

G. BAKUS

ON THE INTRODUCTION OF AN EDIBLE ORIENTAL SHRIMP J. Martin (CARIDEA, PALAEMONIDAE) TO SAN FRANCISCO BAY

E king contra hast

BY

WILLIAM A. NEWMAN Department of Zoology, University of California, Berkeley, U.S.A.

Reprinted from: CRUSTACEANA, Vol. 5, Part 2, 1963



LEIDEN E. J. BRILL

Life Theme contra

ON THE INTRODUCTION OF AN EDIBLE ORIENTAL SHRIMP (CARIDEA, PALAEMONIDAE) TO SAN FRANCISCO BAY ¹)

BY

WILLIAM A. NEWMAN²) Department of Zoology, University of California, Berkeley, U.S.A.

The introduction of a new organism is usually watched with some apprehension, whether it has been introduced intentionally or by chance, for one cannot predict the outcome. It is generally held that the chance introduction of an organism to an established situation, like a genetic mutation, is rarely indifferent, rarely good, and usually bad. Although good or bad may not be measurable in terms of human or natural economy, it is inescapable that any introduction will have an effect on an established ecosystem, and that when an introduction occurs it should be recognized, identified and followed.

San Francisco Bay, as other estuarine systems (Hedgpeth, 1957), supports a relatively restricted fauna in terms of numbers of species. Partially responsible for this is the fact that estuaries in general are unfavorable for most truly marine littoral organisms with regard to temperature, salinity and the diversity of habitats available. Those animals that do tolerate the rigors of the physical environment escape to a large extent the high interspecific competition of the marine situation. On the other hand, the isolation of great estuaries from one another, and their relatively short existence in terms of geological time, prevents their full and efficient biological exploitation, and occupancy of very broad habitats by a few species is ordinarily maintained.

The advent of man and his fisheries and shipping activities has provided species a means of transport from one distant locality to another, and introductions are not infrequent (Elton, 1958). Any introduced species is, in effect, a mutation in a community, for it not only comes into interplay with an already established ecosystem, but is a new part of it, and one can expect a shift to occur to accommodate the newcomer. The introduced form may utilize situations not already fully exploited by native forms, but if it is somewhat better adapted to a particular portion of a broad habitat already occupied by an established species, it may usurp that portion to the detriment of the original holder. Unless such events are studied while they are taking place, it is unlikely that we will ever know how things progressed, much being lost to our knowledge and to our ability to predict the course of events should comparable introductions be made elsewhere.

¹) This investigation was supported, in part, by a research fellowship (GF-12,150) from the Division of General Medical Sciences, Public Health Service.

²) Present address: Department of Oceanography, Scripps Institution, La Jolla, California, U.S.A.

It is the purpose of this note to record the recent introduction of a sizable caridean shrimp to San Francisco Bay. Although its presence has been recognized for a number of years, knowledge of its place of origin and of literature pertaining to it, awaited the determination of its scientific name. This determination has been made, and, having been adequately confirmed, is reported here. The shrimp belongs to the subgenus *Palaemon* s.str. of the genus *Palaemon* Weber, 1795 (family Palaemonidae).

Palaemon (Palaemon) macrodactylus Rathbun, 1902

Palaemon macrodactylus Rathbun, 1902: 52, fig. 24; Balss, 1924: 50; Holthuis 1950: 7. Leander macrodactylus, Parisi, 1919: 76; Kemp, 1925: 291; Kubo, 1942: 36, figs. 7-9, 19 D, O,

20D, 21D, 22D, 23 D, K, 24D, O, 25 D, D', 26 D, Q, 27D, 28C, L, 29D, 30. Leander serrifer longidactylus Yu, 1930: 570, fig. 4. non Leander macrodactylus, Yoshida, 1941: 26, pl. 6 fig. 4 (= Paelaemon gravieri (Yu)).

