2300	2300	0006	40	L. C. Hubbs, Clark Hubbs	3
	15	0009	2350	....	....	0106	..		
Sept.	27	2212	2150	....	....	2325	..	C. L. Hubbs, L. C. Hubbs	
	28	2252	2250	....	....	1008	..	C. L. Hubbs, L. C. Hubbs	
	29	2337	2320	....	....	0025	..	C. L. Hubbs, L. C. Hubbs	

TABLE XVI

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1947

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
Feb.	21	2151	2100	....	• ••	2304	••	B. W. Walker, Earl Hubbs	
	22	2215	2047	2122	2316	2345	50	B. W. Walker, Earl Hubbs	42
	23	2241	2100	2128	2359	0030	50	B. W. Walker, Earl Hubbs	47
	24	2314	2200	....	....	2400	••	B. W. Walker	
March	6	2109	2030	....	....	2145	••	B. W. Walker	
	7	2140	2030	....	....	2210	••	B. W. Walker	
	8	2206	2100	2109*	2250	2320	5	B. W. Walker	
	9	2243	2051	2110	0038	0110	65	B. W. Walker, C. L. Hubbs	
	10	2310	2140	2144*	0105	0141	30	B. W. Walker	
	11	2345	2140	2153	2359	0030	x	B. W. Walker	26
	12	0029	2200	....	....	0040	••	B. W. Walker	
March	22	2105	1945	2035	2111	2147	x	B. W. Walker	4
	23	2130	1930	2025	0003	0030	50	B. W. Walker	
	24	2159	2030	2059	2328	0030	40	B. W. Walker	
	25	2230	2040	2119	0035	0100	10	B. W. Walker	
	26		2117	....	....	0017	••	B. W. Walker	
April	5	2056	2010	....	....	2110	••	B. W. Walker	
	6	2121	2010	2105	2230	2310	x	B. W. Walker	12
	7	2146	2010	2047	2337	0012	50	B. W. Walker	
	8	2214	2100	2119	0007	0035	30	B. W. Walker	
	9	2244	2115	2128	2350	0030	20	B. W. Walker	
	10	2320	2150	....	....	0010	••	B. W. Walker	

TABLE XVI (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1947

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
April	20	2023	1945	....	....	2115	..	B. W. Walker	1 n.o.b.
	21	2052	1950	2111	2311	2345	30	B. W. Walker	
	22	2124	2010	2109	0012	0030	50	B. W. Walker	
	23	2201	2050	2129	0046	0120	20	B. W. Walker	
	24	2247	2140	....	....	0010	..	B. W. Walker	4 n.o.b.
May	5	2042	2000	....	....	2200	..	B. W. Walker	
	6	2106	2010	2055	2301	2345	25	B. W. Walker, F. Fleming	
	7	2133	2055	2100*	0021	0048	45	B. W. Walker, F. Fleming	
	8	2200	2115	2140	0023	0045	20	B. W. Walker, F. Fleming	
	9	2237	2208	2224	0003	0033	x	B. W. Walker	68
	10	2328	2200	....	....	2330	..	B. W. Walker	
May	20	2025	1950	....	....	2130	..	B. W. Walker, F. Fleming	
	21	2106	2030	2056	2333	2353	30	B. W. Walker, F. Fleming	
	22	2147	2115	2142	0029	0055	60	B. W. Walker, C. L. Hubbs	
	23	2239	2215	2246	0056	0120	10	B. W. Walker, F. Fleming	
	24	2339	2300	....	....	0054	..	B. W. Walker	4 n.o.b.
June	4	2041	2110	....	....	2242	..	B. W. Walker	40 n.o.b.
	5	2109	2045	2129	2322	2347	25	B. W. Walker	
	6	2140	2147	2148*	2359	0025	50	B. W. Walker	
	7	2214	2200	2204*	0004	0045	25	B. W. Walker	
	8	2255	2145	2220	2350	0035	x	B. W. Walker	28
	9	2353	2230	....	....	2400	..	B. W. Walker	

