Reproduction, Life History, and Larval Ecology of the California Xanthidae, the Pebble Crabs

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THIS STUDY is concerned with the reproduction, life history, and larval ecology of the California Xanthidae, the pebble crabs. The Brachyura of the west coast of North America are not well known with reference to their behavior and ecology. Because of its economic importance, the edible crab, *Cancer magister* Dana, has been made the subject of a series of studies by Weymouth (1917), Weymouth and MacKay (1934, 1936), and MacKay (1942). The only studies of economically unimportant species are those of Wells (1940) on the pinnotherid crabs of Puget Sound, and Hiatt (1948) on the lined shore crab, *Pachygrapsus crassipes* Randall. The latter study is concerned primarily with ecology and behavior, and its thoroughness makes it a pattern for similar studies. The present paper is the partial result of a study on the family Xanthidae made by the writer while at the Allan Hancock Foundation, University of Southern California. The writer is grateful to Dr. John S. Garth and Dr. Norman T. Mattox for their guidance in this work.

The xanthid crabs of California are common but seldom seen members of the lower intertidal-zone fauna, found along protected rocky beaches. Their superficial resemblance to beach pebbles and their ability to "play dead" make them an interesting group to study. Because of their similarity, the scope of this paper has been broadened to cover the four major species found locally, rather than just one species. Thus, *Lophopanopeus leucomanus leucomanus* (Lockington), *Lophopanopeus bellus diegensis* Rathbun, *Paraxanthias taylori* (Stimpson), and *Cycloxanthops novemdentatus* (Lockington) are discussed collectively as the major California Xanthidae. Information concerning the reproduction and life history of this group is almost totally

lacking. This is also true, with regard to larval ecology, for all Brachyura of western North America.

REPRODUCTION

Sexual Dimorphism and Maturity

The only distinct, sexually dimorphic characteristics of significance in the California Xanthidae are found in the abdomen of mature and submature specimens. The chelipeds of some male crabs are said to be larger than those of the female of the same species. There is considerable variation of length-width ratios of chelae among the local xanthid crabs, but there is no strongly marked trend towards dimorphism. It is generally true that the largest specimens are males. However, if the life span of the male and female crab is approximately the same, then the size difference is easily explained by the work of Hiatt (1948: 165) with *Pachygrapsus crassipes*. Hiatt demonstrated that the normal molt cycle of female crabs is interrupted by periods of egg bearing, and that a longer time is thus required for the female to reach a size equal to a male. If this applies to the Xanthidae as well, then the larger size of the male is not sexual dimorphism, but is due to a normal interruption of the female molt cycle. The abdomen, however, shows definite dimorphic trends, and at the time of maturity differs distinctly in male and female specimens.

In taxonomic work, as well as in natural history, it is often very useful to know if a particular specimen or size-class is mature. Gonad study is impractical because (1) the specimen is destroyed, (2) the sex organs may be dormant at the time of year which the specimen is collected, making determination impossible, and (3) the individual would be of no further use in a natural history study. Therefore, it is useful to have certain external signs with which mature specimens may be separated from im-

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mature. Seventy-five female xanthid crabs were dissected in the month of June to correlate size, gonad development, and abdominal characteristics. An additional 178 females were examined and measurements were taken on 63 of the premature to mature size range. These data will be presented for each species.

Cycloxanthops novemdentatus: This species shows signs of sexual dimorphism beginning at the 6.5 millimeter (carapace width) size class. Prior to this the male and female abdomen are alike, composed of seven segments, the third being the widest segment, while the sixth segment is less than two-fifths the width of the second. From about 6.5 millimeters carapace width the abdominal segments of the female distal to the third segment broaden with each additional molt. From the data given for this species (Table 1) it can be seen that there are two distinct classes, immature and mature, and a transitional submature class.

The immature specimens are those females in which the gonads are undeveloped and lack ova. External signs of this are as follows: (1) the third abdominal segment is the widest of all segments; (2) the marginal abdominal "hair"

TABLE 1

A SURVEY OF MATURE AND IMMATURE FEMALE *Cycloxanthops novemdentatus**

WIDTH IN MM.	WIDEST AB. SEG.	LATERAL "HAIR"	LOCK	SPERMA-THECA	CONDITION OF OVARIES	CONDITION OF EGGS
17.2	3	1/8	×	0	undeveloped	—
18.0	3	1/8	×	0	undeveloped	—
19.1	3	1/8	×	0	undeveloped	—
19.2	3	1/8	×	0	undeveloped	—
19.4	3	1/8	×	0	undeveloped	—
20.8	3–4	5/8	—	0	somewhat developed	—
22.5	3–4	7/8	—	0	somewhat developed	—
23.5	3	1/4	×	0	undeveloped	—
24.0	3	1/4	×	0	undeveloped	—
24.2	3	1/4	×	0	undeveloped	—
25.0	3	1/4	×	0	undeveloped	—
25.8	3	1/4	×	0	undeveloped	—
26.0	3	1/4	×	0	undeveloped	—
26.2	3	1/4	×	0	undeveloped	—
26.4	3	1/4	×	0	somewhat developed	—
27.0	3	1/4	×	0	undeveloped	—
28.5	3–4	1/2	×	0	somewhat developed	—
30.0	3–5	1/2	×	0	somewhat developed	—
31.2	3–5	3/4	×	0	somewhat developed	—
32.8	4–5	1	—	large	ripe, gravid	—
32.9	4–5	1	—	large	ripe, gravid	lg. blastomeres
33.0	3–5	1	—	medium	ripe, gravid	—
33.3	3–5	1	—	large	ripe, gravid	—
34.0	4–5	1	—	medium	ripe, gravid	lg. blastomeres
34.5	4–5	1	—	medium	ripe, gravid	new
35.5	4–5	1	—	medium	somewhat developed	—
36.8	4–5	1	—	large	ripe, gravid	new
37.0	4–5	1	—	large	ripe, gravid	—
37.5	4–5	1	—	large	ripe, gravid	—
38.0	4–5	1	—	large	ripe, gravid	—
38.5	4–5	1	—	medium	ripe, gravid	new
40.0	4–5	1	—	medium	ripe, gravid	—
41.0	4–5	1	—	large	ripe, gravid	lg. blastomeres
42.8	4–5	1	—	medium	ripe, gravid	—
52.3	4–5	1	—	large	ripe, gravid	—

* The lateral abdominal hair length is given as a fraction of the third abdominal segment length; ×, present; —, absent; O, spermatheca empty; lg., spermatheca large, full of sperm; med., spermatheca of medium size, with some sperm.

is 25 per cent or less than the length of the third abdominal segment; (3) the sixth abdominal segment is narrower than the second in young, but immature females; (4) the pleopods are sparsely provided with "hairs"; and (5) the lock mechanism is present. The lock mechanism is typical of male crabs of this species, and consists of a pair of cup-shaped pockets on the distal-lateral margins of the sixth abdominal segment, and a pair of protuberances projecting forward from the fifth thoracic sternite which lies in union with the sixth abdominal segment. When the abdomen is "closed," the cups of the sixth segment fit over the protuberances of the sternite and serve to lock the abdomen in place. The last abdominal segment is free, and is extended for defecation without lowering the entire abdomen. The protuberances of the sternite are the most conspicuous evidence of this mechanism. Generally the maximum carapace width of the immature female is 28.5 millimeters.

