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CHANGES IN THE FISH FAUNA OF WESTERN NORTH AMERICA CORRELATED WITH CHANGES IN OCEAN TEMPERATURE'

By

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Many lines of evidence support the conclusion that temperature is a factor of prime importance in the distribution of marine fishes along the Pacific Coast of North America. The correlation between water temperature and the type of fish found is so definite that I feel justified in drawing inferences, from the known data of fish distribution, regarding ocean temperatures of the past and regarding the temperatures of regions for which the physical data are inadequate. Several patterns in the present distribution of fishes along the coast can be plausibly explained only on the theory that ocean temperatures fluctuated considerably, up and down, during recent geological time. Largely on the basis of warm-water forms reported from 1853 to 1860, I further infer that the ocean temperatures at that time, nearly one hundred years ago, were definitely higher in the southern half of California than they have been during any subsequent series of years.

Some call such two-way use of data unwarranted—a "vicious circle"—but I regard the method, when used with due caution and insight, as both proper and promising. Consistency in results and in explanations is a justification of the procedure. A similar approach was used in a recent correlation of hydrographic history and fish distribution in the Great Basin (Hubbs and Miller, 1948).

Even though I almost completely restrict the treatment zoologically to fishes, geographically to western North America, and temporally to the present and near-present, I must sail rapidly through a sea of extensive, varied and detailed *data*. In particular, the correlation between present temperatures and the present distribution must, for want of space, be treated sketchily. Chief emphasis in this paper is given to fish faunal changes associated with short-term (annual) and long-term changes in surface temperature within historic time.

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REVIEW OF ZOOGEOGRAPHICAL EVIDENCE

The general transition of the fish fauna from Arctic to Tropic waters along the Pacific Coast illustrates well the correlation between temperature and distribution. The relative sharpness of the change in temperature at Point Conception is reflected in the rather rapid transition there between the fish fauna of southern California, with a large representation of subtropical types, and that of central California, with many subarctic forms.

The correlation between temperature and distribution is especially emphasized where the latitudinal transition is locally reversed. Thus, the general southward increase in temperatures and the increasingly tropical aspect of the fauna is reversed in northwestern Baja California, from near the California border southward through at least 2.5° of latitude. Here the offshore temperatures during the critical spring and summer months may run 1° C. cooler than near San Diego (according to unpublished data assembled under the direction of George F. McEwen). More significantly, the inshore temperatures of this region are in general unusually low, very strikingly so in foci of upwelling (McEwen, 1916). The validity of the areas of upwelling charted by McEwen (his plate 9) is being confirmed by recent data. Thus on August 8, 1948, the temperature of the surf was only 15.1° C. at or near the focus of the area of upwelling just south of the border, only 13.6° at Santo Tomás Anchorage south of Ensenada, and generally low in the intervening areas, except in Todos Santos Bay, where partial enclosure and shallow water produce a warm area, with temperatures on August 8 as high as 22.6° (at a point only 13 nautical miles north of Santo Tomás Anchorage). Furthermore, due to the prevalence of upwelling and the general lack of eddies, the temperatures off most of the coast of northwestern Baja California (Todos Santos and Sebastian Viscaíno Bays excepted) can not be expected to attain the occasional heights experienced in southern California (as Harald U. Sverdrup pointed out in discussing this problem). In striking agreement with the oceanographic conditions, we are finding south of the international border, in the areas of upwelling, a very considerable representation of central California fish types. Some of the species, for instance the reef seaperch, *Amphigonopterus aurora*, appear to have a discontinuous range, broken in southern California and probably also in such warm areas of Baja California as Todos Santos Bay. Other fishes and some invertebrates (as the red abalone, *Haliotis rufescens*, and the large sea urchin *Strongylocentrotus franciscanus*) that occur near San Diego only in the cooler infratidal waters reappear between tides in the areas of upwelling in Baja California. Other species

occur in shallower water in those areas. A strikingly parallel picture of algal distribution in northwestern Baja California has been discovered by E. Yale Dawson (personal communication). Our findings have been given brief advance notice, as by Hubbs (1946: 84), Barnhart and Hubbs (1946: 371) and Stephenson and Stephenson (1948: 7).

The prevalence along the Oregon and Washington coasts of upwelling, which lowers the inshore surface temperatures, seems to be associated with the absence there of certain fishes, such as the Californian reef klipfishes *Gibbonsia montereyensis* and *G. metzi*, that reappear in British Columbia. Other southern fishes that occur in British Columbia are listed by Clemens and Wilby (1946: 4). The extremely cold water just south of Monterey Bay is correlated with the occurrence there of such northern reef fishes as *Scylalima cerdale*, *Phytichthys chirus*, *Artedius harringtoni* and *Clinocottus embryum*.

Warmer bays have a far more southern fauna than the adjacent open coast. Thus we note the occurrence of a southern pipefish, *Syngnathus arcta*, and the abundance of the least seaperch, *Micrometrus minimus*, and of a southern flatfish, *Hypsopsetta guttulata*, in Elkhorn Slough and Tomales Bay, central California. Morro Bay has a particularly southern fauna, in harmony with the warmth of its waters, caused by the extensive shoals of blackish mud. Here occur the California killifish, *Fundulus parvipinnis*, otherwise seemingly absent north of Santa Barbara, the southern California subspecies of the staghorn sculpin, *Leptocottus armatus*, and the northernmost population of the pipefish *Syngnathus griseo-lineata leptorhyncha*, separated from the main range of this subspecies by another subspecies, *S. g. barbara*.

