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The Atyid Shrimp of the Genus *Syncaris* in California

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1. Species and distribution of Atyidae

Four species of Atyid shrimps have been recorded from North America north of the Rio Grande: *Syncaris pacifica* (HOLMES), from small streams in Sonoma, Marin and Napa counties in northern California, *Syncaris pasadenae* (KINGSLEY) from lowland streams in Pasadena, Los Angeles and San Bernardino, southern California; *Palaemonias ganteri* HAY from Mammoth Cave, Kentucky and *P. alabamiae* SMALLEY from caves in Alabama. The latter species are blind cavernicolous forms. The last recorded collections of *Syncaris pasadenae* were made in 1933, and the species is probably extinct. *Syncaris pacifica* continues to exist in the restricted environment of a few small streams, remote from other atyids. Until recently these shrimp have been unnoticed by zoologists, and their original descriptions escaped the notice of ORTMANN (1918) who stated that the only species of Atyid in North America was *Palaemonias ganteri*. My attention was called to these shrimp by Dr. JAMES E. LYNCH while at Pacific Marine Station in the summer of 1949. During the past 16 years I have looked for Atyids in streams of California and Oregon, and watched with lugubrious sentiments the steady deterioration of the restricted environment of the extant species in California.

The distribution of Atyidae is somewhat irregular throughout the world; most species are found in the tropics in freshwater streams and lakes. They occur in streams of southern Europe draining into the Mediterranean, in west and central Africa, especially the lakes. Species are found in the Cape Verde Islands, Central America, Brazil, Hawaii, New Zealand, Australia, and in many of the western Pacific islands as far north as Hainan and in Japan. The family is also represented in southern India and Madagascar. There are a number of troglitic species in various parts of the world in addition to the two in North America. The great majority of atyids are strictly freshwater in occurrence, but there are a few tolerant of brackish water conditions, notably *Atyaephyra desmaresti*, which is in the process of invading northern Europe; it was first noticed in

Holland about 1915 and can live in waters of at least 465 mgr Cl/liter (VORSTMAN, 1955). HOLTHUIS (1963), in renaming the species from Hawaii formerly known as *Caridina brevisrostris* as *Halocaridina rubra*, notes collection data which indicates that this species occurs naturally in brackish pools. In this same paper he discusses the occurrence of *Antecaridina lauensis* in saline ponds connected with the sea in such a manner as to suggest that hearily oceanic salinities may be tolerated by this species, which is found in Fiji, in Europa Island near Madagascar, and Entedebir Island in the southern Red Sea. According to Dr. H. STEINITZ (in litteris, Sept 5, 1967), *Antecaridina* was found in the Devil's Crack at Entedebir in pools at salinities of 35.91 and 36.13‰.

ORTMANN (1902) suggested, on the basis of the distribution pattern of the Atyidae (he was unaware of the California species), that the present atyids are descendants of forms which left the sea in Jurassic times. For whatever it is worth, it is interesting to note that the watersheds of northern California in which *Syncaris pacifica* occur drain through strata of possibly Jurassic age, the Franciscan formation (DICKERSON, 1922). However, there were undoubtedly great changes in the drainage pattern of the lowland streams in both Pliocene and Pleistocene times (HIGGINS, 1952; WEAVER, 1949), and it is probable that there were routes for dispersal for freshwater shrimps to all the various small drainage areas in the region.

The distribution of Atyidae in North America is in sharp contrast to that of the Palaemonidae (HEDGPETH, 1957, 1966). The Palaemonidae are as a group much more tolerant of estuarine and marine waters, and are probably much later invaders of fresh waters than the Atyidae.