Submature or transitional females have well-developed ovaries but generally lack developing ova. The morphological changes from the preceding stages are as follows: (1) abdominal segments three and four are of nearly equal width; (2) the lateral "hair" on the sixth segment is almost 50 per cent as long as the third abdominal segment; (3) the pleopods are more fully developed; and (4) the lock mechanism is generally present. The size of this stage ranges between 28.5 and 33.0 millimeters.

The fully mature female *Cycloxanthops novemdentatus* is about 33.0 millimeters wide or wider, and has fully developed, gravid ovaries (in season). Externally these specimens can be determined by the following features: (1) abdominal segments four and five are the widest; (2) the lateral "hair" of the sixth segment is about equal in length to the third abdominal segment; (3) the sixth segment is wider than the third; (4) the pleopods are very full in appearance; (5) the lock mechanism is lacking entirely; and (6) the groove in the sternum occupied by the abdomen is proportionally shallower and wider than in the immature or male condition.

About 4 per cent of the females examined had a carapace width of 19.2 to 21.5 millimeters, but had all of the characteristics of a mature female.

Normally female *Cycloxanthops novemdentatus* are not ovigerous until June in southern California, and the individual young take about the same length of time to develop, probably two years. The small but mature females are probably hatched early in April, and thus are large enough in the following year to be influenced by the warm temperatures of late summer. Hence, the secondary sex characteristics are brought on abnormally early.

Hiatt (1948: 198) used the presence of sperm in the vas deferens as a criterion of maturity in male *Pachygrapsus crassipes*. The writer examined preparations from 15 *Cycloxanthops novemdentatus,* several other xanthid crabs, and several *Pachygrapsus crassipes* (within the mature size range), but concluded that the poor results obtained were not worth the destruction of additional specimens. A study of the external genitalia of the male, however, reveals that the intromittent organs are capable only of anterior-posterior movement. Thus successful copulation could not occur except with equal-sized females. In this species the intromittent organs are fully developed when the individual is 19.5 millimeters wide. Just prior to this they appear normal but are shorter than normal. Thus 20-millimeter males are able to copulate with small, mature females. However, the fertility of males in this size-class has not been established.

Paraxanthias taylori: The anatomical features important in determining the maturity of this species are the same as for *Cycloxanthops novemdentatus.* Signs of sexual dimorphism are seen in 6.5 millimeter specimens when the distal abdominal segments of the female begin to broaden with respect to segment three. There is no clear-cut transitional or submature class, in that the morphological features of such a class in this species are too indefinite to be of value.

Immature females which have underdeveloped ovaries are characterized by the following external signs: (1) the third abdominal segment is the widest; (2) the second abdominal segment is wider than the sixth segment; (3) the lateral "hair" on segment six is one half or less the length of the third abdominal segment; (4) and the lock mechanism is always present.

Females of this species mature between the sizes of 11.5 millimeters to 13.5 millimeters. The

wide range in size is probably due to their long breeding season which allows considerable size variation in each year class. Mature specimens have either gravid ovaries, eggs attached to the pleopods, or both. The anatomical changes and signs of a mature female are as follows: (1) the fourth abdominal segment is as wide as or wider than the third segment in the smaller mature specimens, while the fourth and fifth segments are wider than the third segment in older females; (2) the sixth abdominal segment is wider than the second; (3) the lateral "hair" on the sixth and/or seventh segment is equal to the length of the third abdominal segment; (4) the lock mechanism is lacking; and (5) the abdominal groove in the thorax is shallower and broader than in immature stages.

An attempt to analyze the maturity of males of this species and of the genus *Lophopanopeus* also met with little success. In both cases, however, the intromittent organs were fully developed when the male had reached a size somewhat smaller than the minimal size (11.5 mm.) of a mature female.

Lophopanopeus l. leucomanus and *L. bellus diegensis:* These species were studied independently but the data obtained were so similar that both will be discussed together. Sexual dimorphism is evident when the female reaches a size of 4.5 millimeters. This genus evidently matures more quickly in these latitudes than do the other genera, for ovigerous females having a carapace width of only 8.5 to 9.0 millimeters are common. This fact, together with the fact that this genus has the longest breeding season, explains in part its extensive northerly range.

Immature females have the following characteristics: (1) the third abdominal segment is wider than any other; (2) the lateral "hair" on the sixth segment is one-half or less the total length of the third abdominal segment; (3) the pleopods are underdeveloped; and (4) the lock mechanism is always present.

Mature females change in the following way: (1) the fourth abdominal segment is as wide or wider than the third segment; (2) the lateral "hairs" on the last two abdominal segments equal the length of the third segment; (3) the pleopods are fully developed; and (4) the lock mechanism is absent.

Internal and External Genitalia

The anatomical features of the genitalia are the same for the three genera studied, although there are some minor variations in shape and size of such parts as the male intromittent organs. The genitalia of *Cycloxanthops novemdentatus* will be presented as a representative type of the other genera in this study.

The internal genitalia of the male (Fig. 1, A) consist of the testes, which are dorsal to the liver mass and which join medially over the posterior portion of the stomach. From the testes arise two tightly coiled ducts which are the glandular portion of the vasa deferentia and which secrete a fluid which aids in the conduction of sperm. From these coils, the vasa deferentia pass posteriorly, leave the visceral area, and terminate in the coxae of the fifth pair of pereiopods.