The along-shore cooling effects of upwelling in Oregon and Washington are strikingly evident in the southward extension of the range of many subarctic fishes. Farther offshore, beyond the effects of upwelling, occur fishes of more southern types, such as the mola (*Mola mola*), albacore (*Germo alalunga*), bluefin tuna (*Thunnus thynnus*), and more southern types of sharks.

In the cases of more or less isothermal bathymetric distribution, the effect of temperature transcends that of light and a great variety of other factors. Thus certain forms that inhabit intertidal reefs in central California occur in the cooler infratidal waters in southern California. Examples are a klipfish, *Gibbonsia montereyensis*, and a rockfish, *Sebastes chryselas*. Like the two invertebrates mentioned previously (*Haliotis rufescens* and *Strongylocentrotus franciscanus*), these two species reappear on certain intertidal reefs of Baja California where the water is unusually cool. A midshipman, *Porichthys notatus*, breeds in intertidal waters in central California but not in

southern California. In general, fishes of wide latitudinal distribution occur in deeper water to the southward. Thus the rattfish, *Hydrolagus collicii*, lives close to shore in Puget Sound, but chiefly in about 50 to 100 fathoms near San Diego. The seven-gill cowshark (*Heptanchias maculatus*) is common in the shallow parts of San Francisco Bay, but off San Diego it is taken chiefly off the open coast at depths of about 50 fathoms. A rockfish, *Sebastes mystinus*, abounds in central California close to the rocky shores and near the surface offshore, but is confined in southern California to rather deep water. It is hoped that supporting data will be marshalled in future publications.

The seasonal movements of fishes along the coast are clearly controlled by water temperatures. Thus marlin, *Tetrapturus mitsukurii*, do not appear off San Diego until or unless the surface temperatures approximate 70° F. Albacore, *Germonus alalunga*, are looked for at temperatures approximating 60 to 65° F. The wide movements of the sardine, *Sardinops caerulea*, are also definitely seasonal.

Though the data have been presented so sketchily and though much of the detailed information remains to be gathered and collated, it seems safe to assert that the distribution of marine fishes along the Pacific Coast of North America is determined to a large degree by the sea temperatures. This assertion, of course, is bolstered by the close relations between temperature and distribution established for fishes in other parts of the world, and for other groups of organisms.

INFERENCES FROM FAUNAL EVIDENCE REGARDING PREHISTORIC CHANGES IN SEA TEMPERATURE

On the basis of present distribution it may be inferred that isotherms and fish faunas have been displaced both northward and southward during recent geological time. Unhappily the Pleistocene fish faunas are much too poorly known to bring to bear on this problem, in the way that warm-water and cool-water Pleistocene mollusk faunas have been cited to indicate such thermal and faunal shifts (Smith, 1919; Schenck and Keen, 1937; etc.).

The evidence for past northward shifts in ocean isotherms and fish distribution is found chiefly in the occurrence of southern forms northward, in appropriate waters beyond discontinuities in distribution. Reference has been made already to the occurrence in British Columbia of certain Californian fishes that do not live in the intervening cool regions of maximum upwelling; also, to the northern outliers of southern types in certain warmish bays, particularly Morro Bay. Since none of the southern relicts shows any evidence of differentiation, the past connections, probably during periods of warm climate, were

presumably in late Quaternary time. The warm Postglacial period, generally recognized on the basis of pollen profiles and other evidence, suggests itself as the time when isotherms and fish faunas were displaced northward along the coast.

A small body of fish evidence and a larger amount of mollusk data from Indian kitchen middens support the view that displacements both northward and southward have taken place during Postglacial times.

The occurrence along the northwestern coast of Baja California of northern coastal relicts, likewise undifferentiated, may be taken to indicate a very late Pleistocene or early Recent southward displacement of isotherms and fish faunas. The presence of a rainbow trout, *Salmo gairdnerii nelsoni*, in certain streams of the region has been thought of as confirmatory evidence of such a southward shift, but the inference is not secure (Hubbs, 1946: 85), not nearly so convincing as the inference for past displacements that can be drawn from the presence in Formosa (Jordan and Oshima, 1919: 122; Jordan and McGregor, 1925: 137) of a land-locked salmon (*Oncorhynchus formosanus*).

A more ancient and more extensive southward displacement of isotherms and faunas is indicated by the occurrence of a rather large number of northern relicts in the upper part of the Gulf of California, where the summer water temperatures are high and the winter temperatures low. The types with northern affinities coexist with a somewhat depauperate Panamian fish fauna. Most of the northern Gulf relicts and their respective Californian cognates do not now range into the almost strictly tropical waters about Cape San Lucas. The connection presumably existed at some ancient time, or more probably at several times. Since, according to published and unpublished studies, the level of differentiation grades from full-specific to racial or none—usually weakly specific or subspecific—and since southward displacements are generally accepted as having occurred during the Glacial periods, it seems logical to date the connection or connections as Pleistocene. The occurrence of a specifically differentiated trout of the *Salmo gairdnerii* series in the upper part of the Gila River system seems attributable to a similar displacement. Other northern fish relicts in various streams of the Pacific Coast drainage are probably also of Pleistocene derivation (data in part cited by Hubbs and Miller, 1948).