2. *Syncaris pacifica* — natural history and distribution

Syncaris pacifica is a slender caridean shrimp about two inches long (Figure 1 and 2). It is usually transparent and almost impossible to see in the stream although there may be hundreds of individuals in a pool 10—15 feet wide and 30—40 feet long. The general color out of the water is greenish gray; the uropods

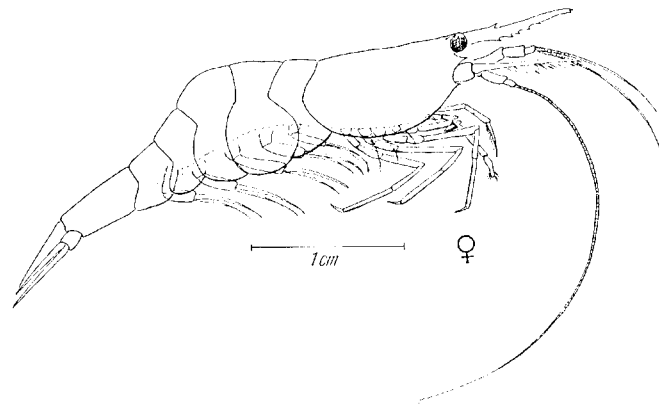


Fig. 1. Habit sketch of a female specimen of *Syncaris pacifica* from Salmon Creek, California

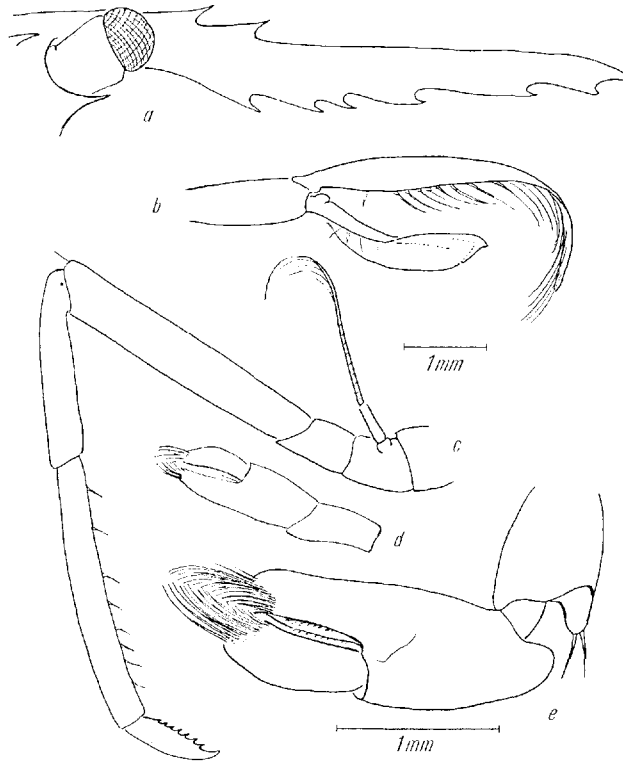


Fig. 2. *a.* Rostrum of male specimen from Salmon Creek; *b.* First pleopod of male; *c.* Fourth pereopod of male; *d.* Chela of 2nd pereopod; *e.* First chela

are pale blue. The shrimp is found typically in the slower reaches on lowland streams, living among such plants as *Chara* and *Potamogeton*. During most of the year these streams are warm and are avoided by salmonid fishes (although Salmon Creek, as its name implies, supports a small run of silver salmon during periods of high water). During the salmon run, however, the streams are usually muddy.

The shrimp are usually found among the attached vegetation, often clinging upside down by their pereopods. A few specimens have been taken in deeply shaded pools in a small stream among the redwoods, but the most characteristic environment is that illustrated in Figure 3. They are not found in cold, rocky streams. They live compatibly with sticklebacks, cottids, and crayfish. EDMONDSON (1929) found that atyids in Hawaiian streams could not persist in streams where there were introduced mosquito fish, since these ate the newly hatched larvae.

The shrimp live well in aquaria, and were it not for their limited populations in a few small streams, would make excellent experimental animals. In the aquarium they cling to plants or such objects as the aerating stone or tubes, remaining motionless for long periods. They may hang upside down, sideways

or head downwards, but most of them maintain an upright, level position. They usually swim forward downwards, but they are capable of quick darting backward movements, and can skip several feet over the surface of a pool when disturbed.