Description (female). - Supra-orbital, sub-orbital and hepatic spines absent; branchiostegal and antennal spines present; mandible with 3-segmented palp; eyes distinctly pigmented, with two horizontal bands, ocellus present; anterior margin of basal segment of antennular peduncle rounded, anterolateral spine small; propodus of fifth pereiopod with transverse rows of setae along distal part of posterior margin. Rostrum about one tenth longer than antennal scale (scaphocerite), equal to or slightly shorter than length of carapace, approximately four times as long as high, strengthened on each side by a rounded keel, superior margin with 9 to 15, usually 10 to 12 teeth (excluding sub-apical tooth), three or occasionally four teeth on carapace behind posterior margin of orbit, the most posterior being somewhat removed from the others; inferior margin supporting 3 to 5, usually 4, teeth, and a double row of setae (fig. 1 A). Antennular peduncle somewhat shorter than scaphocerite, longer than antennal peduncle by slightly more than two segments; second and third peduncular segments equal in length; rami of upper flagellum fused by 5 to 9 articles, shorter ramus of 20 to 31 articles. Length of scaphocerite to width 1/0.31 (fig. 1 G). Third maxilliped longer than antennal peduncle by one half to entire length of terminal segment. First leg longer than scaphocerite by one half to entire length of the finger; carpus to chela 1/0.56, carpus to merus 1/0.9, palm to finger 1/0.8. Second leg longer than scaphocerite by chela and as much as one half of carpus; carpus to merus 1/1, carpus to chela 1/1.2; proximal margin of cutting edge of movable finger with two rounded teeth apposing a single tooth on the immovable finger (fig. 1 H). Posterior margin of propodus of third leg armed with 5 to 8 setae (fig. 1 F). Third, fourth and fifth legs reaching forward equally. Fifth leg reaching beyond scaphocerite by two thirds to entire length of dactyl, dactyl to propodus 1/3.3; distal rows of setae on propodus strongly serrate. Dactyl of third leg to propodus 1/2.4. Anterior pair of dorsolateral spines placed at middle of telson, posterior pair inserted about one half distance between anterior pair and tip. Telson terminating in a short, strong median spine, a pair of short lateral spines, a pair of long, strong mediolateral spines and a median pair of

longer, thin, plumose setae which have two pairs of short thin setae at their bases (fig. 1 C).

Sexual dimorphism. - The first and second pleopodal endites, and the appendix

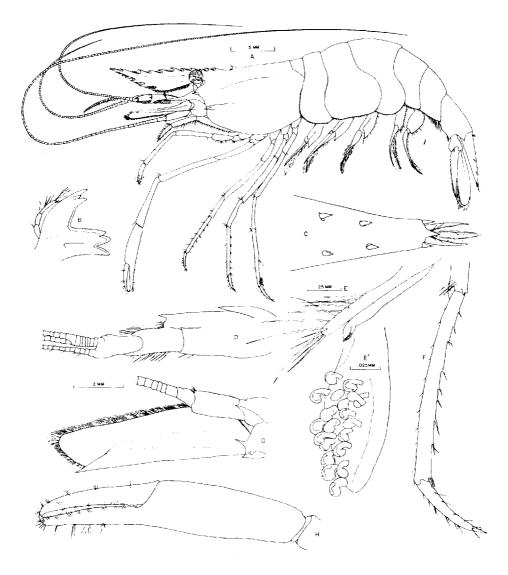


Fig. 1. Palaemon macrodactylus Rathbun from San Francisco Bay. A, ovigerous female (eggs not figured); B, mandible; C, telson; D, antennular peduncle; E, appendices interna and masculina; E', coupling hooks of appendix interna; F, dactyl and propodus of third pereiopod; G, scaphocerite and antennal peduncle; H, chela of second pereiopod. B-D, F-H, female appendages, to same scale; E, E', from second pleopod of same male.

masculina on the latter (fig. 1 E) are described by Kubo (1942). These readily separate the sexes and are considered as primary sexual characteristics here. Second-

ary or other sex limited characteristics have not been described for this species, yet in the San Francisco Bay form, the two sexes are markedly different in a number of ways as tabulated below:

| | Males | Females |
|--|--|---|
| color in alcohol | usually white to yellow | usually pale yellowish- orange to salmon red |
| first pereiopod | equal to or a bit shorter than scaphocerite | longer than scaphocerite by 1/2 to entire length of finger |
| rostrum/carapace | equal to or usually longer (1/0.89) | equal to or usually shorter (1/1.05) |
| carapace | appears relatively slender | appears relatively stout |
| (length/height) antennular peduncle | (1/0.74) | (1/0.8) |
| (2nd/3rd article) | 1/2 | 1/1 |