TABLE XVI (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1947

Date		High Tide	Times of Start Obs.	Times of First Fish	Times of Last Fish	Times of End Obs.	% Run Series	Observer	Remarks
June	19	2056	2035	....	....	2328	..	B. W. Walker	5 n.o.b.
	20	2143	2135	2157	0043	0113	30	B. W. Walker	
	21	2233	2205	2225	0102	0130	55	B. W. Walker	
	22	2331	2245	2259	2356	0115	15	B. W. Walker	
	23	0038	2300	....	....	0035	..	B. W. Walker	
July	4	2059	2035	....	....	2245	..	B. W. Walker	
	5	2148	2120	2147	2332	2410	60	B. W. Walker	
	6	2202	2155	2211	2319	2350	40	B. W. Walker	
	7	2240	2215	2317	2317	2400	x	B. W. Walker	1
July	19	2138	2020	....	....	2150	..	B. W. Walker	10 n.o.b.
	20	2228	2215	2215*	0011	0040	80	B. W. Walker	38
	21	2318	2255	2256*	0015	0100	20	B. W. Walker	7
	22	0016	2250	....	....	0045	..	B. W. Walker	
August	2	2049	2000	....	....	2210	..	B. W. Walker	
	3	2118	2048	2146	2154	2310	25	B. W. Walker	7
	4	2153	2115	2238	2336	2350	70	B. W. Walker	18
	5	2228	2220	2307	2307	2348	5	B. W. Walker	1
August	17	2128	2100	....	....	2230	..	B. W. Walker	
	18	2214	2145	....	....	2350	..	B. W. Walker	
	19	2300	2240	....	....	2400	..	B. W. Walker	
	20	2352	2315	....	....	0045	..	B. W. Walker	

TABLE XVI (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1947

Date			Times of						
		High Tide	Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
Sept.	1	2108	2030	....	....	2200	..	B. W. Walker	
	2	2141	2105	....	....	2310	..	B. W. Walker	
	3	2220	2200	....	....	2400	..	B. W. Walker	

TABLE XVII

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1948

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
Feb.	11	2225	2130	....	....	2300	..	B. W. Walker	
	12	2250	2200	....	....	2335	..	B. W. Walker	
Feb.	26	2234	2200	....	....	2308	..	B. W. Walker	
	27	2310	2250	2303*	2342*	2345	50	B. W. Walker	
	28	2348	2305	2318*	0005*	0010	50	B. W. Walker	
	29	0026	2356	....	....	0102	..	B. W. Walker	
March	11	2132	2105	2110*	2201*	2203	55	B. W. Walker	
	12	2156	2130	2135*	2201*	2215	30	B. W. Walker	
	13	2219	2125	2130*	2240	2256	15	B. W. Walker	
	14	2246	2200	....	....	2325	..	B. W. Walker	
March	26	2150	2100	....	....	2300	..	F. Sisler	
	27	2220	2205	2206*	2350*	2400	60	B. W. Walker	
	28	2255	2100	2130	2334*	2334	20	B. W. Walker	
	29	2333	2310	2310*	0015*	0015	20	B. W. Walker	
April	7	2007	1930	....	....	2110	..	B. W. Walker	
	8	2029	1955	....	....	2115	..	B. W. Walker	
	9	2047	2015	2022*	2151	2230	10	B. W. Walker	
	10	2111	2010	2030	2325*	2325	50	B. W. Walker	
	11	2137	2010	2023	2315*	2315	20	B. W. Walker	
	12	2210	2215	2215*	2325*	2326	20	B. W. Walker	
	13	2252	2215	....	....	2345	..	B. W. Walker	

TABLE XVII (Continued)