Fig. 3. View of Salmon Creek, Sonoma County, California between Bodega and Valley Ford near Witham house, showing characteristic reach inhabited by *Syncaris pacifica*

Syncaris pacifica has a winter breeding season. Ovigerous females bearing 50—70 eggs are common in December and January. No ovigerous females have been observed in July and August, and BORN (1968) has estimated that the breeding season is from September to October. The incubation period is not known, but ovigerous females collected in late December did not release larvae in the aquarium for more than a month. When collected, these eggs were comparable to the 150 hour stage described by NAIR (1949) for *Caridina laevis* in southern India; in *Caridina laevis*, however, hatching occurs about 17 days after the beginning of cleavage. The large numbers of half grown shrimp taken in December suggests that *Syncaris pacifica* may not mature until the second year. VORSTMAN (1955) suggested that as *Atyaephyra desmaresti* moves northward it tends to have a two year breeding cycle, and notes the long breeding season of populations in Holland as compared with those of southern Europe. Some tropical atyids may breed the year round; according to EDMONDSON (1929), this is the case for *Atya bisulcata*. While the winter breeding cycle may account for the long incubation period in *Syncaris pacifica*, it also suggests that the primary adaptation in this species is to the hydrologic cycle of the region. Often in summers the small lowland streams of this area are almost dry, with scattered pools. Populations may be reduced during such times, and it would obviously be disadvantageous for the species to reproduce at the time of year when the environment is at a minimum.

The known occurrences of *Syncaris pacifica* are indicated in Figure 4. Repeated collections over the last 15 years have established this basic pattern, and it can be reasonably stated that *Syncaris pacifica* does not occur south of San Francisco Bay, nor north of the lower Russian River drainage. Almost every suitable stream north into Oregon has been sampled, many of them several

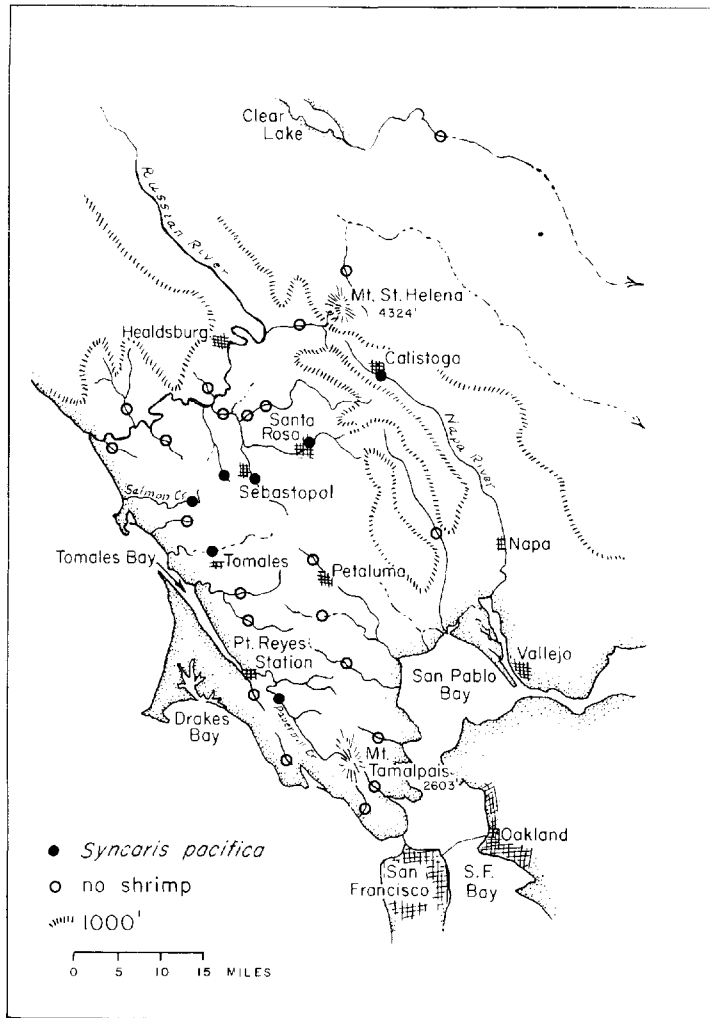


Fig. 4. Distribution of *Syncaris pacifica* in streams north of San Francisco Bay, based on collections from 1949 to 1965