LONG-PERIOD NORTHWARD DISPLACEMENTS OF FISH FAUNAS WITHIN HISTORIC TIME

In agreement with other lines of evidence, data on changes in the distribution of fishes along the Pacific Coast suggest that climatic

oscillations have persisted into historic time. There are strong indications that the ocean temperatures from 1850 (or earlier) to about 1870 were definitely warmer in the southern half of California than during subsequent decades, and there are weaker suggestions of a reverse change in temperature and fauna during the past two or three decades.

The fish fauna of San Diego, as sampled from 1853 to 1860, particularly by the Pacific Railroad Survey from 1853 to 1857 (Girard, 1858; etc.), was definitely more tropical than that of any subsequent decade. Of the 30 odd species reported, six (about 20%) do not now occur so far north or have been so rare recently that one certainly would not expect any to be caught at present by such incomplete and superficial collecting as that of the 1850's and 1860's. Possible sources of gross error have been disregarded after due consideration. The Pacific Railroad Survey secured at San Diego: five specimens of the giant seahorse, *Hippocampus ingens*; few of which were collected north of Magdalena Bay from then until 1880 and none since that year; four examples of a presumably tropical pipefish, *Dermatostethus punctipinne*, which has never been secured again, anywhere; several individuals of an unidentified triggerfish (of the tropical family Balistidae), which seemingly has not been collected again in the eastern Pacific; two spade-fish, *Chaetodipterus zonatus*, of which the only subsequent California record is for a specimen taken in the extremely warm summer of 1931 (p. 467); a puffer, *Spherooides politus*, of which only one doubtful example has been secured in California since 1880 and few before that year; and a jack, *Caranx caballus*, of which single specimens have been reported from California in 1857, 1924, and 1945. The only northern species reported from San Diego by Girard was the seaperch *Taeniotoca lateralis*, but this species was represented by a single adult; this species ranges commonly south to the Santa Barbara Islands and it has been collected recently near San Pedro and in northern Baja California.

Nearly as impressive is the evidence that the fish fauna at Monterey during the first two decades of the second half of the nineteenth century was made up to a considerable degree of fishes now characteristic of the relatively warm waters south of Point Conception. Only about twenty species were reported from Monterey by the Pacific Railroad Survey, but the list includes five or six kinds that do not now occur so far north or are so rare as not to be collectable by any such dribbling survey as that of the 1850's. These southern types are the sand bass, *Paralabrax nebulifer*, the California sculpin, *Scorpaena guttata*, the bay blenny, *Hypsoblennius gentilis*, the garibaldi, *Hypsypops rubicunda*, the horned shark, *Heterodontus francisci*, and perhaps the guitarfish,

Rhinobatos productus (recorded as from either Monterey or San Francisco). The evidence that the California flyingfish, *Cypselurus californicus*, occurred prior to 1864 north as far as Santa Cruz on Monterey Bay has been cited (Hubbs and Kampa, 1946: 209) as an example of former occurrence of southern forms north of their present range. As noted by Steinbeck and Ricketts (1941: 48) and by Schmitt (1921: 163), *Pleuroncodes planiceps*, a very conspicuous crustacean that swarms at the surface in warm water, was washed ashore in considerable numbers in March 1859 at Monterey, hundreds of miles north of its usual present range. Ordinarily this species is uncommon north of central Baja California, though it penetrated into southern California in abundance in the spring and summer of 1941 (notes in California State Fisheries Laboratory).

For the region of San Francisco, in contrast, the evidence (more extensive than for the other ports) indicates a relatively stable fauna throughout the last hundred years. Approximately one hundred species have been reported as collected about San Francisco from 1853 to about 1860 (here much local collecting, particularly by W. O. Ayres, supplemented that of the Railroad Survey). With about seven exceptions, the species reported are still rather common about San Francisco. One of the seven, the opaleye, *Girella nigricans*, has not since been collected about San Francisco, but adults straggle to Monterey, and Ayres had only one example from San Francisco. Four (namely *Squatina californica*, *Rhinobatos productus*, *Synodus lucioceps* and *Stereolepis gigas*) are now very seldom found north of Point Conception, which further suggests a slight southward facies, though all of the species were reported as rare in the 1853-1860 period. Partly counterbalancing this indication of a southern facies were the early records of two northern species for San Francisco. Girard and Ayres each reported from there a snakeblenny, *Lumpenus gracilis*, which has never since been collected south of Puget Sound, and Ayres had one, the sanddigger, *Trichodon trichodon*, which has since been taken only once at San Francisco.