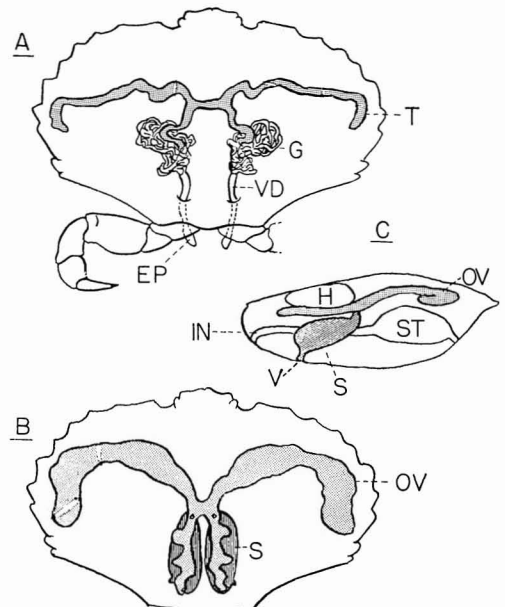The first (Fig. 2, A) and second abdominal appendages are modified to transfer sperm to

FIG. 1. Internal genitalia: A, Internal genitalia of a male *Cycloxanthops novemdentatus;* B, internal genitalia of a female *Cycloxanthops novemdentatus;* female genitalia, longitudinal view. EP, external papilla; G, glandular portion of the vas deferens; H, heart; IN, intestine; OV, ovary; S, spermatheca; ST, stomach; T, testes; V, vulvae; VD, vas deferens.

the female. The first pair, the intromittent organ, is nearly as long as the abdomen. Each pleopod consists of three segments: the coxopodite, basipodite, and flagellum (after Cochran, 1935: 46). The coxopodite is more or less coalesced with the abdominal segments. The basipodite and flagellum are closely associated and appear as a single unit. Along the median margin of the flagellum of the first pair of pleopods is a canal through which sperm passes, and into which is inserted the flagellum of the second pleopod. The second pleopod moves up and down in the canal during copulation and thus serves as a plunger or pump to force sperm through the canal. There is an external pair of papillae on the coxae of the last pereiopods which transfer sperm from the vasa deferentia to the intromittent organs. These are permanently situated in a funnel-shaped opening on the anterior side of the basipodite of the intromittent organs. Thus, during copulation sperm is conducted through the vasa deferentia, through the external papillae, into the intromittent organs, and there pumped to the terminal end by the second pair of pleopods, and transferred to the vulva of the female.

The internal genitalia of the female are similar to those of the male. There is a pair of ovaries (Fig. 1, B and C) which are U-shaped and lie over the liver anteriorly, and below the heart posteriorly. They unite just behind the dorsal side of the stomach where they give rise to a pair of oviducts. Each oviduct enlarges into a spermatheca as it passes ventrally, narrows again, and terminates in a vulva which opens on the sixth thoracic sternite (Fig. 2, B).

Mating Posture, Time, and Frequency

The writer had occasion to see pairs of *Paraxanthias taylori* and of *Lophopanopeus bellus diegensis* in copulation on 12 different occasions in the laboratory. On one of these occasions the entire act was witnessed. There is no prenuptial pairing or courting in the Xanthidae as reported for other crabs by Williamson (1903: 101), Hay (1904: 405), and Churchill (1918: 105). The writer has seen the courting of *Cancer antennarius* on four occasions in the field. During the prenuptial pairing the male of this species carries the slightly smaller female around in his

chelae. When disturbed he runs to a hiding place with the female tightly in his grasp. If separated the female is very passive and will offer no defense. The male "courts" the female until she completes ecdysis, at which time they copulate. Two mating pairs of this species were found at Palos Verdes in which the female was completely soft, having just molted. In each intance the crabs were in copulation.

The California Xanthidae breed while in a hard-shell state, and not after molting. The one complete act observed progressed as follows: A male *Paraxanthias taylori* approached a female of this species. The female raised her chelae, which were grasped by the male's chelae, and was lifted above the substratum. Without breaking stride the male pushed the female over backwards and proceeded to straddle her body. The male then lowered his abdomen, catching the female's abdomen with it as he did so. By extending his abdomen under hers, he forced the female to open her abdomen away from her body and thus expose the vulvae. The intromittent organs were lowered automatically with the male's abdomen and were quickly inserted into the vulvae.

In the laboratory, xanthid crabs were seen in copulation for periods up to 3 hours. The male was always dorsal to the female, which is a position typical for most Brachyura, but is unlike that of *Pachygrapsus crassipes* (Hiatt, 1948: 199). Copulation was often repeated by one pair of crabs on several successive days. Forty per cent of the ovigerous females examined had full or partially full spermathecae, which suggests that copulation may not be required for each batch of eggs.