times. The largest resident population of *Syncaris pacifica* occurs in Salmon Creek, Sonoma County. Probably the next best location for these shrimp is in Lagunitas or Papermill Creek just south of Pt. Reyes Station in Marin County. Since I began to observe these animals, the population in Santa Rosa Creek at the city of Santa Rosa was extirpated by the urban renewal project which converted the stream (that might have been the scene for a charming park in the manner of San Antonio, Texas) into a large square culvert hidden beneath parking lots and other progressive developments. The shrimp may still occur in Santa Rosa Creek, but no longer at the convenient site beneath the town bridge across the stream. The location at Calistoga, (Napa County) in the small stream

called the Napa River, is very similar: a bridge almost in the middle of the commercial district. I am informed by JOHN BORN that he could not find any shrimp there recently. However, records for this locality go back to 1897, and it is to be hoped that *Syncaris pacifica* still lives somewhere in this drainage.

The persistence of these shrimp in lowland streams, subject to heavy run off in winter, and almost complete cessation of flow during drought years, attests to their ability to survive natural events. However, a number of the populations appear to be very small, or perhaps sporadic. That is, populations in such areas as the Laguna de Santa Rosa (the possible type locality) or Atascadero Creek west of Sebastopol may not occur there every year, but may be the result of migrations from time to time via connecting streams. While it would be of interest to study the variation in these separate populations, I have been reluctant to collect large numbers of specimens in some of the smaller streams.

3. *Syncaris pasadenae* (incl. *S. trewi*)

Inasmuch as no specimens of *Syncaris pasadenae* have been collected since 1933, and repeated efforts by myself, CADET HAND, J. C. YALDWYN and others in all possible streams from the Mexican Border to Santa Barbara have yielded negative results (Figure 5), it must reluctantly be assumed that the species is extinct. It is represented by a number of collections in the United States National Museum (Table 1). The small collection of 10 specimens, undated, from "San Diego, California" is somewhat puzzling. It is possible that this locality was that of the collector's domicile rather than the site of collection.

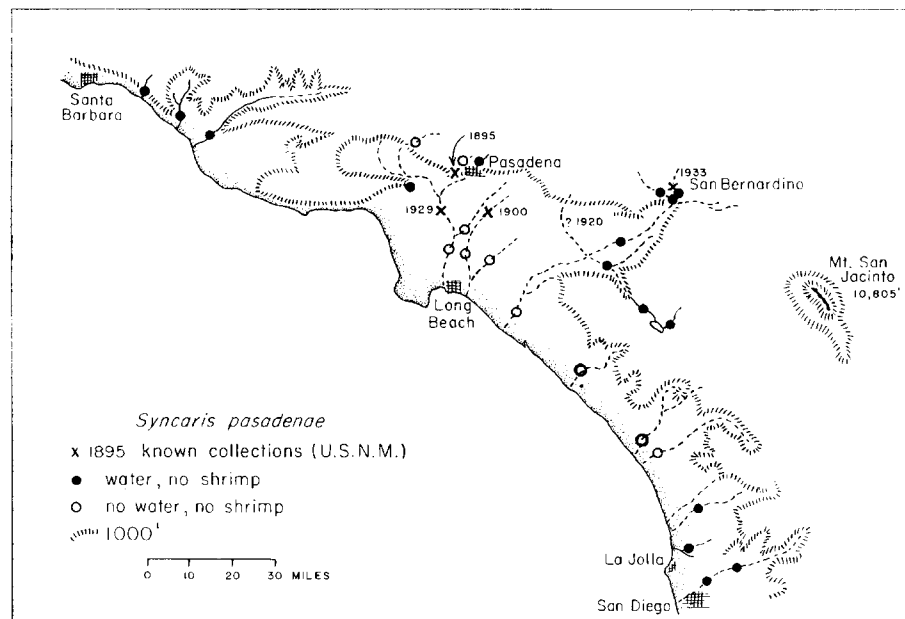


Fig. 5. Last known records and streams sampled for existence of *Syncaris pasadenae* since 1951

None of the streams in the Los Angeles area are in their original state. The type locality appears to have been about where the Rose Bowl now stands. Several of the streams are now large concrete flood canals, dry most of the year. Streams near San Bernardino were visited in 1957, and the channels were being re-organized by bulldozers for flood control purposes. Many of the localities indicated by open circles on Figure 4 were found to be dry arroyos.

