STUDIES ON THE TALITRIDAE (AMPHIPODA, CRUSTACEA) IN JAPAN

IV. THE DEVELOPMENT OF GNATHOPOD II IN *ORCHESTIA PLATENSIS* KRØYER[1)2)]

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With Text-figures 1–7 and Table 1

Introduction

Detailed analyses of life history and breeding activity of *Orchestia platensis* Krøyer revealed that the reproductive activity in the breeding season of this animal was sustained by populations of two successive generations overlapped. And some of the important life history events and breeding activity of the female, for instance, growth rate, commencement and duration of the breeding, and life span, showed seasonal variation that was significantly attributable to the climatic condition (Morino, 1978). The variation thus recognized in female sexual activities may well suggest the possibility of the corresponding phenomena in the male.

The present paper deals with the development of a male sexual character and its variation in *Orchestia platensis*. Growth and development of gnathopod II is selected for the purpose, since the appendage of this species shows sexual dimorphism, as in some other talitrid genera, and a character, that is, a depression on the palmar margin of the 6th article of gnathopod II in the male, is conveniently used in the species identification. Presence or absence of sexual dimorphism of gnathopod II, and their phylogenetic interrelation seem to be a cornerstone for phylogenetic analysis of the Family Talitridae (Hurley, 1959; Bousfield, 1968). The examination on the constancy or the range and nature of morphological changes of those characters seems to be important to afford the more sound basis for the taxonomy and phylogenetic considerations of this group of animals. Possible derivation and phylogentic relationships of the Japanese Talitridae will be fully discussed in a subsequent paper, from the view point of geographical distribution.

I would like to express my sincere gratitude to the late Professor Emeritus H. Utinomi of Kyoto University who had led me to the present study. Professor Emeri-

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tus T. Tokioka of Kyoto University and Associate Professor S. Nishimura of Yoshida College in Kyoto University gave me invaluable advices, to whom I am very much indebted. I would also like to thank Dr. E.L. Bousfield of the National Museum of Canada for his helpful comments during the study. My hearty thanks are due to Professor E. Harada of the Seto Marine Biological Laboratory, whose criticism and encouragement have enabled the present study to be completed.

Materials and Methods

Materials from Hatake-jima Island in Tanabe Bay, which had already been examined from the view point of the breeding activity and life history, were utilized again. Detailed explanation of the sampling site and methods was given in the preceding paper (Morino, 1978). In addition, specimens collected at Ezura shore on the south coast of Tanabe Bay, Misaki on Miura Peninsula in Kanagawa Prefecture and Onagawa in Miyagi Prefecture have been examined.

Specimens were sexed as the female or the male by the presence of oöstegite or penis, respectively. When neither was recognized, the specimen was treated as the juvenile. The number of flagellar segments of the antenna II was counted. Measurements were done on the following items.

1) Body length: from the tip of the head to the postero-median margin of pereionite VII.

2) Length of the frontal margin of the 6th article of gnathopod II (Fig. 1, A and B).

3) Depth of depression on the palmar margin of the 6th article of gnathopod II in adult male (Fig. 1, C).

In the laboratory, behavior was observed under the binocular microscope.

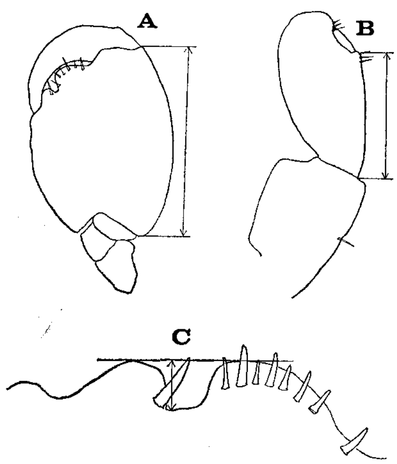

Fig. 1. Measurement sites for the morphometric study of gnathopod II.

Results

Changes in Size and Shape of Gnathopod II during Growth

Sixth articles of the gnathopod II of *Orchestia platensis* of various sizes and molting ages from Hatake-jima Island are illustrated and compared seasonally in Fig. 2