Living material of Palaemon macrodactylus from San Francisco Bay is generally translucent or nearly transparent without conspicuous markings or color pattern, although the tail fan and antennary area have a reddish hue. However, material collected from Palo Alto Yacht Harbor contained several unusual specimens appearing dark green or olive drab. These proved to be remarkably beautiful, variegated non-ovigerous females. Closely spaced chromatophores of the cardiac, gastric, hepatic and antennal regions of the carapace, and the abdomen, ranged from dark green through olive drab to brown, except for a median dorsal light stripe of more scattered orange chromatophores. The branchial region had a vermiculated pattern similar to that seen in P. serrifer (Stimpson, 1860) the linear markings being composed of orange chromatophores; this same color outlined the posterior and lateral margins of the abdominal segments. Distal portions of the telson and pleopods were bright red as were the proximal portions of both pairs of antennary flagella and the setose margin of the scaphocerite. The remainder of the scaphocerite, both antennary peduncles and the eye stalks were colored green by well-spaced chromatophores. The finger tips of the second chelipeds were white, followed by reddish-brown to the joint of the movable finger. At this point, a white band circumscribed the entire chela, while the palm was slate or greenishgray. The basis for this intense coloration was not apparent. In that so few have been observed to be in this condition one supposes it may be fright or courtship coloration rather than a general response to the environment.

Size. — Rathbun (1902) gives measurements for a female 55 mm in length. Kubo's (1942) measurements are 21.4 to 30.2 mm for males and 18.8 to 38.2 mm for females. Data from San Francisco Bay specimens are given below. The local form falls within the range known for females of *P. macrodactylus*, but certain males are remarkably large, one specimen being nearly as large as the largest female observed. From Kubo's data, *P. gravieri* (Yu, 1930) has somewhat larger females, while *P. serrifer* would appear to be a somewhat smaller species, although Kubo had relatively few individuals to study.

In the following tabulation is given the length of 135 specimens from Aquatic Park and Corte Madera Creek, collected in 1960 and 1961, and (in parentheses) of 26 specimens from Montezuma Slough, Suisun Bay collected June, 1961. Measurements are in millimeters, taken from the tip of the rostrum to the tip of the telson.

| Condition and sex | Range | Mean | Number |
|-----------------------|---------|--------|--------|
| ovigerous females | 31-51 | 38.6 | 37 |
| (ovigerous females) | (40-49) | (44.5) | (6) |
| non-ovigerous females | 18-53 | 30.8 | 50 |
| males | 18-40 | 33.6 | 48 |
| (males) | (35-51) | (41.0) | (20) |

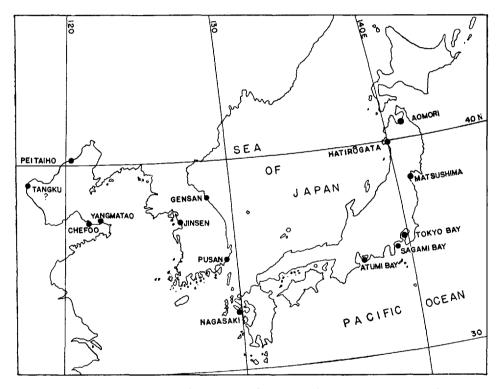


Fig. 2. Localities reported for Palaemon macrodactylus Rathbun in China, Korea, and Japan.

Although males from Aquatic Park are smaller than females, attaining but four-fifths their length, there is a substantial over-lap in size with ovigerous females. However, the males from Montezuma Slough are remarkable for their large size. Females apparently become reproductive when about 30 mm in length as deduced from the first occurrence of an ovigerous condition. The size at which reproductive activity begins in males was not determined.

Distribution. — Locality records from the Orient indicate that *Palaemon macrodactylus* is widely distributed in Japan, Korea and the north coast of China (fig. 2). The following localities have been given by the authors indicated. Aomori, Matsushima, Nagasaki, Fusan (= Pusan), Gensan (= Yuensan), Chemulop (= Jinsen) — Rathbun, 1902; Sagami Bay — Parisi, 1919; Yangmatoa (= Yangmatao?), Peitaiho, Tangkou (= Tangku), Chefoo — Yu, 1930; Tokyo Bay, Atumi (= Atsumi) Bay — Kubo, 1942. Yu's Yangmatoa could only be located as Yangmatao.

As far as it is known on the west coast of North America, *P. macrodactylus* occurs only in San Francisco Bay (fig. 3). It is therefore the northernmost representative of the subgenus on this coast, being separated from *P. ritteri* Holmes, 1895, in the south by some 500 miles. However, one might expect *P. macrodactylus* eventually to become distributed southward and perhaps somewhat northward, and also to appear in such places as Hawaii, if it has not already done so.