Little can therefore be said of the natural history of this species. Specimens collected in the Los Angeles River in 1925, dated "March 13 and June, 1925" include two ovigerous females, and the lot collected near Warm Creek, San Bernardino County on February 6, 1933, included one ovigerous female. This suggests that *Syncaris pasadenae*, like its northern congener, had a winter breeding season.

Table 1. Collections of *Syncaris pasadenae* (KINGSLEY) in the U.S. National Museum

Locality	Date	Coll.	Specimens	Remarks
San Diego, Calif.	ca. 1895	(C. R. ORCUTT)	1♂ 9♀	Cotypes <i>S. pasadenae</i>
Pasadena, Calif.		(J. S. KINGSLEY)	1♂ 2♀ (1 ovig.)	
San Gabriel, Los Angeles Co.	(ca. 1900)	N. C. TREW	4♀ (1 ovig.)	Cotypes <i>S. trewi</i> HOLMES
Los Angeles River	Mar. 13 & June 1925	H. R. HILL	22♂ 19♀ (2 ovig.)	
Los Angeles River	Apr. 11, 1929	K. & M.	1♂	
Warm Creek, San Bernardino Co.	Febr. 6, 1933	A. E. BERGH- DUFF	24♂ 8♀ (1 ovig.)	

4. Notes on the salinity tolerance of *Syncaris pacifica*

The erratic distribution of *Syncaris pacifica* in a few small streams in a comparatively small area, most of them flowing directly into the sea, raises the question whether these animals might possibly have spread from one stream to the other via the sea. To test this, some preliminary experiments were conducted. About one hundred specimens, including ovigerous females, were collected on December 20, 1950. The experiments are summarized in Table 2 and Figure 6.

For each experiment, 11 or 12 individuals, including several ovigerous females, were selected and placed in large finger bowls with 1,000 cc. of solution. Each bowl was aerated by means of a foam stone. Small sprigs of *Nitella* were placed in each bowl for food. Solutions were made of the original water from Salmon Creek and the supply of Pacific Ocean sea water (of about 33–34‰, as follows: 10%, 25%, 50%, 75%, 100%, and control). Attempts were made to prolong the survival in 75 and 100% sea water by moving animals up from 50% after about a day. Since the exact time of mortality was not always recorded, the results are best interpreted in terms of survival, and the accompanying table of data indicates, therefore, the number of experimental animals remaining alive at the time the mortalities were recorded.

No mortalities occurred in the controls, the reserve stock, or in dilutions of 10, 25, and 50% sea water for the duration of the experiment (about 13 days,