SUMMARY OF OBSERVATIONS AT LA JOLLA - 1948

Date		High Tide	Times of Start Obs.	First Fish	Last Fish	End Obs.	% Run Series	Observer	Remarks
April	23	2040	2030	....	....	2145	..	B. W. Walker	
	24	2111	2100	....	....	2230	..	B. W. Walker	
	25	2147	2100	2149	0018	0030	30	B. W. Walker	
	26	2211	2130	2225	0004	0025	50	C. L. Hubbs	
	27	2244	2220	2220*	0040*	0040	20	B. W. Walker	
	28	2330	2330	....	....	0030	..	B. W. Walker	
May	8	2011	1930	....	....	2115	..	B. W. Walker	
	9	2040	2000	2315	2315	2330	20	B. Walker, B. Boren	
	10	2115	2030	2056	0007	0020	45	B. W. Walker	
	11	2153	2130	2130*	0100	0115	30	B. W. Walker	
	12	2238	2230	2242	0020	0035	5	B. W. Walker	
May	24	2111	2100	2140	2303	2330	x	C. L. Hubbs	150
	25	2147	2100	2139	0020	0035	40	J. L. McHugh	
June	8	2105	2220	2220*	2313*	2315	10	B. W. Walker	
	9	2149	2205	2205*	2350	0010	60	B. W. Walker	
	10	2240	2320	2320*	0050	0110	30	B. W. Walker	
June	24	2206	2200	?	?	0040		A. A. Allanson	
July	7	2102	2100	....	....	2145	..	B. W. Walker	
	8	2149	2200	2207*	2333*	2333		B. W. Walker	
	9	2236	2240	2240*	0008*	0008		B. W. Walker	
	10	2332	2325	2339	0003	0015		B. W. Walker	6

TABLE XVIII

REPORTS ON OBSERVATIONS ON OTHER BEACHES - 1947

Date		Location	Start	Stop	Reported by	Remarks
March	25	Mission Bay E. of Bridge	?	?	G. Wernham	"Good run"
April	7	Marine Base San Diego Bay	?	?	Prodonovitch	"Saw thousands"
	8	Marine Base San Diego Bay	?	?	Prodonovitch	"Saw thousands"
	9	Marine Base San Diego Bay	?	?	Prodonovitch	"Saw thousands"
May	23	Bayshore Drive	2206	0115	C. L. Hubbs	Light run
May	20	Cabrillo Beach	"sev.	hrs."	J. E. Fitch	2 fish on beach, 1 n.o.b.
	21	Cabrillo Beach	2130	2400	J. E. Fitch	Very good run from around 10:00 p.m. till I left beach Still coming in and spawning when I left.
	22	Cabrillo Beach	?	?	Game Warden	"Very great numbers" 10:15 p.m. till nearly 2:00 a.m.
	22	Redondo Beach	?	?	Game Warden	"Excellent run"
	22	Newport Beach	?	?	Game Warden	"Greater numbers than any previous runs witnessed"
	23	Cabrillo Beach	?	?	J. E. Fitch	First fish 10:45 - "Countless thousands" up to end of observation

TABLE XVIII (Continued)

REPORTS ON OBSERVATIONS ON OTHER BEACHES - 1947

Date		Location	Start	Stop	Reported by	Remarks
June	4	Ensenada	?	?	Fishermen	"Small run"
	5	Ensenada	?	?	Fishermen	Very heavy run
	6	Ensenada	2200	2330	J. E. Fitch	Very heavy run
	7	Ensenada	2245	0030	J. E. Fitch	Saw several hundred fish - very light run
	21	Cabrillo Beach	?	?	F. A. Everest	"Large run"
July	5	Estero-Ensenada	?	?	J. E. Fitch	Good run
	18	Strand	?	?	E. E. Keeton	No fish - spent 1½ hours on beach
	19	Strand	?	?	E. E. Keeton	No fish
	20	Strand	?	?	E. E. Keeton	Good run (heaviest)
	21	Strand			E. E. Keeton	Good run
	20	5 mi. N. of Santa Monica	2230	0030	F. A. Everest	Saw 1 fish
August	4	Strand	?	?	E. E. Keeton	"Good run"
	5	Strand	?	?	E. E. Keeton	"Few n.o.b."