Reproductive Season

There is considerable variation among the major genera of the California Xanthidae in the duration of their reproductive seasons. The writer has observed ovigerous females of *Lophopanopeus l. leucomanus* and of *L. bellus diegensis* collected from February to October inclusive. *Paraxanthias taylori* has the next longest season, with ovigerous females common from April to September. *Cycloxanthops novemdentatus* does not become ovigerous until the middle part of June. Females of this species were collected with
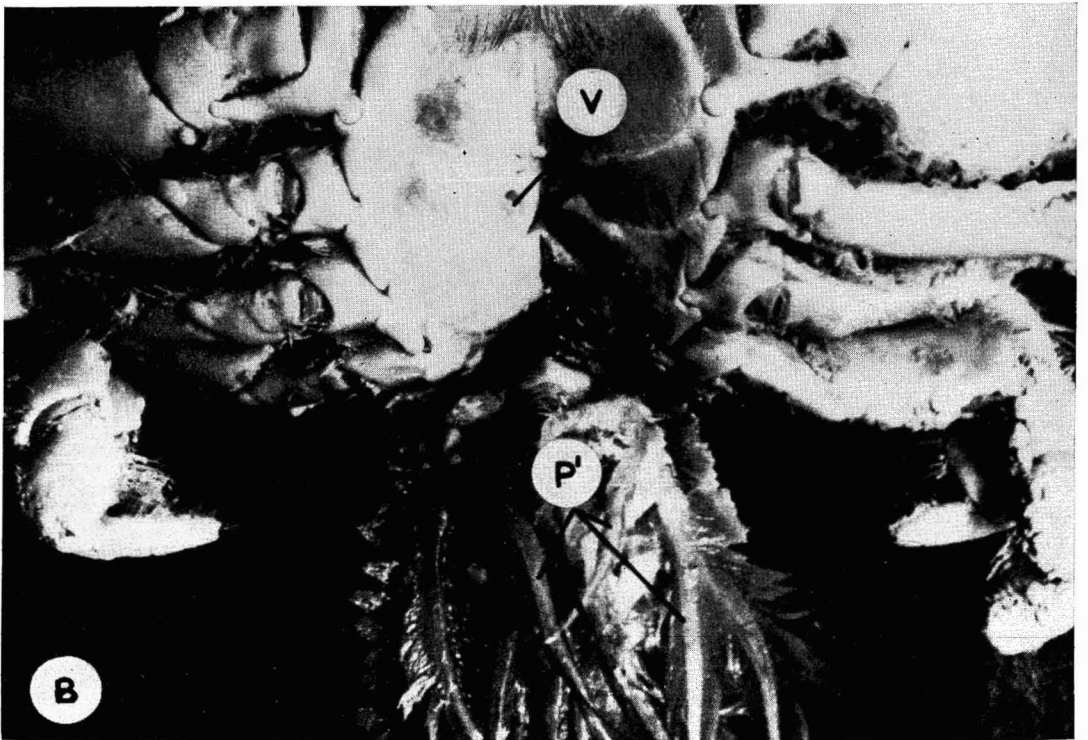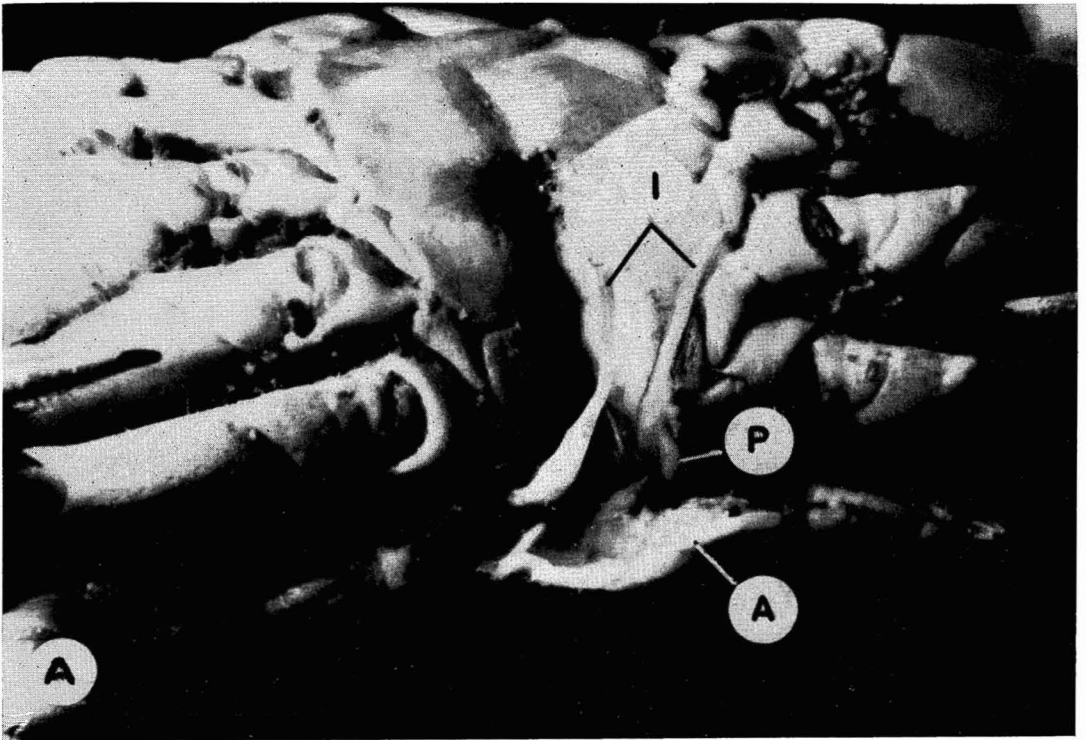
eggs in September, but no later record of egg bearing is available. The local *Lophopanopeus* and *Paraxanthias* remain in the normal tidal range, while ovigerous *Cycloxanthops novemdentatus* migrate to about the minus 3- to 6-foot tide level before extruding their egg masses. Only one ovigerous female of this species has been deposited in the Hancock Foundation collection. Almost all of the ovigerous specimens collected by the writer were obtained by skin diving rather than by collecting on shore. During the reproductive season the sex ratio at the higher tide levels is unbalanced, while in the winter and spring months there is an equal ratio of male and female crabs.

Egg Mass

The egg mass attached to the pleopods of the female varies in proportion to the size of the individual and, to a lesser degree, between different individuals of the same size-class. Table 2 gives the estimated number of eggs carried by 15 xanthid crabs. In each case the eggs were stripped from the pleopods and 300 were counted. The volume of the 300 eggs divided into the total volume multiplied by 300 gave the approximate total number of eggs. In all cases the crabs used were smaller mature individuals rather than older and larger individuals. It can be seen that the total number of eggs is roughly proportional to the size of the individual. Mature *Lophopanopeus* spp. would thus carry from 1,000 to 6,400 eggs within their normal size-range, while an average-sized individual may carry around 3,500 eggs. An average *Paraxanthias taylori* may carry about 21,000 eggs and an average-sized female *Cycloxanthops novemdentatus* about 45,000 eggs.

Egg Extrusion and Attachment

At the time of extrusion of the egg mass the individual eggs pass through the oviduct and into the spermathecae. Then they pass out of the body by means of the vulvae, and drop into a "basket" formed by the abdomen and its appendages. The process of egg extrusion was observed on four occasions, but in each instance the eggs were aborted, and were not fastened to the pleopods. However, this process was essentially the same as when eggs are attached, except that the female crab periodically shook the eggs from her pleopods and allowed them to fall to the floor of the aquarium.

During egg extrusion the female tilts her body backwards and elevates it above the substrate by extending her walking legs beneath her. The abdomen is lowered to about a 50 degree angle below the body plane. The sixth and seventh abdominal segments are turned upward, and together with their marginal "hair" serve to catch the eggs. The exopodites of the four pairs of pleopods are heavily set with "hair" on their anterior and posterior margins. When these are extended laterally they complete the "basket" which receives the eggs. Thus the basi-abdominal segments form the posterior wall, the median segments form the floor, the terminal segments form the anterior wall, and the exopodites form the lateral walls of the egg "basket." Eggs stream from the vulvae and are received by the abdomen. As they do so the endopodites of the pleopods move up and down through the loose egg mass. The endopodites are set with long smooth "hairs" to which the eggs are attached. When a part of an egg mass is examined microscopically it can be seen that there is an umbilical-like thread attached to each egg. This thread is wrapped around and attached to the pleopod "hairs." However, the end of the thread is not attached to the "hairs" but remains free. One of the mysteries, still unsolved, is the origin of this thread, and the method of its attachment to the egg and to the pleopod "hair." Broekhuysen (1936: 277) gives an excellent review of the literature, outlining nine possible answers to the problem, but concludes that the theories are still unsatisfactory for the Brachyura. The present writer observed that there is a sticky consistency to the entire egg mass shortly after being extruded, but he has not had opportunity to study this more fully. This sticky material may be a cement product secreted by the crab, as is the case of the lobster (Herrick, 1895: 48). How-

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FIG. 2. External genitalia: A, External genitalia of a male *Cycloxanthops novemdentatus*; B, external genitalia of a female *Cycloxanthops novemdentatus*. A, abdomen; I, intromittent organs; P, second pleopod inserted into the first pleopod; P', pleopods to which the eggs are attached; V, vulvae.