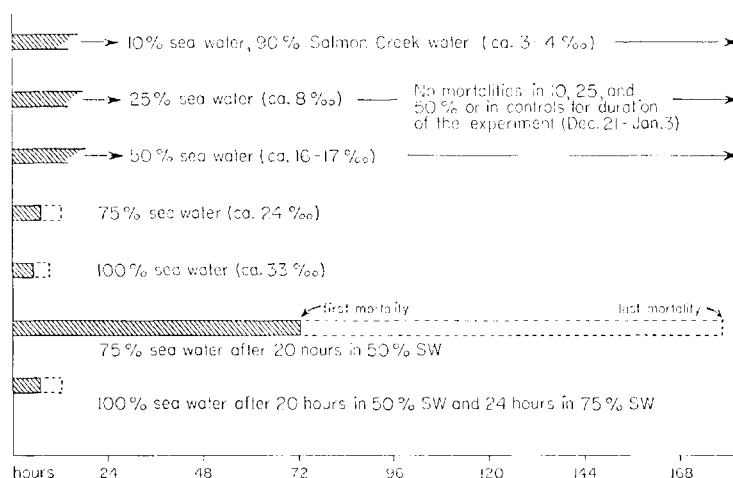
Syncaris pacifica - salinity tolerance

Fig. 6. Tolerance to various salinity concentrations by *Syncaris pacifica*

from December 21 to January 3). When subjected to a 75% solution of sea water (a salinity of about 24‰), the shrimp began to die after seven hours and were all dead within 12 hours. In undiluted sea water, the shrimp did not survive more than 9 hours. A group of 7 shrimp was removed from the 50% dilution after 20 hours and placed in a 75% solution of sea water. All the shrimp survived 71 hours before any mortality occurred, and the last specimen died 178 hours after the start of this experiment. An attempt was made to acclimatize five specimens to undiluted sea water by moving them from 50 to 75% after 20 hours, and on to 100% after 24 hours in 75%. All five specimens survived 7 hours, but all were dead within 13 hours after their introduction to undiluted sea water. After ten days six specimens in 50% sea water were returned to their original medium. One of these died after 15 hours, but the rest were still alive when returned to the stock tank.

In all experiments involving solutions up through 50%, feeding and molting activities appeared to be normal, and several shrimp in the experimental dishes moulted without apparent ill effects. In the 75 and 100% solutions, the shrimp soon began to turn opaque, and clung to the aerator. No feeding was observed in these higher solutions.

There appears to be a differential mortality, since the ovigerous females usually died first. Two ovigerous females were kept for the duration of the experiment in a small finger bowl in an effort to hatch the larvae, without apparent ill effects, which would appear to indicate that under natural conditions the ovigerous females are at least as hardy as the rest of the population.

Although this can only be considered a preliminary experiment, it is in substantial agreement with similar investigations by EDMONDSON (1929) of *Atya bisulcata* in Hawaii. EDMONDSON found that the Hawaiian species survived in 10% sea water mixture with regular moulting and regeneration of lost parts for an indefinite period. In a 25% solution, adults lived as long as five months

Table 2. Salinity tolerance of *Syneoris pacifica*.
(Numbers indicate mortalities recorded at times indicated)

No. of spec. at start	Control (Stream water)	Percent of sea water mixed with native stream water						100% from 75
		100%	25%	50%	75%	100%	75% from 50	
	10	11	12	12	8	11	5	5
	1 p. m. Dec. 21 — Jan. 3	12 Noon — no mortality	11 a. m. Dec. 21 — noon Jan. 3	- no mortality	11 a. m. Dec. 21 — noon Jan. 3	- no mortality	11 a. m. Dec. 21 — noon Jan. 3	- no mortality
5 15					2 (1 ov, ♀)	2 (1 ov, ♀)		
5 45					1 ov, ♀	1 ov, ♀		
6 07					2 (1 ov, ♀)	2 (1 ov, ♀)		
6 20					1 ov, ♀	1 ov, ♀		all alive
6 40					2	2		?
7 00					1	1		
7 15					1	1		
7 35					2 (1 ov, ♀)	2 (1 ov, ♀)		
8 00					1	1		
9 10					2 ov, ♀	2 (1 ov, ♀)		
10 50					2 (1 ov, ♀)	2		
12 00								X
12 25					2			
15								
71							1 ov, ♀	
97 30							1	
118 30							2	
166							1	
178							1	

and eggs developed normally. In the 50% mixture, the shrimp survived from 40 to 188 days. All the animals died within 5 days in 75% sea water, and within 12 hours in undiluted sea water. My experiments suggest that *Syncaris pacifica* may be even less tolerant of sea water than the Hawaiian forms. This is supported by field observations of avoidance of the brackish water reaches of Salmon Creek by *Syncaris pacifica*. If this loss of ability to adjust itself to sea water antedates the various changes in the drainage system which have occurred in California in Pleistocene times, it would mean that inland drainage changes are the only means of dispersal for this species from one stream to another. However, it is also possible that during rare periods of very excessive rainfall the shrimp might move from the mouth of one stream to another in overlying fresh water on the surface. This might have been a possible method of dispersal from one stream to another flowing into Tomales Bay, yet at the present time the shrimp have not been found in Walker Creek near the mouth of Tomales Bay, although they are in Papermill Creek at the upper end of Tomales Bay. Possibly they have been extirpated from Walker Creek by other causes in recent years. In any event, they were not observed by JONES (1962) in his study of the lower reaches of Walker Creek, and were not collected at any time in the last 20 years in the upper parts of the stream. In the recent past this area has been subject to heavy erosion, especially during the late 1870's and 1800's, when so much topsoil was lost from the area that Walker Creek became shoaled at the mouth and agricultural practice changed from potato growing to dairy farming (see DICKINSON, 1967 for various accounts of heavy rains that periodically interrupted rail service in the area).