Taxonomic considerations. — A comparison of the San Francisco Bay Palaemon with five syntypes of Palaemon macrodactylus Rathbun (U.S.N.M. Cat. No. 26162) has been made. For the Bay form a series included six females and one male for forty-three linear characters, and nine females and ten males for four meristic characters. In addition, one hundred and fifty specimens, mostly from Aquatic Park, Berkeley, ranging in size from 18 to 53 mm were inspected, sexed and measured. No particular differences between these samples and the syntypes of *P. macrodactylus* were noted. Because the Bay form is quite distinct from the known American members of the subgenus (cf. Holthuis, 1952) and because it can be readily assigned to a known Oriental species, there is little question that it has been introduced from the Orient. Dr. Fenner A. Chace, Jr. has been consulted regarding the determination and Dr. L. B. Holthuis, working independently on material sent him by the State of California Department of Fish and Game, has arrived at the same conclusion.

The present species can be distinguished from other central California intertidal Caridea given in Light et al. (1957) by modifying their key (: 176) and adding the eleventh and twelfth dichotomies, as indicated below:

| Delete: 6. Carpus of 2d legs not annulated, in fresh water |
|---|
| Read: 6. Carpus of 2d legs not annulated |
| Add: 11. Upper margin of rostrum with 1-2 teeth; supra-orbital spine present (fresh water) |
| Syncaris pacifica (Holmes) |
| 11. Upper margin of rostrum with at least 8 teeth; supra-orbital spine absent (marine or |
| brackish water) |
| 12. Rostral teeth $\frac{8-10}{3-4}$, two teeth behind orbit, no sub-apical teeth; branchiostegal spine |
| originating on anterior margin of carapace Palaemon ritteri Holmes |
| 12. Rostral teeth $\frac{9-15}{3-5}$, at least three reeth behind orbit, sub-apical teeth usually present; |
| branchiostegal spine originating behind anterior margin of carapace |
| Palaemon macrodactylus Rathbun |

Palaemon macrodactylus is presently known to have a relatively restricted geographical distribution in the Orient. However, it is quite similar in general appearance to the widely distributed Indo-West Pacific species *P. serrifer* (Stimpson). It seems quite possible, due to confusion between the two, or due to our general lack of records, that *P. macrodactylus* is more widely distributed than now supposed. Kubo (1942 : 41) gives five characters by which these two species can be separated. In addition, *P. macrodactylus* can be distinguished from *P. serrifer* by the double rather than single row of setae along the inferior margin of the rostrum, by the origin of the branchiostegal spine behind rather than on the anterior margin of the carapace and by the general lack of a distinctive color pattern in vivo.

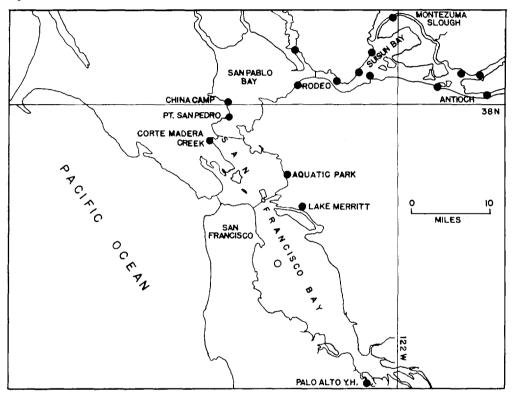


Fig. 3. Localities reported for *Palaemon macrodactylus* Rathbun in San Francisco Bay, California. The open circle in South San Francisco Bay represents a collection made in December 1961 in which only *Crangon nigricauda* Stimpson and *Heptacarpus stimpsoni* Holthuis (= Spirontocaris cristata (Stimpson)) were taken.

Palaemon macrodactylus is also similar to P. gravieri (Yu, 1930) which, although not found in Japan has a relatively restricted but comparable distribution in the Orient. Kubo (1942 : 50) gives five characters by which these two forms can be separated. In addition, females of P. macrodactylus can be distinguished from P. gravieri by the antennular peduncle being subequal to, rather than one half the length of the scaphocerite, by the terminal antennular segment being equal to rather than twice the length of the second segment, by the first leg exceeding the scaphocerite by as much as the entire length of the dactyl rather than being just equal, by the branchiostegal spine originating well above rather than near the antero-lateral angle of the carapace, and by the translucent white rather than uniformly red color in vivo.