TABLE 2

NUMBER OF EGGS PER MASS OF DIFFERENT SIZES
OF XANTHID CRABS

SPECIES	CARA-PACE WIDTH	EGGS COUNTED	ESTI-MATED TOTAL
L. l. leucomanus	8.5 mm.	300	1,250
L. l. leucomanus	9.2 mm.	300	2,100
L. l. leucomanus	10.0 mm.	300	1,000
L. l. leucomanus	10.0 mm.	300	3,000
L. l. leucomanus	11.5 mm.	300	3,600
L. l. leucomanus	12.0 mm.	300	3,300
L. l. leucomanus	12.5 mm.	300	3,500
L. l. leucomanus	13.5 mm.	300	4,200
P. taylori	15.0 mm.	300	3,800
P. taylori	18.5 mm.	300	6,450
P. taylori	19.0 mm.	300	7,200
P. taylori	29.5 mm.	300	20,300
C. novemdentatus	32.9 mm.	300	22,500
C. novemdentatus	34.5 mm.	300	23,400
C. novemdentatus	38.5 mm.	300	40,680

ever, the eggs are never stuck together after attachment, and are never attached to the exopodites, which are equally as "hairy" as the endopodites. Williamson (1903: 109) suggests that the endopodite "hairs" puncture each egg, and that the "umbilical" thread is then produced by material which streams from the egg. Broekhuysen (1936: 281) has raised many objections to this idea, concluding that it is a physical impossibility.

LIFE HISTORY, STAGES, AND DURATION

The life cycles of four of the most common xanthid crabs in the southern California area were worked out and compared by the writer. Of the four published life cycles of British Columbia Brachyura by Hart (1935: 414), one is of a xanthid crab, Lophopanopeus bellus bellus (Stimpson). The data given by Hart compare favorably with those obtained by the writer, thus permitting a discussion which may be applicable to the entire family.

The eggs are attached to the pleopods and there incubated from 25 to 30 days. The female periodically flexes and extends her abdomen as if to allow fresh sea water to wash and aerate the eggs. From time to time the female plucks eggs or other material from the egg mass with her chelae, and conveys this to her mouth. The exact reason for such action is not known, but it

may be a method of cleaning the eggs. In the field it was noted that ovigerous females of Lophopanopeus b. diegensis, Lophopanopeus l. leucomanus, and Paraxanthias taylori were often stranded by minus, low tides. These animals make no attempt to enter tidepools a few inches below them, but rather remain in their hiding places. The abdomen of such animals is closed over the egg mass, thus keeping considerable water around the eggs. In the laboratory a tall rock-filled water jar was stocked with ovigerous xanthid females. The sea water was then slowly siphoned out in an attempt to simulate the lowering of tides. Paraxanthias taylori and Lophopanopeus l. leucomanus did not follow the receding water, but stayed out of water where they finally died. Eggs kept out of water in moist algae up to 6 hours were viable when returned to water. Thus periodic withdrawal of water under normal tidal conditions has no apparent effect on the eggs.

Hatching occurred most frequently at night shortly after dark. Occasionally a few individuals of a given egg mass will hatch during the daylight hours, but these are followed by mass emergence of the other larvae at night. Hatching begins as the egg capsule splits about halfway around, above the dorsal surface of the larva. The larva struggles out of the capsule, dorsal side up, and swims free of the mother crab. During the peak of the hatching period the flexion and extension of the female's abdomen increases very noticeably. With each flexion many larvae are washed away from the egg mass.

The prezoea (the larva just after hatching) has its maxillipeds, antennules, antennae, telson, and spines telescoped. There is no apparent ecdysis between this stage and the first zoea. Rather, the folded extremities are extended by haemocoelic fluid as is the case after normal ecdysis. Hiatt (1948: 204), however, reports true ecdysis after the prezoeal stage in Pachygrapsus crassipes. Healthy prezoeae swim for 30 minutes to 2 hours before the expansion is complete. When the larvae are completely expanded they are called zoeae.

There are typically four zoeal stages and one megalops stage in the xanthid life history. The zoeae are pelagic, photopositive forms which

feed on smaller animals or plants. Each zoeal stage resembles the previous one, but shows a marked increase in size. The megalops more closely resembles a crab, having chelae and four pairs of walking legs. This stage settles and molts, thus becoming the first crab stage which resembles the adult. In the laboratory an average of 5 weeks was required to complete the larval stages of the four species. The first zoeal stage lasted from 4 to 6 days. The megalops stage lasted from 7 to 10 days. The first crab stages lasted 13 days, but each stage beyond this required an increase in time for completion.

LARVAL HABITS AND ECOLOGY

Locomotion

The zoea uses two forms of locomotion. The first is a form of directional swimming in which the larva moves in a straight line. Swimming is always carried out in the direction of the dorsal spine so that the body is either in a normal or inverted position (Fig. 3, A, B). The first and second maxillipeds are used as paddles and rapidly move up and down as the larva swims.
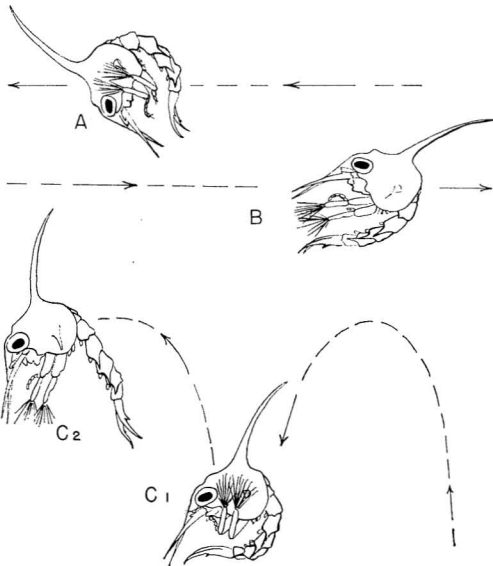

FIG. 3. Methods of zoeal locomotion: A, Normal maxilliped locomotion; B, inverted maxilliped locomotion; C_1–C_2, maxilliped-telson or hop-up-and-sink locomotion.

On the distal end of the exopodite of the maxillipeds are four or more plumed natatory "hairs." These "hairs" fan out as the blade of an oar and give the zoea added thrust. After each ecdysis several new natatory "hairs" are added to help propel the additional mass of the zoea.