In recent years the streams draining into the northern part of San Francisco Bay have been invaded by an oriental palaemonid, *Palaemon macrodactylus* (NEWMAN, 1963). The history of this species in California is in striking contrast to that of the native *Syncaris pacifica*. Whereas the atyid is a restricted species that cannot tolerate salinities above 24‰, the palaemonid can live in sea water and can also adjust to almost fresh water conditions. As a consequence, it is actively invading the lower salinity areas of the San Francisco Bay drainage. It would appear unlikely, however, that the species will establish large populations in strictly fresh water. It is to be hoped that no one helps it over the hills into the streams now inhabited by *Syncaris pacifica*.

When he was collecting fresh water biota in the area in 1949, Dr. JAMES E. LYNCH found one palaemonid shrimp in Lagunitas Creek. Unfortunately he dissected the specimen before realizing what it was. Repeated collections in this stream have failed to turn up any palaemonid shrimp, and Dr. LYNCH's specimen remains a mystery.

For that matter, *Palaemonetes hiltoni*, described from San Pedro, Los Angeles County, and once collected in Del Mar Slough, San Diego County, does not seem to have been found in recent years (HOLTHUIS, 1952). It is a possibly estuarine species.

5. Geological events in the range of *Syncaris pacifica*

The area in which *Syncaris pacifica* now occurs is one of complex geological history, and has been the subject of several studies (see especially DICKERSON, 1922; WEAVER, 1949; HIGGINS, 1952; DAETWYLER, 1966). The main events

with reference to the survival of a fresh water species such as *Syncaris pacifica* may be summarized roughly as follows (Figure 7): During Pliocene times there was a broad transgression of the sea inland to the present sites of Sebastopol and Petaluma, along the western edge of the Santa Rosa valley. Possibly this transgression was continuous to San Francisco Bay. There is, however, no good

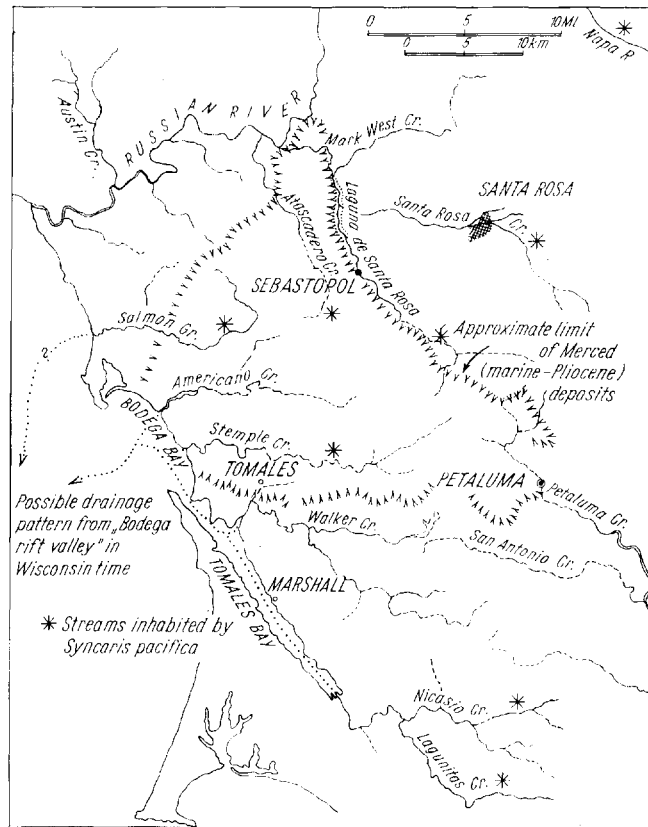


Fig. 7. Geological events in the range of *Syncaris pacifica* (from HIGGINS, 1952, and DAETWYLER, 1966)