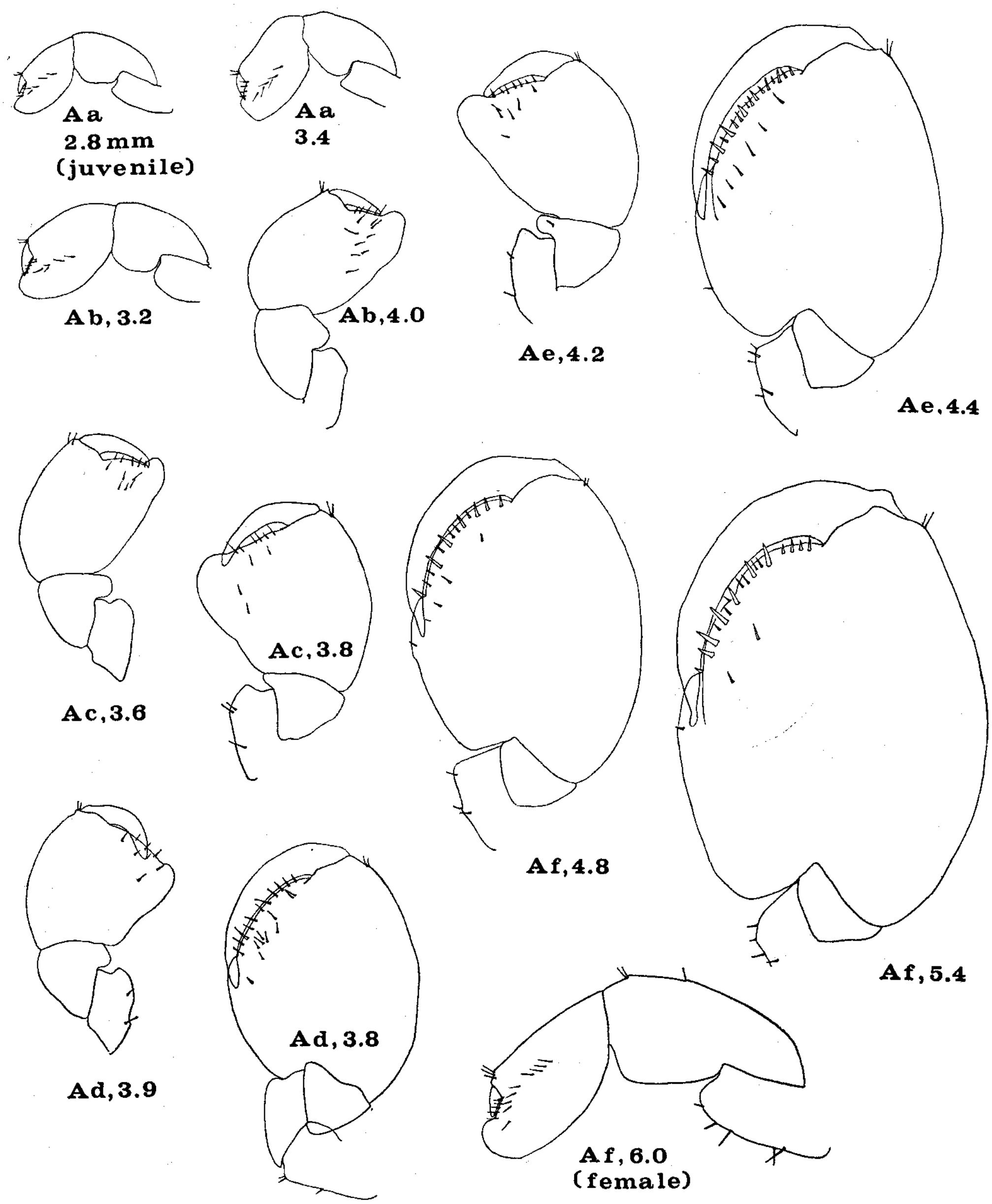

Fig. 2. Gnathopod II of *O. platensis* of various sizes and numbers of flagellar articles, from Hatake-jima Island, 13 Jan. 1973. All males, unless otherwise indicated; a; 8 articles, b: 9, c: 10, d; 11, e: 12, f: 13; inserted numerals mean body length,