The relatively large number of subtropical types that were taken about San Diego and of southern California types that were secured about Monterey, from 1853 to about 1860, and the stationary habits of these species, make it appear very improbable that the northward occurrences represented merely single-season waves, such as are mentioned below. A further reason for believing that the warm-water faunas were long-lasting and real is that a considerable representation of southern types seems to have persisted through the 1870's until 1880, when Jordan and Gilbert conducted the most thorough reconnaissance of the century of the West Coast fishes. A study of the

reports by Jordan and Gilbert (1881 a, b) and by their contemporaries indicates that the fauna from San Diego to San Francisco had a slightly more southern tinge than at present, despite the fact that 1880 was an unusually cold year (Figs. 1-3, 5). No particularly

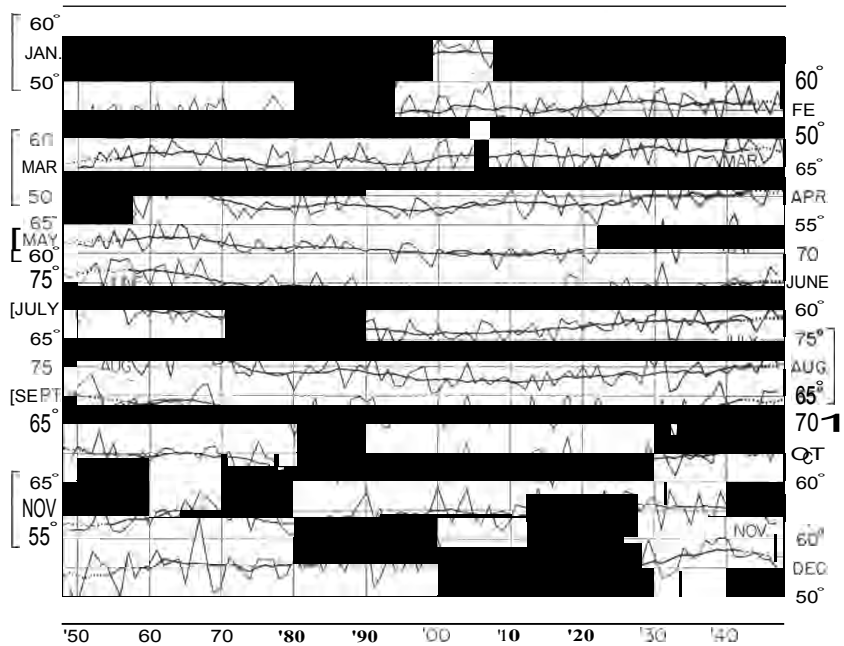


Figure 1. Fluctuations of mean air temperatures at San Diego from 1849-50 to 1947-48, for each month, with trends computed by running averages of 11. Data from World Weather Records (Smithson. misc. Coll., 79, 1927: 934-935; 90, 1934: 347; 105, 1947: 373) and from Climatological Data (U. S. Weath. Bur., vols. 45-52, 1941-1948); all data corrected to means of 24 hours.

northern type was reported for 1880, except possibly a cod, *Theragra chalcogramma* (recorded as rarely taken about San Francisco), but in contrast a considerable number of distinctively southern types were reported for that year. A Spanish mackerel, *Scomberomorus concolor*, occurred in some numbers in Monterey Bay then and during the following several years, but it is now excessively rare even in southern California. *Cynoscion parvipinnis* was common in southern California, where it now seems to have been absent for many years, though it remains abundant in central Baja California. The barracuda, *Sphyræna argentea*, was said to be especially abundant in Monterey Bay, whereas now it lives chiefly in southern California and southward.

The bonito, *Sarda lineolata*, now chiefly southern, was reported to be very abundant everywhere in summer. The elasmobranch fauna as reported seems distinctly more southern than at present.

Several tropical types reported as occurring rarely in southern California in the last third of the nineteenth century possibly also represent holdovers from the warm-water fauna of the middle of the last century. Among these are three that have not since been taken in the state: *Eucinostomus argenteus*, *Chilomycterus affinis* and *Diodon hystrix*.

During the last two decades a considerable number of tropical types have been collected in southern California, suggesting the possibility that a slightly more tropical assemblage is becoming re-established. However, the captures are attributable, in part at least, to more thorough collecting, to chance migrations, and to the single-season northward dispersals that are discussed in the following section. Four bottom fishes previously unknown north of central Baja California, however, have been found recently in some numbers in San Diego County, with indications of recent establishment. These are the zebraperch, *Hermosilla azurea*, a porgy, *Calamus brachysomus*, and two giant groupers, *Mycteroperca xenarcha* and *M. jordani*.

SINGLE-SEASON NORTHWARD DISPERSALS OF FISH FAUNA

During occasional warm years, unusual numbers of free-swimming fishes and other pelagic animals appear along the Pacific Coast far north of their customary range. A year particularly noted for this phenomenon was 1926 (Hubbs and Schultz, 1929). Southern types, including the siphonophore *Verella*, abounded as far north as British Columbia. *Mola mola* appeared off the British Columbia and Washington coasts. Anchovies, *Engraulis m. mordax*, were unexpectedly abundant in the mouth of the Columbia River. Albacore, *Germo alalunga*, were caught near the Oregon shore for the first time on record and the catch off central California increased sharply. Mackerel, *Pneumatophorus japonicus die go*, and jacksmelt, *Atherinopsis californiensis*, previously unrecognized there, appeared in numbers in Coos Bay. A thresher, *Alopias vulpinus*, was also taken there, as a novelty, and many hammerheads (*Sphyrna* sp.) were caught in southern California.

Five years later, in 1931, an unusual number of southern fish strays were captured along the coast of southern California (Walford, 1931). In 1941 red crabs, *Pleuroncodes planiceps*, abounded off Los Coronados and Santa Catalina islands, far north of their usual range. In British

Columbia there was an intrusion of southern forms, as also in 1936 (John L. Hart, personal communication).