It will be observed that *P. macrodactylus* cannot be keyed out in Kemp (1925). The original description states that the carpus of the second leg exceeds the manus in length. Kemp apparently interpreted manus, as used here by Rathbun, to be equivalent to chela. In all of the material examined, including the syntypes available to me, the chela exceeds the carpus in length. This fact, and the confusion of terms, probably accounts for the difficulty in Kemp's key. Kemp (1925 : 291) utilized Rathbun's original description (1902 : 52) in order to include P. macrodactylus in his key under dichotomy D, which reads: "Carpus of second leg longer than chela". P. macrodactylus can only be placed under this dichotomy by inference because there are some difficulties in interpretation of the original description. Rathbun (1902 : 52) states, for the first leg: "... the carpus is one and two-thirds as long as the chela; the palm is a little longer than the fingers...", and for the second leg: "The carpus... exceeds the manus in length... Palm..., longer than fingers". These two constructions appear essentially parallel and lead one to conclude that chela is equivalent anatomically to manus, and is composed of palm and fingers. This interpretation is apparently that of Kemp, and it gains some support from the fact that manus is Latin for hand. On page 50 in the same paper, but for another species, Rathbun says, "...the carpus... (is) longer than the palm of the hand; the fingers longer than the palm". Certainly Rathbun intended hand to be equivalent to chela here. The construction of this description is basically parallel to those given above. It would appear then that three terms (chela, manus, and hand) refer to the same anatomical structure, and that this structure is divided into palm and fingers. However, it seems that in 1902 Rathbun had not settled on strict definitions for the anatomical features concerned here, and in 1902 she may have meant manus to equal palm rather than chela: sixteen years later (1918) she does consider manus and hand to be synonymous with palm rather than chela. Therefore, on the basis of her 1918 terminology, the descriptions of 1902 quoted above become confused and no firm interpretation of what was meant can be made. In any event, the carpus of the second leg in P. macrodactylus is shorter than the chela, rather than longer, and this accounts for the difficulty in Kemp's key.

It will also be observed that males of P. macrodactylus cannot be keyed out in Kubo (1942), or at least this is true of the San Francisco Bay form. In males examined, the rostrum exceeds the carapace in length, while it does not in females, and Kubo relies on the rostrum-carapace ratio in his key.

Biological considerations. — Incidental to the taxonomic aspects of this study, some observations on the biology of *Palaemon macrodactylus* were made. Some of these may be of general interest and some suggest how the shrimp was introduced into San Francisco Bay.

Although there is no existing estimate on what part of the dwindling commercial shrimp catch is made up by *P. macrodactylus*, it does occur with *Crangon* spp. in the middle and upper reaches of the Bay. In aquaria these two forms behave quite differently. While *Crangon* tends to bury itself in a soft substratum during daylight hours, *Palaemon* does not, but prefers rather to hide in spaces between large pieces of rubble or to nestle in depressions. Although *Palaemon* occurs with *Crangon* in fishing areas covered by open water, it is taken alone in protected harbors, ponds and tidal creeks around the Bay; frequently being found in old tires, tin cans and other artificial shelters as well as on pilings, walls and among rocks or calcareous tubes of *Mercierella*. One is impressed by the fact that, although the two shrimps do occur together, *Palaemon* also occupies environmental situations not utilized by the native forms. It is of interest that the same is true of many other introduced organisms; for instance, a number of arthropods and molluscs, that have been introduced over the years, are observed to over-lap existing populations but they also occupy habitats not originally held by the native species.

The estuarine distribution of Palaemon macrodactylus indicates that it is adapted to wide variations in salinity and temperature. This is readily borne out in the laboratory. Adults can be maintained in normal or dilute sea water at temperatures ranging from 14 to 26° C for indefinite periods of time. Ovigerous females in aquaria at room temperature feed readily on bits of fish and occasionally there is cannibalism if many are kept together. Such females have hatched zoea larvae on a number of occasions and in one instance an attempt was made to rear them. The zoeae were transplanted to finger bowls with sea water kept at room temperature without aeration. Initial losses were high. This may have been partially due to crowding and a heavy protozoan infection, and perhaps to factors tending to select for a "laboratory type", but it was also probably due to the slowness of getting brine shrimp (Artemia) cultures going to be supplied as food. In approximately two weeks after hatching, the nine larvae remaining in one finger bowl, having been fed exclusively on Artemia up to three days old, had metamorphosed into juvenile shrimp resembling the adults. No attempts were made to note the number of moults or changes in form during this period although the material lent itself to this sort of study. Although cannibalism was not observed among the developing larvae, it was evident among the young shrimp. By the end of the third week, six were left, and by the end of the ninth week, of the three remaining specimens, the largest measured 16 mm in length. At this size, not only could they feed on freshly hatched Artemia but on full grown Artemia as well. It should be mentioned that although some attention was paid to the rearing of these shrimp, they endured relatively poor conditions: no aeration, occasional missed feedings, wide temperature fluctuations, some increased salinity due to evaporation, and infrequent water changes. Indeed this is a very hardy species, a fact that makes it a valuable laboratory animal and probably attributes in part to its successful introduction.