TABLE XIX

REPORTS ON OBSERVATIONS ON OTHER BEACHES - 1948

Date	Location	Start	Stop	Reported by	Remarks
Feb. 26	Abreojos Pt., L. C.,	?	?	L. W. Walker	No fish
27	Abreojos Pt., L. C.,	?	?	L. W. Walker	No fish
27	Imperial Beach	?	?	E. C. LaFond	No fish
27	Ocean Beach	?	?	E. C. LaFond	Caught 20 fish
27	Mission Beach	?	?	E. C. LaFond	Caught 36 fish
28	Imperial Beach	?	?	E. C. LaFond	20 fish caught
28	Ocean Beach	?	?	E. C. LaFond	3 fish caught
28	Mission Beach	?	?	E. C. LaFond	Small run
March 11	Mission Beach	?	?	E. C. LaFond	No fish
11	Imperial Beach	?	?	E. C. LaFond	No fish
11	Malibu Beach	2100	2300	F. A. Everest	Saw 2 fish
12	Pacific Beach	?	?	E. C. LaFond	No fish
12	Imperial Beach	?	?	E. C. LaFond	Fair run, fish ran before high tide
12	Malibu Beach	2145	2315	F. A. Everest	Everest saw none, but saw a party that had caught 12
13	Imperial Beach	?	?	E. C. LaFond	Caught 2 fish
13	Malibu Beach	2215	2345	F. A. Everest	No fish
14	Malibu Beach	2245	0015	F. A. Everest	No fish

TABLE XIX (Continued)

REPORTS ON OBSERVATIONS ON OTHER BEACHES - 1948

Date	Location	Start	Stop	Reported by	Remarks
March 26	Imperial Beach	?	?	E. C. LaFond	No fish
26	Mission Beach	?	?	E. C. LaFond	No fish
26	Malibu Beach	2200	2330	F. A. Everest	Saw few grunion at 11:30
27	Imperial Beach	?	?	E. C. LaFond	Fair run - caught 61
27	Mission Beach	?	?	E. C. LaFond	Light run - caught 5
27	Pacific Beach	?	?	E. C. LaFond	Light run - caught 6
27	Malibu Beach	2230	0030	F. A. Everest	Many grunion observed from 2330 on. Some seen prior to this by other observers
28	Imperial Beach	?	?	E. C. LaFond	Caught 235 - heavy run
28	Malibu Beach	2200	0100	F. A. Everest	Exceedingly heavy run throughout observation. Near end, "two of us picked up 508 fish in about half an hour
29	Imperial Beach	?	?	E. C. LaFond	Caught 160 (Good run)
29	Malibu Beach	2300	0030	F. A. Everest	Good runs from start of obs.
30	Imperial Beach	?	?	E. C. LaFond	"Quite a lot but no count" This observation questionable
April 11	Imperial Beach	?	?	E. C. LaFond	One party caught 80, another 115
12	Imperial Beach	?	?	E. C. LaFond	One party caught 7, another 4
26	Imperial Beach	?	?	E. C. LaFond	Three parties caught 693 - "very good" run

TABLE XIX (Continued)

REPORTS ON OBSERVATIONS ON OTHER BEACHES - 1948

Date		Location	Start	Stop	Reported by	Remarks
May	10	Malibu Beach	2100	2230	F. A. Everest	Moderate heavy run - didn't dig in much
	11	Imperial Beach	?	?	E. C. LaFond	"Best run seen this season"
	25	Malibu Beach	2200	0040	F. A. Everest	Very heavy run - started about 2300 and continued when we left
	26	Malibu Beach	2230	0045	F. A. Everest	Very heavy run throughout period
	27	Malibu Beach	2330	0030	F. A. Everest H. B. Holmes	Moderate heavy run - not as heavy as 25th and 26th
June	8	Malibu Beach	2115	2400	F. A. Everest	Very few grunion - Just few isolated fish
	9	Malibu Beach	2215	0045	F. A. Everest	Light runs - (Beach badly undercut)
	10	Malibu Beach	2300	0200	F. A. Everest	Good spasmodic runs from 2400-0200, Beach undercut
July	22	Morro Bay	2130	2335	C. L. Hubbs	Picked up 182 - Fish confined to one small area
	22	Malibu Beach	2115	2315	F. A. Everest	Single grunion seen at 2230
	23	Malibu Beach	2200	0020	F. A. Everest	First fish 2345, heaviest run at 2400 - fair run