Weldon (1889: 169) states that steering is effected by means of the telson and abdomen. This may be the case where positive phototaxis is not involved. Mast (1938: 209–216) has shown that photopositive animals with bilaterally located photoreceptors and locomotor organs are affected by the amount of light that each photoreceptor receives. Thus when more light strikes the right eye the left bank of locomotor organs become more active until the body is turned to a point where both eyes are equally illuminated. To test this for the Xanthidae, many zoeae were placed in an 8-inch cylindrical jar in a darkened room. When a light was turned on the larvae swam towards it, but when one light was replaced by a second light 90 degrees away, the larvae turned and swam in that direction. When a light was rotated around the jar the larvae swam in circles in a horizontal plane. When the light was slowly passed over, around and under the jar the larvae swam in vertical circles.

The second form of zoeal locomotion is a random hop-up-and-sink type of movement which follows no definite direction. As a zoea sinks, it draws its abdomen up against its thorax and raises its maxillipeds (Fig. $3C_1$). Simultaneously the abdomen and maxillipeds are thrust downward, resulting in an upward propulsion of the larva (Fig. $3C_2$). The process is repeated so that the zoea remains at approximately the same level in the water column.

Megalops do not use their mouth parts for locomotion but swim by means of pleopods and walk by means of pereiopods. Newly molted megalops are photopositive while older individuals become somewhat photonegative. When swimming, the pereiopods (Fig. 4A) are folded against the body and the abdomen is fully extended. When the megalops turns upward (Fig. 4B) or downward (Fig. 4C) the abdomen is bent up or down, as the elevator of an airplane, to effect the change in direction.
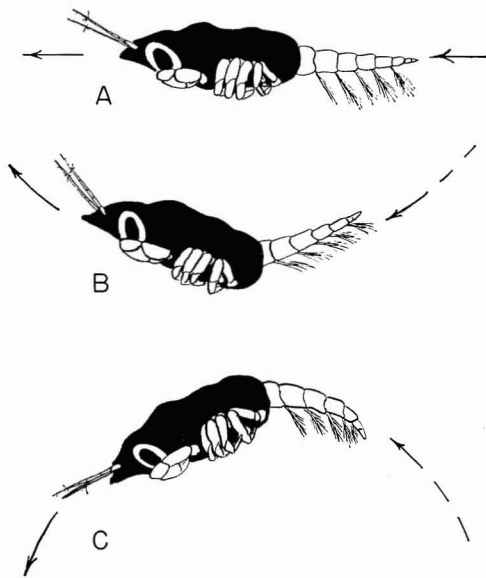
FIG. 4. Locomotion of the megalops stage. See text.

The rate of directional swimming is remarkable. Zoeae placed in a piece of glass tubing 1 inch in diameter and one meter long swam the meter distance in a horizontal plane in 45 to 60 seconds. For this experiment a light was used to maintain the direction of swimming and a wrist watch for timing. These times compare exactly with those recorded by Foxon (1934: 842) for *Galathea, Eupagurus, Pandelus,* and *Porcellana* larvae. Xanthid larvae swam up a 1-meter column in 50 to 60 seconds, while swimming down the column required only 12 to 15 seconds. Xanthid megalops were only timed on one occasion, at shipside while at anchor. The average approximated rate was 2 meters per minute, or about twice the speed of zoeae. Foxon (1934: 843) suggests that the larval swimming rate is sufficient for diurnal migration, which actually does occur (Russell, 1927).

Orientation

Mast (1938: 215) suggests that a portion of the eye functions as a receptor which detects the direction of light. When a light source is present the larvae show no response to gravity as seen above, and as reported by Weldon 1889: 169), Spooner (1933: 395), and Foxon (1934: 838). However, Foxon demonstrates that when light is

absent a normal dorsal-up orientation is maintained. Gurney (1902: 475) suggests that the carapace spines play some role in orientation, since statocysts are not present in the zoea. Foxon demonstrated that drugged zoeae, or those with the maxilliped exopodites excised, sank uncontrollably, suggesting awareness and functional exopodites are required also. However, more testing of these theories is necessary.

Food and Feeding Habits

Lebour (1928: 500) states that the natural food of zoeae consists of planktonic organisms, such as diatoms and other microscopic algae, larval and small adult animals. In the laboratory, mixtures of protozoans, turbellarians, diatoms, and other aquarium dwellers were fed to the zoeae. However, the nauplius larva of brine shrimp, *Artemia,* proved to be an excellent source of food for the zoeae. Megalops fed upon *Artemia,* zoeae, and small sessile algae.

Zoeae were observed under the microscope while feeding on nauplius larvae. A zoea catches a nauplius by swimming just a little above it, tilting backward, and dropping down upon it from above. The nauplius is caught between the maxillipeds (which are used for feeding as well as for locomotion) and held by the endopodites. The rostral spine and antennae prevent the nauplius from escaping anteriorly. The abdomen and telson are curled beneath the nauplius, preventing escape posteriorly and ventrally. The mandibles are then in position to feed upon the nauplius. During the feeding process the exopodites of the maxillipeds are used for the locomotion or balance of the zoea.

Ecdysis

In the laboratory the periods of larval ecdysis are the times of the greatest mortality. The molt from the first to the second zoeal stage is the most critical, while the molt and transition from the fourth zoea to the megalops stage is next. During the act of molting a great deal of energy is spent in an attempt to get free of the old "skin." Zoeae which pause to rest generally expand to a point where withdrawal becomes impossible. Larvae in this stage live for a while with the old skin attached to them, but feeding and future molting is generally impossible. Other larvae are so weakened after ecdysis they are

defenseless or unable to capture food, and eventually die.

On a few occasions zoeal ecdysis was seen microscopically. The writer's notes and the examination of zoeae preserved while partially through ecdysis reveal that the process is essentially the same for larvae and adults (Knudsen, 1957: 133–142). The carapace is elevated dorsally above the abdomen. The abdomen and pereiopods are drawn out of the old skin as the new zoea expands upward and backward. As the zoea backs out of the split in the old skin the new dorsal spine is extracted from the old case. The eyes, antennae, and rostral spine are the last parts to be withdrawn. The haemocoelic pressure quickly extends the body to its new size as the molting process is completed. Once free of the old skin the zoea swims away and begins feeding in less than a day's time.

Enemies

To an individual pelagic larval crab, or any other animal, every organism is a possible source of food because it is smaller, or of neutral status because of equal size and strength, or a predator because it is larger. The diatom is generally thought of as the basis of the oceanic food chain. Above this come the tiny, filter-feeding animals, which in turn, serve as food for larger planktonic animals. Thorson (1950: 19) names depredation by other animals as the most important form of wastage of planktonic larvae. The filter feeders, from tiny crustaceans on up to fishes (herring, mackerel) and even whales, probably take the great percentage of larvae.