Although the habitat of the present form is not strictly specified in the systematic literature, *Palaemon macrodactylus* is clearly a marine organism like most other

species of the subgenus. It would seem clear from its distribution in San Francisco Bay and from its behavior in the laboratory that it is, more specifically, an estuarine form. Its occurrence and abundance in warm shallow areas in the Bay such as Aquatic Park and Lake Merritt, along with such equally tolerant forms as the barnacle *Balanus amphitrite denticulata* Broch and the tube worm *Mercierella enigmatica* Fauvel, as well as in cooler more marine- and estuarine-dominated situations, demonstrates very broad ecological tolerances quite typical of estuarine organisms in general.

Mode of introduction. — The methods currently utilized in the commercial transport of oysters from Japan, where spat on shells in lattice crates are simply hosed down daily while in transit, do not seem adequate to transport such shrimp across the Pacific. A mollusc, crab or barnacle might survive since many of these are adapted to short or even extended periods of exposure, but not a shrimp of this fragile physical nature, which, like most fish, is normally always submerged and is not only utterly helpless but perishes shortly when out of water. Transport by a heavily fouled ship seems more likely because the shrimp is strictly a subtidal form. But then it seems improbable that a natant organism, one that tends to swim, would be transported great distances across the open ocean on the bottom of a fast moving vessel, for in the event it should happen to swim free, it would surely be left behind to be lost at sea.

If it seems unlikely that the shrimp arrived with oyster spat or that it clung to the bottom of a vessel, how could it have been transported? This we will never know definitely, but an incident of some years ago suggests a way that a chance introduction of this sort could have occurred.

In 1954 I was retained as a consultant by a company engaged in cleaning out the sea water system of a naval vessel docked at Alameda, California. The system had become fouled at some undetermined port in the Orient. My job was to identify the fouling organisms. Unfortunately the system had been partially treated at Alameda and only the hard parts of the organisms remained. These lined the entire interior surfaces of the large pipes in a layer an inch and a half thick, reducing the bore to about two or two and a half inches. The remains were identified as calcareous tubes of a worm comparable to *Mercierella enigmatica* Fauvel and the shells of the barnacle *Balanus amphitrite denticulata* Broch.

According to Utinomi (1960), this same barnacle has been introduced to Japan and to San Francisco Bay by ship, and it is an interesting coincidence that the barnacle, the tube worm *Mercierella* and *Palaemon macrodactylus* are found intimately associated at Aquatic Park, Berkeley, and Lake Merritt which connects with the Oakland-Alameda Estuary. Such evidence surely suggests a means by which *Palaemon* could have arrived from the Orient, for in a sea water system, normally protected by screens, large or sessile organisms can arrive or leave only as larvae. This eliminates the problem of a swimming organism, such as the shrimp, of being lost at sea. Also, it is likely that such a system that has become fouled, in a fast traveling vessel, would be expected to transport sorts of organisms that would otherwise not make the trip on a ship's outer skin, and that some of these would be introduced to new localities where favorable conditions were met. If such special conditions are necessary, we have gained some insight as to why such an introduction has been long delayed, for such sea water systems are not ordinarily allowed to become fouled, that is, they are turned off while in port and perhaps even filled with fresh water. This substantially reduces the probability of the appropriate sequence of events taking place, even though ships have long traversed the Pacific between the Orient and California.

Time of introduction. — Palaemon macrodactylus first came to our attention through Dr. R. Bacigalupi of the Jepson Herbarium who was questioned about its identity by a local shrimp fisherman in the fall of 1957. The fisherman, Mr. E. Wetton, who is also the proprietor of the "Shrimp Shack", Berkeley, has informed me that he first noticed the shrimp in his local commercial catch about that time. The records of interest, both before and after the shrimp was first noticed are summarized below (the abbreviation S.F. stands for San Francisco, p.c. for personal communication, and u.m. for unpublished manuscript data):

| Time | Source | Region explored Palae | mon macrodactylus |
|-----------|--|--|-------------------|
| 1912-1913 | Schmitt (1921) | entire S. F. Bay | not recorded |
| 1950-1958 | H. K. Chadwick (p.c.) | San Pablo Bay and Delta region | not recorded |
| 1952-1953 | E. S. Herald and K. F. Innes (u.m.) | Lower San Pablo, S.F., and South S. F. Bays | not recorded |
| 1953 | N. J. Marchette (u.m.) | Lake Merritt, Oakland | not recorded |
| 1957 | Light et al. (1957) | Central California | not recorded |
| 1957 | present report | North S. F. Bay | present |
| 1958 | H. Wright (p.c.) | Aquatic Park, Berkeley | present |
| 1959 | H. K. Chadwick (p.c.) | Lower San Pablo Bay | present |
| 1960 | present report | Corte Madera Creek, S. F. Bay | present |
| 1960-1961 | H. K. Chadwick (p.c.) | throughout Suisun Delta region | present |
| 1961 | H. Wright (p.c.) | Lake Merritt, Oakland | present |
| 1962 | present report | Palo Alto Yacht Harbor, South S. F. Bay | present |