TABLE XX

SUMMARY OF COASTWISE OBSERVATIONS - NIGHT OF APRIL 22, 1947

Location	Time of Start Obs.	Time of Stop Obs.	Time of High Tide	Time of Start Run	Time of Finish Run	Observers	Remarks
Bodega Bay Sonoma County	2342	0115	2342	....	....	W. I. Follett	No run
Del Monte Beach	2205	2405	2258	....	....	R. Prasad, W. Vishniac, D. Wootton, F. H. Tarp	No run
Carmel Beach	2200	2400	2258	....	....	N. Riser, H. Orcutt	No run
Palm Beach to Port Rogers, Monterey Bay	2205	0010	2257	....	....	J. B. Phillips	No run, 1¼ mi.
Morro Beach, San Luis Obispo Co.	2140	2315	2226	....	....	L. E. Lahr, H. V. Shebley	No run, 1½ mi.
Oceano Pier, South Pismo Beach	2145	2315	2226	....	....	W. L. Scofield, L. A. Golden	No run, ½ mi.
Surf (Station), Santa Barbara Co.	1945	0015		....	....	W. L. Neely	No run, 1 mi.

TABLE XX (Continued)

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 22, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Refugio Beach, Santa Barbara Co.	2030	2330	2200	....	....	E. R. Noble, L. Davenport	No run
Hendry Beach, Santa Barbara Co.	1945	2315		....	....	R. E. Bailey	No run
Ledbetter Beach, Santa Barbara Co.	2007	2326	2156	2211	?	B. D. Blanchard	Saw 200 at 2326 so not end of run -- Many fish
Ledbetter Beach, Santa Barbara Co.	2007	0015	2156	2145 2252	2335	M. M. Erickson, H. Decker	Few fish seen
Carpenteria State Beach	1930	0015	2156	2140	2335	E. M. Lynch	½ mi. Rain 1930-2030
Coral Beach, Point Dume	2050	2305	2140	....	....	R. B. Cowles	No run, 5 n.o.b. at 2140-2150
5 mi. North of Santa Monica	2030	2330	2136	....	....	S. Houston	No run
½ mi. North of Santa Monica Canyon	2134	2330	2136	2134?	2330?	Hice, Browne, Farnham	1st obs., fish seen; last obs., many seen

TABLE XX (Continued)

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 22, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
100 yards North of Santa Monica Canyon	2000	2325	2136	....	....	J. Hall	No run, 2 n.o.b.?
Santa Monica Canyon to 1 mi. South	1930	2400	2136	2145	2350?	G. P. Weisel	
1 mi. South of Venice, Los Angeles Co.	2000	2330	2136	2145	2330?	T. H. Bullock	Not end of run
Manhattan Beach	2010	0015	2141	2111	2349	P. P. Powell	Good
Hermosa Beach	2000	0010	2141	2207?	0010?	P. M. Roedel	Fish still on beach at end of obs. Fair run
Cabrillo Beach	1950	0100	2141	2123	0051	F. N. Clark	<u>Very</u> heavy run. Heaviest ever seen
Long Beach	2020	0025	2141	2143	0020?	D. H. Fry, Jr., W. E. Ripley	<u>Very</u> heavy run
Long Beach	2010	0020	2141	2131	0020?	C. R. Clothier	<u>Very</u> heavy run

TABLE XX (Continued)

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 22, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Belmont Shores	2002	0008	2141	2145	0008?	R. D. Collyer	Fish very numerous at end of obs.
Belmont Pier and South	2133	0010	2141	2133?	0010?	H. C. Godsil	Very heavy run
Huntington Beach	2000	0005	2141	2130	0005?	F. E. Durham, J. Mohr	3 mi. Very heavy run. Many fish at last obs.
Santa Ana River Mouth	2020	2300	2141	2135	2300?	J. Garth, R. Menzies	Fair run. Still in progress at last obs.
Newport Pier to Santa Ana River	2003	0035	2126	2205	2400	J. E. Fitch, Mrs. Fitch	Very heavy run near Pier
Newport Pier to Balboa Jetty	2020	2355	2126	2304	2332	A. Daugherty, J. Janssen	3 fish seen
Corona del Mar, Inside Bay (Site 1)	2020	2415	2136	2141	2342	G. MacGinitie, Mr. Johnson	150 yards Very heavy run
Corona del Mar, Inside Bay (Site 2)	2020	2415	2136	2137	2359	N. MacGinitie, B. Ewing	50 yards Very heavy run

TABLE XX (Continued)