Obviously the xanthid zoeae are no exception, but fall prey to any stronger or larger predator. In the laboratory zoeae and megalops fed frequently on other zoeae. Many first zoeae were seen to eat the dorsal spine of other living first zoeae. When *Artemia* larvae became too large they too preyed on the zoeae. Copepods experimentally placed in culture jars also took a toll of zoeae.

Mortality of Larvae

Table 2 gave approximate numbers of eggs produced at one time by various sized females. An investigation of the gonads and spermathecae of ovigerous females suggests that more

than one egg mass is carried per year. Judging from the length of the breeding season, it appears that *Lophopanopeus* and *Paraxanthias* produce more than two egg masses each year. Thus a 40-millimeter female *P. taylori* may produce up to 120,000 eggs per year.

There is no direct method of measuring the mortality of pelagic larvae. Thorson (1950: 12–19) states that food conditions, temperature conditions, metamorphosis, unfavorable current transport, and predators are the sources of waste of pelagic larvae. Where commercial records are kept for a species for a long period of time some estimate of the total adult population, the yearly spawn, and the larval mortality can be made. However, if the entire population of a species remains relatively constant over a long period of years, then, barring short-term fluctuations, the following supposition can be made: only one pair of F-1 individuals produced throughout the life span of one breeding pair reaches maturity and reproduces. Thus the annual larval mortality rate equals the total number of eggs produced by an entire species population that year, minus the total mortality of mature individuals of that species. Periodic fluctuations in adult populations, by this line of reasoning, are due to a modification of one of the larval waste factors outlined above, or to some change in conditions which affect the early crab stages. In the case of the Xanthidae, these factors are the total amount of habitat available, food conditions, temperature conditions which may speed up or retard development and reproduction, population pressures, depredation, and competition for food. Thus, the reasoning used is based on a long-term basis in which fluctuating conditions and the resulting population change will balance out.

Current Transport

There are two main ocean currents which are responsible for water movement off the coast of California. These are the California Current, which transports water to the south, and the Davidson Current, which transports water to the north. The California Current prevails from February to October during the seasons of westerly winds and upwelling. In the fall when the westerly winds and upwelling cease, a counter current develops which, in November through

January, transports water as far north as the 48th parallel (Sverdrup, Johnson, and Fleming, 1942: 454, 502, and 726 for maps). In spite of some occasional nearshore reversal of currents, due to various meteorological conditions, the dominant flow of the California Current during the xanthid larval season is to the south. This would mean that any xanthid larva entering such a system during its five-week developmental period would be swept southward and metamorphose 50 to 100 miles from where it hatched. *Paraxanthias taylori* and *Cycloxanthops novemdentatus* at Monterey, California, would thus produce larvae settling at Point Conception, California, and those larvae from Point Conception would settle at Palos Verdes, California, and so on. Obviously this is not the case, for (1) there is no point of larval supply for Monterey, and (2) at 3- to 4-year intervals the distribution of these species would recede 50 miles or more southward. There must, then, be a current system or some other factor peculiar to the nearshore waters which maintains larvae spawned in a local area until they finish their cycle.

To see if such a factor exists, a series of simple float studies was employed in the first bay south of Resort Point, Palos Verdes Hills, California.

Experiment 1. Drift bottles were set out 3 hours before low tide and 3 hours after low tide on November 11, 1955. The bottles used were small, eighth-pint bottles, with colored markers inside. They were launched by means of a leather thong slingshot. Two observers plotted their drift pattern from the cliff top from 9:30 a.m. to 5:30 p.m. Though all of the markers remained in the bay, some of those placed closer to the point entered an eddy system in the mouth of the bay, while others moved towards the head of the bay and there entered a smaller eddy system, but none were washed to shore or out to sea.

Experiment 2. In May 1956, forty "drift arrows" were set out. The arrows consisted of 36-inch, weighted, wooden shafts with small cloth flags at the top. These were shot from the cliff into the bay with a hunting bow, and their drift recorded. These were not very satisfactory in that they were hard to see at distances greater than 200 yards. Most of the arrows in the bay were carried beyond Resort Point, and then southward, out of sight within 20 minutes. A few arrows came into the breaker zone and were washed ashore.

Experiment 3. On July 10, 1956, thirty drift cards were released at 6:00 a.m., one hour after low tide. In this case, the cards were placed just beyond the breaker zone and all floated out to sea and out of sight. Four of these cards were found that same afternoon by swimmers within a one-half mile radius of the bay. A fifth, and more significant card, was found 12 days later still adrift just off shore in the next bay south.

Experiment 4. On July 18, 1956, forty-five drift cards were set out at 10:00, 11:00, 12:00 and 1:00 o'clock but in each case were swept ashore, regardless of their launching point. On the first three attempts half of the cards were set in the middle of the bay and half at the mouth (by swimming out with them). Within 40 minutes after launching they were in the surf zone along the south side of the bay where they were gathered up. On the last attempt the writer placed the cards about 200 yards out beyond Resort Point opposite the mouth of the bay. These also drifted in towards shore where some were picked up by swimmers and returned.

Experiment 5. Thirty drift cards were set out in the bay at 12:00 noon, September 1, 1956. These drifted out of sight within 30 minutes after being released. Four of these cards drifted back into the bay late in the afternoon, and were picked up by swimmers. One more was found in the water within the bay, 8 days later. Another card was found on El Morro Beach 16 days later, and still one more was returned from Carlsbad Beach 19 days later.

Experiment 6. Thirty drift cards were released in the mouth of the bay at 1:40 p.m., September 1, 1956. These cards drifted into the beach and were collected there.

A great deal of additional work is needed before any conclusions can be reached as to the current patterns near Resort Point. The results obtained were of three types: (1) floats remained in a continuous eddy system; (2) floats left the bay but returned at a later time; and (3) floats drifted directly into the bay. It is interesting to note that a float was recovered in the water in the bay almost 2 weeks after being released. Others which had floated from the bay

returned and were picked up in the water. Still other cards were caught in an offshore current and carried far to the south.

It is evident that the currents around Palos Verdes are irregular and frequently shift direction within a short time. Wind, tide level, and bottom topography may all serve to create and alter these currents. It is also evident that the currents observed are peculiar to a narrow strip of water embracing the headland, and that the California Current has little or no effect here. That the California species of Xanthidae are not rapidly disappearing from Palos Verdes suggests this also. The writer believes that a portion of xanthid larvae are caught in a southerly current (Experiment 5) and die in the first crab stage when a suitable habitat is not found. This is suggested by first crabs and megalops clinging to drift algae, and by the deep water distribution of *L. b. diegensis*.