It is a fact that *Palaemon macrodactylus* was present in San Francisco in the fall of 1957, yet there is no possible way of determining just when it was first introduced. Any estimate of the time of introduction can be only a guess, yet some guess seems better than none at all. Considering the available evidence, I would be inclined to consider the following sequence of events as most probable. Vessels, perhaps manned by relatively inexperienced personnel who allowed sea water systems to operate and become fouled while in Oriental harbors, carried the shrimp across the Pacific to California. Ships entering San Francisco Bay must have brought the shrimp in at least once, perhaps about 1954. This date is suggested because it seems highly unlikely to me that the shrimp could have been overlooked at Lake Merritt by Marchette in 1953, and essentially throughout the Bay, by Chadwick in 1950-58 and by Herald and Innes in 1952-53.

CRUSTACEANA, 5

Taking 1954 to be the best approximation of the time of introduction, there remain three years for the shrimp to become abundant enough to be taken in the commercial catch from San Francisco and San Pablo Bays late in 1957, when the form first came to our attention. From then on, the population, apparently well established, virtually exploded. The data of the State of California Department of Fish and Game as provided me by Mr. H. K. Chadwick apparently follow the rise of this explosion, from San Pablo Bay in 1959 and then throughout the Suisun Delta Region and up into the mouths of the San Joaquin and Sacramento Rivers in 1960-61.

The winters of 1955 and 1957 were particularly wet, while 1960 and 1961 have been drought years. We might suppose that heavy runoff of long duration impeded the riverward spread of *Palaemon*, while the recent dry periods have probably been favorable for it in the upper reaches of the system. This may account, at least in part, for the apparent delay between the time the form was first noticed and its appearance in the Delta Region.

Acknowledgments. — The presence of *Palaemon macrodactylus* Rathbun in San Francisco Bay was discovered by the commercial fisherman, Mr. E. Wetton of Berkeley. Mr. Wetton pointed specimens out to Dr. R. Bacigalupi of the Botany Department, University of California, Berkeley who in turn gave them to Dr. Cadet Hand of the Zoology Department. I am grateful to these people whose curiosity and interest led to the sequence of events that brought this exotic shrimp to my attention.

A great deal of credit and many thanks are due to Mr. Keith Ansell of Walnut Creek, who, while participating in a career exploration course under the sponsorship of Acalanes Union High School District, Lafayette, California, and the Engineering and Science Extension, University of California, Berkeley, collected and studied the yet unidentified shrimp, and in comparing it to descriptions in the literature provided him, concluded that it was closest to Rathbun's species from the Orient.

I would like to thank the Division of Marine Invertebrates, United States National Museum for the loan of syntypes of *P. macrodactylus* and specimens of the same form from Corte Madera Creek, Marin Co., California, collected by Mr. E. W. Kirschbaum. I am particularly grateful to Dr. Fenner A. Chace, Jr., for kindly looking over the systematic data after the determination had been made, for his encouragement during the course of the study and for consulting Dr. L. B. Holthuis of the Rijksmuseum van Natuurlijke Historie, Leiden about my studies on the Bay form. I am pleased to acknowledge the correspondence with Dr. Holthuis, in which he pointed out the similarity of the present form to *P. gravieri* (Yu) and which brought attention to the interesting sexual dimorphism in the former.

Dr. Earl Herald and Mr. Kenneth Innes of the Steinhart Aquarium, California Academy of Sciences, Mr. Allyn G. Smith of the Department of Invertebrate Zoology, C.A.S., and Mr. H. K. Chadwick of the State of California Department of Fish and Game kindly allowed me to examine specimens of their various collections, and provided data concerning the occurrence of shrimp in San Francisco Bay from which I have borrowed freely. Without their help a reasonable approximation of the time of introduction of *P. macrodactylus* to San Francisco Bay could not have been made.