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 22, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Corona del Mar, Outside Bay	2030	2410	2136	2126	2345	G. Townsend	½ mi. beach Very heavy run
Doheny State Park	2005	2400	2144	2125	2318	C. McMillen, J. Stackelberg	Light run
Carlsbad	1945	2400	2144	2126	2318	H. R. Moses, W. Klock	
Del Mar	2035	0031	2124?	2109	0010	F. H. Stoye, A. Krom	Heavy surge Very light run
Scripps Beach	2010	0015	2124	2109	0012?	B. W. Walker	Good run
La Jolla Shores	2010	0015	2124	2109	0012?	S. C. Crane, A. S. Lockley	Good to heavy run
North end of Mission Beach	2100	2400	2134?	2145	2326?	R. Steach, Mrs. Steach	Fair run
South end of Mission Beach	2025	2330	2134?	2158	2330?	H. Kritzler, M. W. Williams	Good run
Yacht Basin, San Diego Bay	2035	2310	2144	....	....	S. Houston, B. McConaghy	No run

TABLE XX (Continued)

SUMMARY OF COASTWISE OBSERVATIONS - NIGHT OF APRIL 22, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Harbor Drive, San Diego Bay	2125?	0024	2150?	2146	0012	R. Baum	Very heavy run
Coronado Strand	2120	2355	2134?	2132	2336	M. A. Taylor, J. Homesley	Heavy run
Silver Strand	1945	2330	2134?	2105	2320?	D. Bailey, F. Ratty	Very heavy run
Imperial Beach	2050?	2315	2134?	2130	2315?	O. Ball, R. Crawford	Heavy run
Rosarito Beach, L.C.	2030	2350	2134	2250*	2300*	F. Haymaker, F. W. Fleming	3/4 mi. *Only 2 fish on beach. 7 n.o.b. seen
San Miguel Beach, L.C.	2050	2325?	2134	2055	2315	A. Allanson, D. Sayhor	Heavy run
Estero Beach, near Ensenada, L. C.	2027	0005	2134	2110	2335	C. L. Hubbs, L. C. Hubbs	Very heavy run
San Quintin Bay, L.C.	....	....	2124	....	....	C. I. Johnson and party	No run

TABLE XXI

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 23, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Bolinas Bay, Marin County	0012	0215	0012	....	....	W. L. Follett	No run
Seacliff Beach, Soquel Cove, Monterey Bay	2235	0015	2332	....	....	J. B. Phillips K. W. Cox	No run
Delmonte Beach	2220	0020	2332	....	....	N. Riser H. Orcutt	No run
Carmel Beach	2332	0030	2332	....	....	R. Prasad D. Wootton F. H. Tarp W. Vishniae	No run
Morro Beach	2237	0005	2305?	....	....	L. E. Lahr H. V. Shebley	No run
Oceano Pier, South Pismo Beach	2150	0010	2305	....	....	W. L. Scofield L. A. Golden	No run
Ledbetter Beach, Santa Barbara	2105	0030	2235	2235	0030	M. M. Erickson and party	Few fish
Carpenteria State Beach	2130	0100	2235	2304	0010	E. M. Lynch	Good run, ½ mi.

TABLE XXI (Continued)

SUMMARY OF COASTWISE OBSERVATIONS - NIGHT OF APRIL 23, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Coral Beach, near Point Dume	2030	0030	2210?	2330	0010	R. B. Cowles	Very light run
North of Topanga Canyon, Santa Monica	2200	2350	2210	2248	2330	K. S. Norris R. Lindberg	Light run
½ mi. North of Santa Monica Canyon	2249	2400	2210	2249?	2400?	R. Farnham	Fish still spawning at last obs. Fair run
¼ mi. N. W. of Santa Monica Canyon	2130	0015	2210	2255	2320	Eileen Cox	Short heavy run
100 yds. N. of Santa Monica Canyon	2230	0000	2210	....	....	Jim Hall	3 n.o.b. No run
S. E. of Ballona Cr., Los Angeles Co.	2030	0100	2210	2210	0040	J. Brauner	Heavy run
Redondo Beach	2100	2400	2222?	....	....	Sam Houston	500 yards No run
Manhattan Beach	2100	0100	2225	2205	2320	P. Powell	Fair run. 1/10 previous night
Hermosa Beach	2100	2350	2225	2210	2326	P. M. Roedel	Good run

TABLE XXI (Continued)