evidence that the Russian River flowed southward into San Francisco Bay, although the lowland terrain between Santa Rosa and Petaluma would suggest such a route. According to HIGGINS (1952), F. A. JOHNSON, 1934, not seen, postulated a lagoon, possibly fresh water, along the eastern margin of the Merced transgression. Higgins finds no evidence for this. In any event, during Merced times *Syncaris pacifica* would have had to live considerably eastward of its present range, in the area of the present highlands east of Santa Rosa. If the species did indeed exist at that time, this might account for its present isolated occurrence in the Napa River. All this area has undergone volcanic action many times, including both Pliocene and Pleistocene.

As sea level fell during the Pleistocene, new drainage patterns were established to the west. DAETWYLER (1966) suggests that during Wisconsin time there was a subaerial rift valley at the present site of Tomales and Bodega Bays, and that there may have been a major stream channel seaward between the present headlands of Tomales Point and Bodega Head (Figure 7). Possibly there was at this time an area of rolling hills and lowland streams to the west, draining into the Bodega submarine canyon, about twenty miles west of Bodega Bay. Subsequent eustatic rise of sea level would produce the present pattern of small separated streams and account for the present separated populations of *Syncaris pacifica*.

In any event, it would appear that the vicissitudes of geological changes have been less inimical than the activities of man to the persistence of comparatively small populations of atyid shrimp in California streams. Drainage patterns have been altered and streams obliterated in southern California to such an extent that *Syncaris pasadenae* can be found no more. Some of the plans proposed for streams and valleys in the home range of *Syncaris pacifica* may be just as fatal to this species. From time to time it has been proposed, for example, to utilize the course of Salmon Creek as the route for a sewer line to drain the Santa Rosa urban area. This would possibly involve converting parts of the stream into a large culvert, and certainly would mean disruptive construction work that would interfere with the continuity of the environment. Highway widening, which sometimes involves coffer dams while work is carried on in the stream bed, could extirpate populations in a stream which in some years has almost no flowing water in it. One can only hope that various schemes that have been discussed prove to be too impractical or expensive and that we will have found more sensible ways of handling the wastes of our civilization than destroying our own environment with them.

Acknowledgements

I am indebted to many who over the years have helped me in the pursuit of *Syncaris* in various parts of California. Dr. CADET HAND and I sought out many dry arroyos in San Diego County in 1951–52, and later Dr. J. G. YALDWYN visited streams and the remains of streams in the Los Angeles basin to verify my previous negative findings. I wish to thank Dr. FENNER A. CHACE for providing the information from the collections of the U. S. National Museum. I also wish to thank Dr. RALPH I. SMITH for assistance in preparing some of the illustrations (which were done by Mrs. EMILY REID at the Department of Zoology at Berkeley), and Mr. JOHN BORN for access to his paper. I am also indebted to a number of persons whose names I have forgotten who sent me on interesting wild goose chases because of the popular use of the term “shrimp” for gammarid amphipods.

6. Summary

1. *Syncaris pacifica* (HOLMES) occurs as several separated populations in certain small lowland streams in Marin, Sonoma and Napa counties, California.
2. The reproductive season of *S. pacifica* is in winter; it is thought that this represents an adaptation to the hydrologic cycle since the young are hatched during the more favorable part of the year.
3. *Syncaris pasadenae* KINGSLEY was known to occur in several streams in the Los Angeles Basin, but has not been collected since 1933, and is presumed to be extinct.

4. *Syncaris pacifica* shows limited powers of adjustment to increased salinity, but cannot survive exposure to salinities of about 24‰; this suggests that the species cannot have achieved its present distribution in separated streams by migration from one stream to the other via the sea.
5. The area in which *Syncaris pacifica* presently lives was transgressed by the sea in the Pliocene and probably to a more limited extent in post Wisconsin time.
6. Present and proposed activities of man endanger the survival of *Syncaris pacifica*.

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