Macrocystis Beds

Along the major portion of the range of the California species of Xanthidae are found large beds of the giant brown kelp, *Macrocystis pyrifera*. This alga grows in water from 30 to 90 feet deep all along the rocky shores. In the summer it forms a very thick mat of growth at the surface which divides the outer oceanic water from a thin strip of water between the kelp beds and the shore. A single bed often extends for many miles along the coast without interruption.

Such dense, uninterrupted growths could serve to (1) protect larvae, (2) offer hiding places where the cycle could be completed, and (3) alter currents to maintain an inshore eddy system. Andrews (1945: 36) concludes that kelp beds at Monterey, California, check currents and wave action, and offer protection to developing larvae. Limbaugh (1955: 13) reports the "dumping" of long waves which reach the kelp beds, but states that short waves pass through them with little interference.

Of the animal life in the canopy of *Macrocystis* there are such forms as pelagic and nearshore fishes and invertebrates, especially larval forms (Limbaugh, 1955: 14). The writer's plankton net collecting did not indicate plankton to be more abundant in kelp beds, but the amount of work done is so small (18 net hauls,

half in kelp beds), and accomplished under such awkward conditions (small skiff and inner-tube raft), that it is of no significance. Limbaugh records less plankton collected in the kelp beds than such places as over rocky nearshore bottom where plankton is abundant. He explains this by the abundance of fish which filter feed in the kelp beds and thus reduce the plankton there. However, difficulty in using a net in kelp beds may also explain this difference. The significant points demonstrated are (1) that schools of fish are attracted to feed in the kelp beds, denoting a concentration of plankton which probably seek shelter there, and (2) the presence of a large number of larvae inshore from the kelp beds. It seems apparent that the kelp beds and/or peculiar nearshore currents are holding the larvae and thus preventing a reduction of species along our coast.

Inshore Migration

Unless a mechanism such as that suggested above keeps the xanthid larvae close to their habitat area, the megalops stage must migrate inshore at the time of metamorphosis. The drift card Experiment 4 shows that currents are, at times, very favorable to inshore migration of the larvae. Rafting on drift algae may be a second method employed by xanthid crabs to migrate inshore. Cunningham (1898: 205), Lebour (1928: 499; 1947: 528–535), and Hiatt (1948: 204) report finding megalops and/or first crab stages along the beach. The writer has also recovered the megalops of *Pachygrapsus crassipes*, *Hemigrapsus nudus*, and *Lophopanopeus l. leucomanus* at the bay, thus suggesting that the megalops stage completes metamorphosis after reaching the adult habitat.

Early Crab Stages

The early crab stages of *Paraxanthias taylori*, *Lophopanopeus l. leucomanus*, and *Cycloxanthops novemdentatus* were found on many occasions along the Palos Verdes shore. These resemble the mature adults in carapace proportions and gross appearance. The young *Paraxanthias taylori* resembles the adult in color also while the young of *Cycloxanthops novemdentatus* and of *Lophopanopeus l. leucomanus* are of many different bright colors. These little animals are found in the smallest of cracks or

spaces between snail tubes, or even, in the case of *Lophopanopeus l. leucomanus,* in the dense coralline turf on top of rocks in the xanthid habitat. Edcysis is probably carried out in the security of such places. The early crab stages molt every 10 to 15 days and grow rapidly in their first year. The smallest crab stages feed on microscopic red algae which grow in the shaded areas of their habitat. The small crabs are easily attracted to raw meat, such as abalone, but it is doubtful if their diet contains much of this. The megalops and first crab stages have many enemies in blennioid fishes and other crabs. While making periodic underwater observations, it was noted that blennioid fish occupy the xanthid habitat at high tide. These fish spend much of their time lying in wait on top of algal covered rocks. At times they were seen to dart away from their hiding place to catch isopods. When small xanthid crabs were dropped nearby the fish made a serious effort to capture them. This suggests that the blennioid fish may be preying upon the xanthid crabs. To test this suggestion, stomach examinations were made on 51 blennioid fishes of the following species: 31 *Clinocottus analis* (Girard), 5 *Olygocottus maculosus* (Girard), 3 *Artedius lateralis* (Girard), 5 *Gibbonsia eligans* (Cooper), and 7 *Gibbonsia metzi* Hubbs. The stomachs contained many limpets, snails, polychaetes, crustaceans, and small fishes. Of the Crustacea there were isopods, amphipods, *Caprelia,* stomatopods, shrimp, porcellanids, hermit crabs, and the following Brachyura: *Pachygrapsus crassipes, Lophopanopeus* spp., *Pugettia producta,* and *Herbstia* sp. In the stomach contents crustaceans were dominant, while mollusks were second in volume. Both adults and megalops of the genus *Lophopanopeus* were found, thus establishing the blennioid fish as enemies of the Xanthidae.

SUMMARY

1. Sexual dimorphism of the California Xanthidae is manifested in the abdomen of mature and submature specimens.

2. The immature, submature, and mature specimens of *Cycloxanthops novemdentatus, Lophopanopeus l. leucomanus, L. bellus diegensis,* and *Paraxanthias taylori* may be separated by noting the width of the abdominal segments, the length of the lateral abdominal hair, the presence or absence of the abdominal lock, and the condition of the pleopods.

3. The internal and external genitalia are similar in all species of the California Xanthidae and are described for both sexes.

4. Xanthid crabs breed in a hard shell condition. The male is always above the female, transferring sperm to her vulvae by means of the intromittent organs.

5. *Lophopanopeus* spp. begin breeding earlier in the season and have more broods per season than the other genera. *Cycloxanthops novemdentatus* has the shortest breeding season.

6. Eggs vary in number, with the species and with the size of the individual, from 1,000 to 45,000. They are attached to the pleopods and there aerated and cleaned by the female until hatching.

7. Hatching occurs generally at night. There is no molt between the prezoeal and first zoeal stages. There are four zoeal and a single megalops stage in the xanthid life cycle (which requires about five weeks to complete).

8. The xanthid zoeae are photopositive and swim by means of the maxillipeds or with maxillipeds and telson. The megalops use their pleopods for locomotion.

9. Zooplankton probably constitutes the larval food in nature. Zoeal feeding methods are described herein.

10. The process of molting of the zoeae and megalops is essentially the same as in the adult.

11. Data collected suggest that peculiar eddy currents exist in bays and coves along the California coast which hold the developing larvae close to shore and prevents their removal by the southerly California Current.

12. *Macrocystis* beds help isolate developing larvae, offer wave protection and perhaps hiding places as well.

13. Megalops of the Xanthidae probably metamorphose in the adult habitat since the first crab stages were found there in abundance.

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