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 23, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Cabrillo Beach	2125	0030	2215	2327	0010	F. N. Clark R. Sulentor	Fair run
Long Beach	2120	0010	2220	2224	2316	C. R. Clothier	Light run
Huntington Beach	2103	0120	2215	2140	0055	John Mohr E. LeVeque J. LeVeque	Fair run
Newport Pier and 1 mi. N. W.	2115	2345	2205	2226	2345?	A. Daugherty J. Janssen	
Newport Pier to Balboa Pier	2115	0100	2205	2255	0005	J. E. Fitch Mrs. Fitch	Light run
Balboa	2115	2345	2215	....	....	F. E. Durham	No run
Corona del Mar, Inside Bay (Site 1)	2120	0045	2215	2215	0005	G. MacGinitie	
Corona del Mar, Inside Bay (Site 2)	2120	0020	2215	2207	0002	N. MacGinitie	
Corona del Mar, Outside Bay	2000	0030	2215	2335	0030	V. Ellsworth M. Ellsworth	

TABLE XXI (Continued)

SUMMARY OF COASTWISE OBSERVATIONS -
NIGHT OF APRIL 23, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
Doheny State Park	2112	0055	2210	2144	0023?	J. Stackelberg	Good run
Carlsbad	2100	2335	2210	2136	2316?	H. R. Moses Elfin Moses	
Del Mar Pier	2056	0020	2201	2200	2353	R. S. Arthur	Light run
Scripps Beach	2050	0120	2201	2129	0046	B. W. Walker	
La Jolla Shores	2045	0024	2201	2146	2350	F. W. Fleming	Light run
North end of Mission Beach	2107	0055	2211	2150	0025	Anna Kutz R. Kraus	Light run
South end of Mission Beach	2121	2347	2211	2149	2346?	H. Kritzler M. Williams	Light run
600 yds. S. of Hotel Coronado	2200?	2342	2211	2200?	2342?	H. T. Galpin	Good run
Silver Strand	2123?	2400	2211	2128	2325	E. Marshall R. Page	Fair run
Imperial Beach	2055	0015	2211	2135	2354	M. Taylor J. Doria	Light run

TABLE XXI (Continued)

SUMMARY OF COASTWISE OBSERVATIONS - NIGHT OF APRIL 23, 1947

Location	Start Obs.	Stop Obs.	Time of High Tide	Start Run	Finish Run	Observers	Remarks
San Miguel Beach, Lower California	2045	0030	2211	2132	2356	A. Allanson D. Allanson	Light run
Ensenada, Lower California	2240	2337	2211	2240?	2311	J. Frautschy S. Hinton H. Gould	Good run
Estero Beach, near Ensenada, Lower California	2125	0106	2211	2143	0006	C. L. Hubbs L. C. Hubbs	Very heavy run

TABLE XXII

DATES OF GRUNION RUNS, WITH MIDPOINT DATA (CALCULATED TO TENTHS OF DAY) 1946 - 1948

Runs in 1946			Runs in 1947			Runs in 1948		
March	4- 7	(6.0)	*Feb.	22-23	(23.4)	*Feb.	27-28	(28.5)
March	19-21	(20.8)	March	8-11	(10.2)	March	11-13	(12.6)
April	2- 5	(4.5)	March	22-25	(24.6)	March	27-29	(28.6)
April	17-20	(19.5)	April	6- 9	(8.7)	April	9-12	(11.5)
May	2- 5	(4.1)	April	21-23	(22.8)	April	25-27	(26.9)
May	16-19	(19.2)	May	6- 9	(7.9)	May	9-12	(11.2)
June	1- 3	(3.1)	May	21-23	(22.8)	May	24-27	(26.8)
June	16-18	(17.5)	June	5- 8	(7.0)	June	8-10	(10.2)
*July	1- 2	(2.8)	June	20-22	(21.8)			
*July	15-17	(17.5)	*July	5- 7	(6.4)			
*July	31	(32.0)	*July	20-21	(21.2)			
*Aug.	14-15	(15.9)	*Aug.	3- 5	(4.8)			
*Aug.	29	(30.0)						
*Sept.	13-14	(14.4)						

* Very light runs, omitted in comparisons of timing.