Similar reports stem from off the Oregon, Washington and British Columbia coasts for the summer of 1947, when July was exceptionally clear and warm. According to fishing reports, swordfish and even flyingfish appeared for the first time off Oregon, along with an especial abundance of albacore and numbers of bluefin tuna. A "yellowtail," presumably *Seriola dorsalis*, was caught off southern Washington, far north of the previously known northern limit of range. California pompano, *Palometa simillima*, appeared in unprecedented abundance in British Columbia (Hart, in press).

The appearance of southern fish on the Pacific Coast far to the north of their usual range, during warm years, has usually been attributed to the northward dispersal of individuals. Movement of this sort may be involved, at least for such fish as the sardine, *Sardinops caerulea*, and the mackerel, *Pneumatophorus japonicus die go*, that are known to migrate regularly up and down the coast. An alternative explanation, for animals with a very short life cycle, is that local populations in the north, too small to be conspicuous, may suddenly erupt when temperatures rise. More commonly, however, it is probable that the warm-water types merely move closer to shore from the warmer waters that lie outside the coastal zone of upwelling. Thus the albacore that occasionally appear close to the Oregon and Washington coast probably come chiefly from the population of the offshore, warm "blue water," rather than from southern coastal waters. This is even more likely true of *Mola* and *Veleva*. The dispersal may be essentially short and transverse, like the seasonal migration of many western birds which, instead of undertaking long north and south movements, merely fly back and forth between mountains and valleys.

Whatever the course of movement may be, there is little doubt that in years when the surface temperatures are high, particularly during the spring and summer months, southern types of animals occur near the Pacific Coast far north of their usual limit of range. However, there is no regular northward dispersal comparable to that effected along the Atlantic Coast by the Gulf Stream.

TEMPERATURE DATA BEARING ON CHANGES IN FISH FAUNA

Water temperatures are available for correlation with some of these short-period shifts in fish fauna along the Pacific Coast but are inadequate to explain unequivocally any of the long-term changes. ~~Air-~~ ~~temperature~~ data, within limits, can be used as a substitute for lacking

or inadequate water-temperature data, or can be used to corroborate limited data on sea temperatures, not only for current and recent years but also for the latter half of the nineteenth century. Estimates of prehistoric changes in the ocean temperatures rest on our knowledge of the temperatures of waters now inhabited by the same or similar faunal assemblages and will probably continue to rest on that basis, though some corroboration may be expected from intensive study of middens and fossil deposits and eventually from correlations of the sea-levels and associated deposits with Pleistocene history.

The noteworthy northward displacement of the marine fauna in 1926 was clearly due to exceptionally high sea temperatures along the whole length of temperate North America during the first half of that year. Hubbs and Schultz (1929) reached this conclusion from an analysis of sea temperatures at Pacific Grove, California, and of air temperatures at coastwise stations in Oregon and Washington. Sea

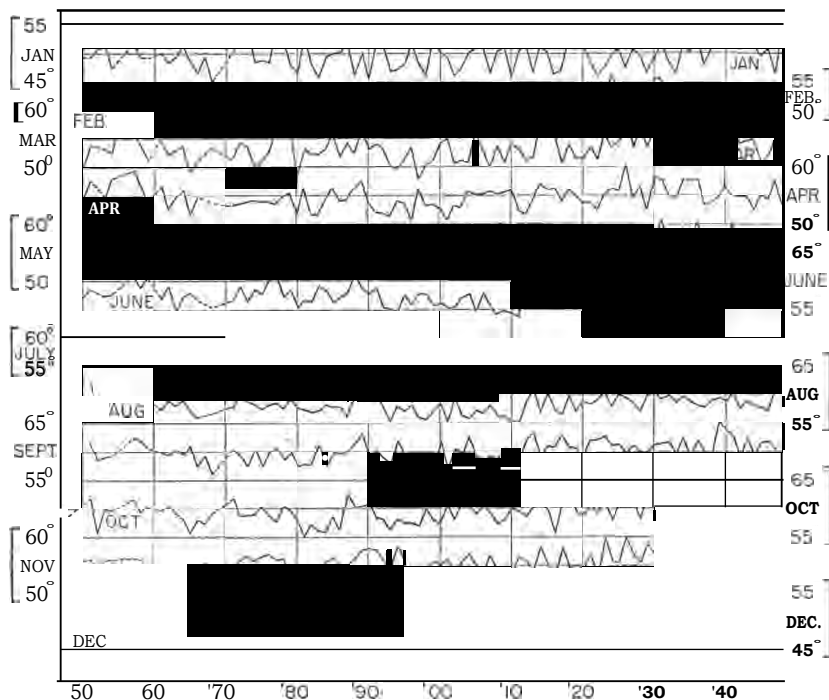


Figure 2. Fluctuations of mean air temperatures at San Francisco from 1847 (in part) to 1947-48, for each month. Data from *World Weather Records* (Smithson. misc. Coll. 79, 1927: 939-940; 90, 1934: 348; 105, 1947 374) and from *Climatological Data* (*U. S. Weath. Bur.*, vols. 45-52, 1941-1948); all data corrected to means of 24 hours.