I am pleased to acknowledge the help received from Dr. Chace and Mr. Chadwick who kindly consented to read and criticize the manuscript of this report. To Dr. R. I. Smith and Dr. Cadet Hand I am much indebted for their patience, advice, and criticism of the manuscript.

résumé

Une crevette orientale comestible, *Palaemon macrodactylus* Rathbun, est apparue récemment dans la baie de San Francisco, Californie. L'époque et la manière de son introduction ont été considérées. Depuis son apparition, cette espèce s'est largement répandue et est devenue abondante. Bien qu'on la trouve parfois dans des situations à dominance marine, elle semble être plus typiquement une forme d'estuaire, tendant à occuper des habitats inexploités auparavant par des espèces de crevettes indigènes.

Son succès considérable laisse supposer que non seulement elle continuera d'être un élément important de la faune du système d'estuaire de la baie de San Francisco, mais qu'elle se répandra probablement plus largement encore en Californie et ailleurs.

Les larves ainsi que les adultes de Palaemon macrodactylus sont extrêmement robustes et se soumettent aisément à la culture de laboratoire quand on leur fournit exclusivement des Artemia comme nourriture; elles seront sans doute très utiles pour les investigations physiologiques et ontogéniques.

LITERATURE CITED

- BALSS, HEINRICH, 1924. Ostasiatische Decapoden. V. Die Oxyrhynchen und Schlussteil. (Geographische Übersicht der Decapoden Japans). Arch. Naturgesch., 90 (A) (5): 20-84, text-figs. 1, 2, pl. 1.
- ELTON, CHARLES S., 1958. The ecology of invasions by animals and plants : 1-181, text-figs. 1-51, pls. 1-50. (Methuen & Co., London).
- HEDGPETH, JOEL W., 1957. Estuaries and lagoons. II. Biological aspects. In: JOEL W. HEDGPETH (ed.), Treatise of marine ecology and paleoecology. Volume I. Ecology. Geol. Soc. Amer. Mem., 67 (1): 693-729, figs. 12-30.
- HOLTHUIS, L. B., 1950. The Decapoda of the Siboga Expedition. Part X. The Palaemonidae collected by the Siboga and Snellius expeditions with remarks on other species. I. Subfamily Palaemoninae. Siboga Exped. Monogr., **39** (a9): 1-268, figs. 1-52.
- —, 1952. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. II. The subfamily Palaemoninae. Allan Hancock Found. Publ. Occ. Pap., 12: 1-396, text-fig. 1, pls. 1-55.
- KEMP, STANLEY, 1925. Notes on Crustacea Decapoda in the Indian Museum. XVII. On various Caridea. Rec. Indian Mus., 27 (4): 249-342, figs. 1-24.
- KUBO, ITUO, 1942. Studies on Japanese Palaemonoid Shrimps, III. Leander. Journ. Imp. Fish. Inst. Tokio, 35 (1): 17-85, figs. 1-33.
- LIGHT, S. F., R. I. SMITH, F. A. PITELKA, D. P. ABBOTT & F. M. WEESNER, 1957. Intertidal Invertebrates of the Central California Coast, (ed. 2): i-xiv, 1-446, figs. 1-138. (University of California Press, Berkeley).
- PARISI, BRUNO, 1919. I Decapodi giapponesi del Museo di Milano, VII. Natantia. Atti Soc. Ital. Sci. nat. Milano, 58: 59-99, text-figs. 1-8, pls. 3-6.

- RATHBUN, MARY J., 1902. Japanese stalk-eyed crustaceans. Proc. U. S. Nat. Mus., 26: 23-55, figs. 1-24.
- ----, 1918. The grapsoid crabs of America. Bull. U. S. Nat. Mus., 97: i-xxii, 1-461, text-figs. 1-172, pls. 1-161.
- SCHMITT, WALDO L., 1921. The marine decapod Crustacea of California. Univ. Calif. Publ. Zool., 23: 1-470, text-figs. 1-165, pls. 1-50.
- UTINOMI, HUZIO, 1960. On the world-wide dispersal of a Hawaiian barnacle, Balanus amphitrite hawaiiensis Broch. Pacif. Sci., 14 (1): 43-50, figs. 1-3.
- YOSHIDA, HIROSHI, 1941. Important marine shrimps and lobsters of Tyôsen (Korea). Bull. Fish. Exper. Sta. Gov.-Gen. Tyôsen, 7: 1-36, text-figs. 1-15, pls. 1-13. (In Japanese; not seen).
- YU, SHOU-CHIE, 1930. Note sur les crevettes chinoises appartenant au genre Leander Desm. avec description de nouvelles espèces. Bull. Soc. Zool. France, 55: 553-573, figs. 1-4.