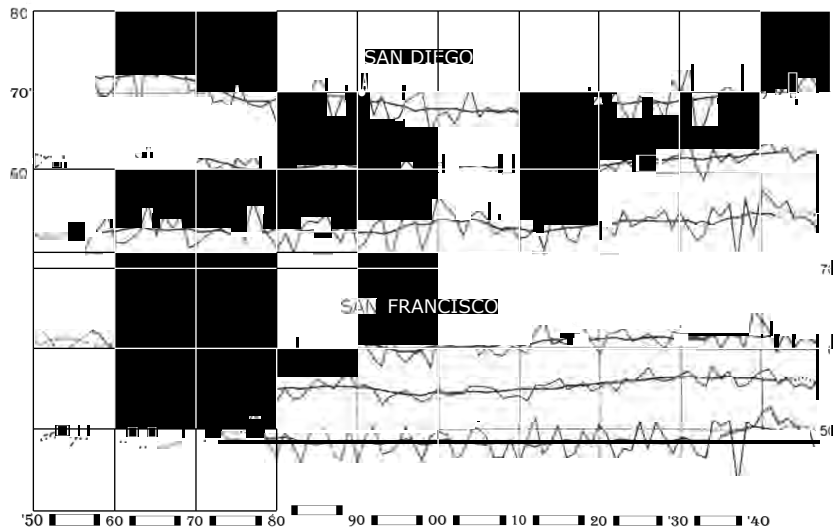


Figure 3. Fluctuations of mean temperatures at San Diego and at San Francisco, with trends computed by means of 11. Shown for each city are the means for the warmest month of each given year; the means for the year; the means for the coolest month. Source of data as for Figs. 1 and 2.

temperatures were high during the first half of 1926 at other stations in California (in general the correlation between stations is very close). Thus, at San Diego, the annual mean was unusually high in 1926 (Figs. 3, 5) as a result of extremely warm water during the early months of the year (Fig. 4). A similar pattern was displayed by the air temperatures at San Diego (Figs. 1, 3-5) and at San Francisco (Figs. 2, 3). At Victoria, British Columbia, the air temperatures were at or near record height from January through June and in November; about median in the other months.

During most of 1931, when many tropical fishes appeared off San Pedro, California, as well as during the latter part of 1930, the air temperatures were definitely above normal at Los Angeles and at San Diego (Walford, 1931). Sea temperatures at La Jolla (Fig. 4), closely corresponding with the air records for San Diego (Figs. 1, 3-5), were likewise extremely high from January through September 1931. The temperature increase in 1931 was less widespread than in 1926 and no record seems to have been made of any general appearance of southern forms in 1931 at any point in California north of the southern part of the state. At San Francisco the air temperatures ran about normal in most months (Figs. 2, 3). In British Columbia, however,

air and sea temperatures were above normal and there was an intrusion of southern forms (John L. Hart, personal communication).

During the early months of 1941 the air temperatures were again very high (Fig. 1) at San Diego and the mean air temperature there,

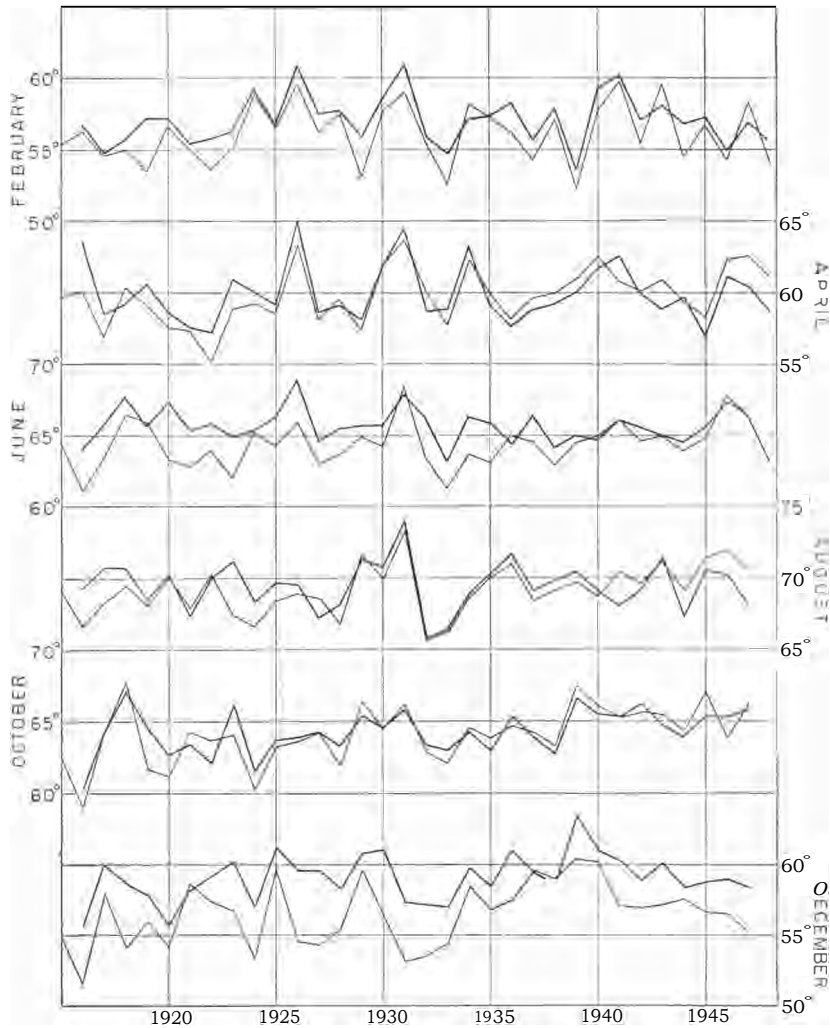


Figure 4. Fluctuations of mean temperatures for alternate months. Lighter lines represent air temperatures at San Diego from 1915 to 1947-48 (source of data same as for Figs 1-3); darker lines represent the monthly means of the sea-surface temperatures taken at 7:00 A.M. each day at the end of Scripps Pier, La Jolla.

as well as the mean sea temperature at La Jolla, was very high (Fig. 5). This is the year when the warm-water red crab, *Pleuroncodes planiceps*, abounded during the spring and summer off southern California (p. 467).

Data collected by John L. Hart of the Fisheries Research Board of Canada, from the albacore fishing grounds of the northwest coast and from the Nootka, British Columbia, lighthouse, confirm fishermen's reports of unusually high summer temperatures in 1947, when southern forms were common in the north.

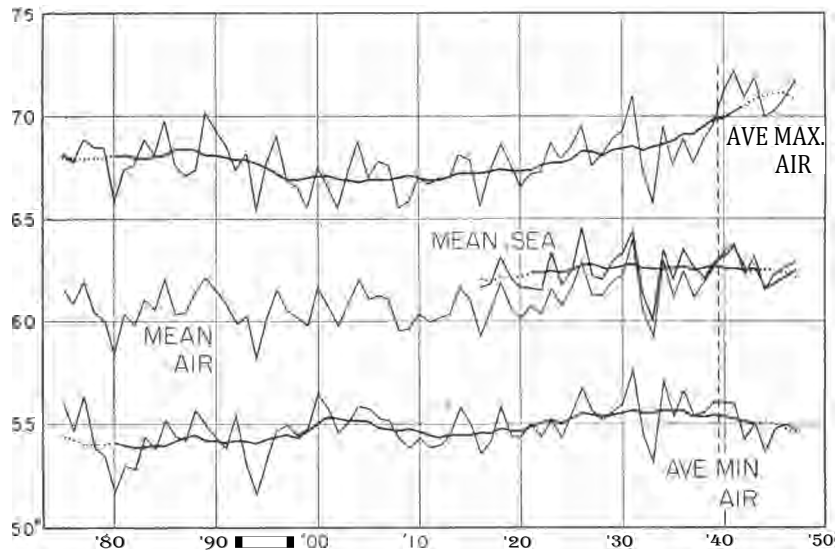


FIG. 5. MEAN AIR, MEAN SEA, AND AVERAGE MAXIMUM AND MINIMUM AIR TEMPERATURES AT LA JOLLA, CALIFORNIA, 1875-1947. (Data from Hart, 1947, p. 467.)

Greater complexities and uncertainties are involved in the effort to correlate long-term changes in the fish fauna with changes in the ocean temperatures. Air temperature data from the weather records (Figs. 1-5) stand in striking agreement with the limited though impressive data on fish faunal changes. Air and sea temperatures along the Pacific Coast are very closely correlated, as is generally known and confirmed by the data presented below, but doubts as yet unresolved

pertain to the correlation of air temperature records of the last century with contemporary changes in sea temperatures.

The air-temperature data for San Diego (Figs. 1, 3-5) strongly suggest long-term climatic changes that correlate nicely with the observed faunal changes. The mean temperature seems to have been high during the early years of record, beginning in 1849-50 and continuing through the 1850 and most of the 1860 decades; that is, during the period when the fish faunas at San Diego and at Monterey were distinctly more southern than during any of the subsequent decades. From just before 1870 the general indicated trend was toward cooler weather until about 1910, after which there seems to have been a moderate reversion toward warmer conditions. In possible correlation, there is evidence—rather slight to be sure—that some subtropical fishes are becoming established in the San Diego area.

Considering the data by months (Fig. 1) we find that the changes in the trend for the mean annual temperature at San Diego characterize also the trend for each month from April through October. For two

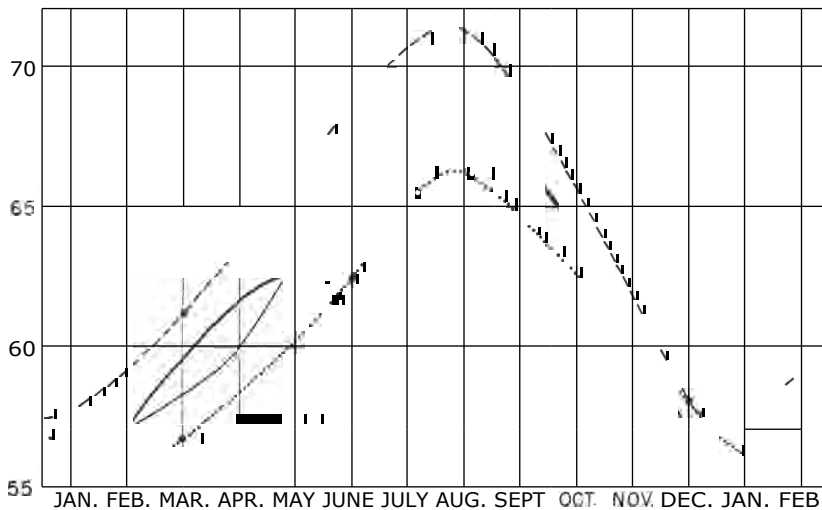


Figure 6. Variation through the year of the average sea-surface temperature about San Diego. The lighter solid line represents the trend at Scripps Pier, La Jolla, from 1916 through 1947. The heavier solid line shows the data for San Diego Bay entrance from 1854 to 1860 (probably depressed during late spring and summer for reasons given in the text). The dotted line indicates roughly the temperature cycle at present to the south of the bay entrance, computed from observed quarterly differences from the Scripps Pier data for the same year (1946-47). The dashed line is a maximum inference of the sea-surface temperatures at La Jolla, based on the assumption that the bay-entrance water came from the southward in 1854-1860, rather than from off Pt. Loma as it apparently does at present.

reasons this evidence is of particular importance in the present connection. In the first place, the months from April to October comprise the period of rapidly increasing and high sea temperatures in southern California (Fig. 6), that is, the season when the warmer-water forms of life reproduce and pass through critical stages of development. In the second place—a point that Martin W. Johnson has suggested—the indicated period of increased warmth was long enough to be of real biological significance. The fact that the months from November through March were not warmer from 1850 to 1870 than during subsequent decades, perhaps even cooler, might not have affected the northward displacement of the fauna nearly a century ago, because the region from which the southern forms would have been derived—southern Baja California—is characterized by cool winter sea temperatures as well as by warm summer seas; the subtropical forms occurring there must be adapted to cool winters.

At San Francisco (Figs. 1, 3), where there seems to have been only a slight change in the fish fauna over the last century, the air temperature data since about 1850 do not indicate a marked long-term trend downward from the 1850-1870 decades to about 1910. There seems to have been a slight downward trend, with notable irregularities, in the months from April through August.

That the air and sea temperatures along the Pacific Coast are correlated very closely is well known from the work of George F. McEwen and others and is strongly confirmed by recent analyses. There are some irregularities, for example, when offshore winds from the desert (Santa Anas) markedly raise the air temperatures but cause upwelling of cool water. Comparing the mean monthly air temperatures at San Diego with the mean monthly morning (7:00 A. M.) sea temperatures at the Scripps Institution Pier (Fig. 4, showing the data for alternate months), we find a very close agreement for the period from 1916 to 1947-48. Major discrepancies occur in certain months, notably January, June and December, but in other months the fluctuations in air and sea temperatures correspond remarkably well. For periods of several years the means and the changes from year to year may be almost identical. The curves for the annual means from 1916 through 1947 (Fig. 5) parallel one another with great precision. The mean sea temperature averaged 0.64° C. higher than the mean air temperature from 1916 through 1939 and 0.10 lower from 1940 through 1947, during which period the air temperatures were taken at a new, warmer location, as explained below.

The correlation coefficient (c) between the average air and sea temperatures is very high. Between the mean annual sea temperatures at La Jolla and the mean annual daily minimum air temperatures at San

Diego, for the period from 1916 through 1946, $c = 0.87$ (the minimum temperatures were only slightly reduced by the move of the Weather Bureau station). There was a similar high correlation between the mean sea temperatures and the annual average of the daily maximum temperatures: $c = 0.87$ for the period from 1916 through 1939 and $c = 0.86$ for the period from 1940 through 1946. For five years, from 1940 to 1944, the correlation coefficient between the monthly average daily sea temperatures at La Jolla and the monthly average of the daily evening radiosound surface air temperatures (approximately 2° F. higher than the minimum air temperature) at San Diego reached the astonishingly high value of 0.98. These data were computed by Dale F. Leipper of the Scripps Institution and were kindly made available by him.

Since the air and sea temperatures are so very closely correlated about San Diego, one might assume that the high air temperature records for the 1850 and 1860 decades and the low air temperature from about 1870 to about 1910, with a slight increase since, might be taken as a clear index of changing sea temperatures. Possible errors, however, are involved. From July 1849 through September 1871, the records were kept by the Army Medical Corps at various locations, by methods and with instruments that are not recorded in detail (Carpenter, 1913: Chap. I). The exact location of the station was changed several times, but fortunately the station remained at about the same elevation and within a one-half mile radius, from 1860 (about the middle of the indicated warm period) through January 1940 (Carpenter, 1913, and Dean Blake, personal communication). Thus the warm summers, the cool winters and the wide difference between the warmest and coolest months, indicated for the early years of the San Diego records (Fig. 1), can hardly be attributed to a change in the location of the station. It is suspicious that the temperature records were generally high until taken by the standard methods of the Weather Service (first under the Army Signal Service), beginning October 1, 1871. Bespeaking the significance of the indications of a prolonged warm period from 1849 through 1868, however, are the facts (1) that moderate temperatures were reported in 1869 and 1870, before the Weather Service took charge, and (2) that, with fluctuations, the trend continued downward after the methods were standardized. Considering also the striking agreement between the recorded weather data and the indicated change in fish fauna, I regard the balance of evidence as favoring the view that the trend of both air and sea temperature was downward from about 1870 to about 1910.

However, some actual data on water temperatures from 1854 to 1860 do not yield unequivocal support for the view that the sea

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