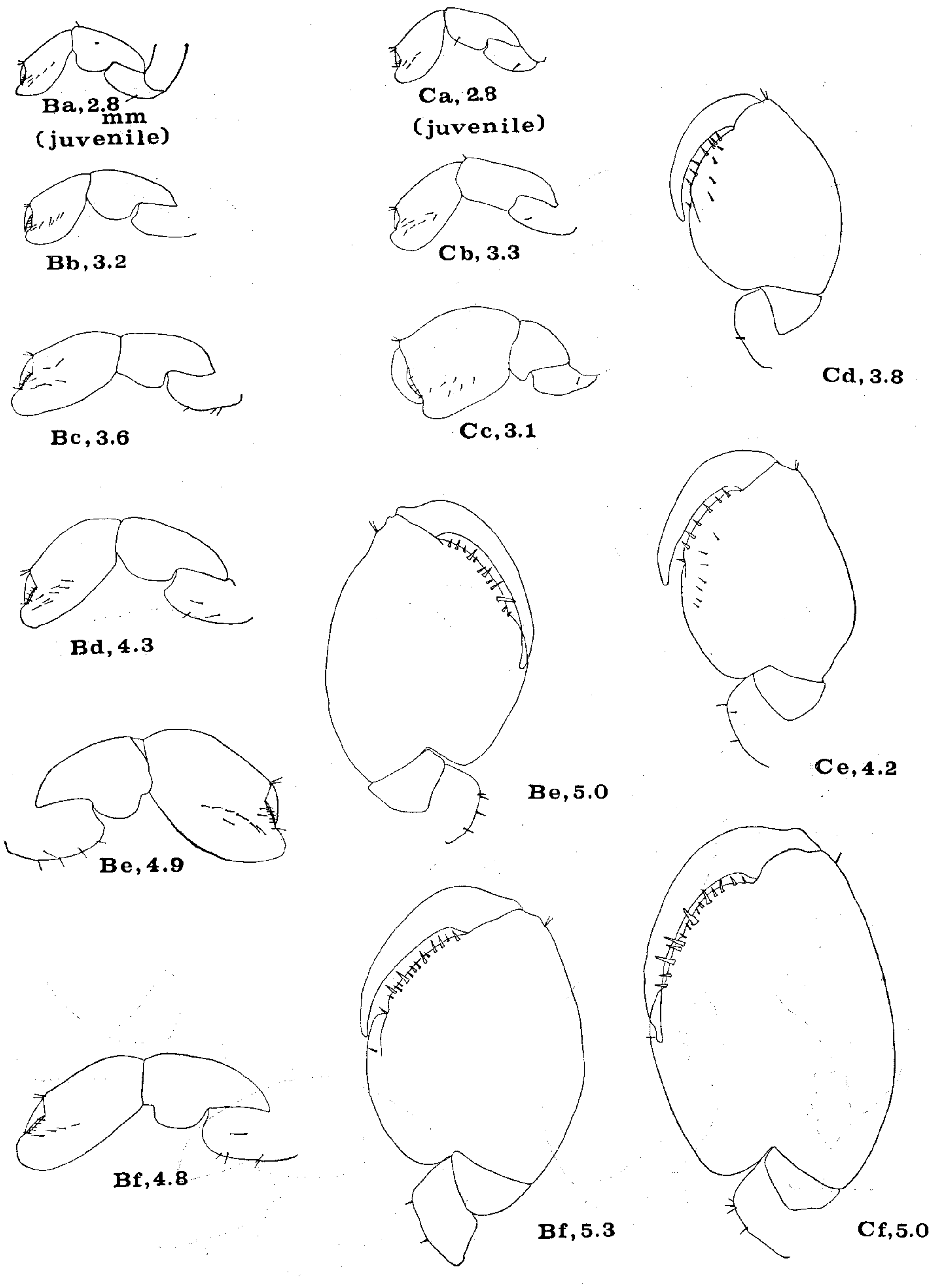

Fig. 3. Gnathopod II of *O. platensis* from Hatake-jima Island; B: 13 Jun. 1972, C: 13 Oct. 1972, All males, unless otherwise indicated. For legend see Text-fig. 2.

(January) and Fig. 3 (June and October). As is shown in Fig. 2, adult female (Af, 6.0 mm) has the article of the same shape to that of the juvenile (Aa, 2.8 mm), but of the larger size than the latter. On the contrary, the article of adult male (Af, 4.8 mm, 5.4 mm) differs both in size and shape from that of the juvenile. It becomes quite massive and the development of palmar margin is remarkable, which is in harmony with the enlargement of the 7th article. The palmar margin is furnished with a depression in the middle. The modification of the article is gradual, and transitional steps are seen from Ab (3.2 mm) to Ae (4.2 mm). General shape of the article in Ad (3.8 mm), Ae (4.4 mm) and Af (4.8 mm) is similar to that of Af (5.4 mm) except for the size, but their palmar margins are without the depression which appears only in larger specimens. So far as the specimens in January are concerned, the transitional steps are correspondent to the body length, but not to the molting age, since the same steps are frequently seen between specimens of nearly the same body length of different molting age (for example, between Ac, 3.8 mm and Ad, 3.9 mm), but not vice versa (see Ae, 4.2 mm and Ae, 4.4 mm).

In June, however, rather large males have the articles of juvenile- or mitten-like shape (Be, 4.9 mm and Bf, 4.8 mm). Massive article (Be, 5.0 mm and Bf, 5.3 mm) corresponding to those of adult males in January (Af, 4.8 mm and 5.4 mm) appears to develop directly from that of mitten-like shape. Thus the transitional steps of modification corresponding to Ab (4.0 mm) or Ae (4.2 mm) in January are largely omitted in June. In October, the way of modification of the article is similar to that in January, and the transitional steps are seen (Cc, 3.1 mm). Thus the pattern of the development of the article shows a seasonal variation remarkably in Hatake-jima Island.

In order to compare the patterns of the development of the article shown in populations of other localities with that of Hatake-jima Island, the relation between the size of the 6th article and the body length of each specimen is shown in Figs. 4 and 5. The seasonal comparisons are also made on a population from Ezura shore. Summer populations from Misaki (35°10′N, 139°40′E) and Onagawa (38°24′N, 141°30′E) are also cited for the geographical comparison. These two localities are northerly located to Tanabe Bay (33°40′N, 135°20′E). Fig. 4 shows that the relationships in the juvenile and the female can well be represented by a single straight line in logarithmic coordinates. By contrast, the relationship is divisible into three distinctive phases in the male. They are the juvenile phase, in which most individuals are unable to be sexed and the relationship is shown by a regression line with the least steepness, the intermediate phase exhibiting the steepest line, and the following mature phase showing the regression line of medium steepness. Measurements of the specimens depicted in Fig. 2 show that most of the articles in the transitional steps fall into the intermediate phase in the relationship, and massively developed articles with or without the depression on the palmar margin into the mature phase. The relationships of the juvenile or female phase, as well as the mature one, are not different significantly throughout seasons for the population of Ezura shore. However, as has been set out above, some seasonal variations are recognizable in the

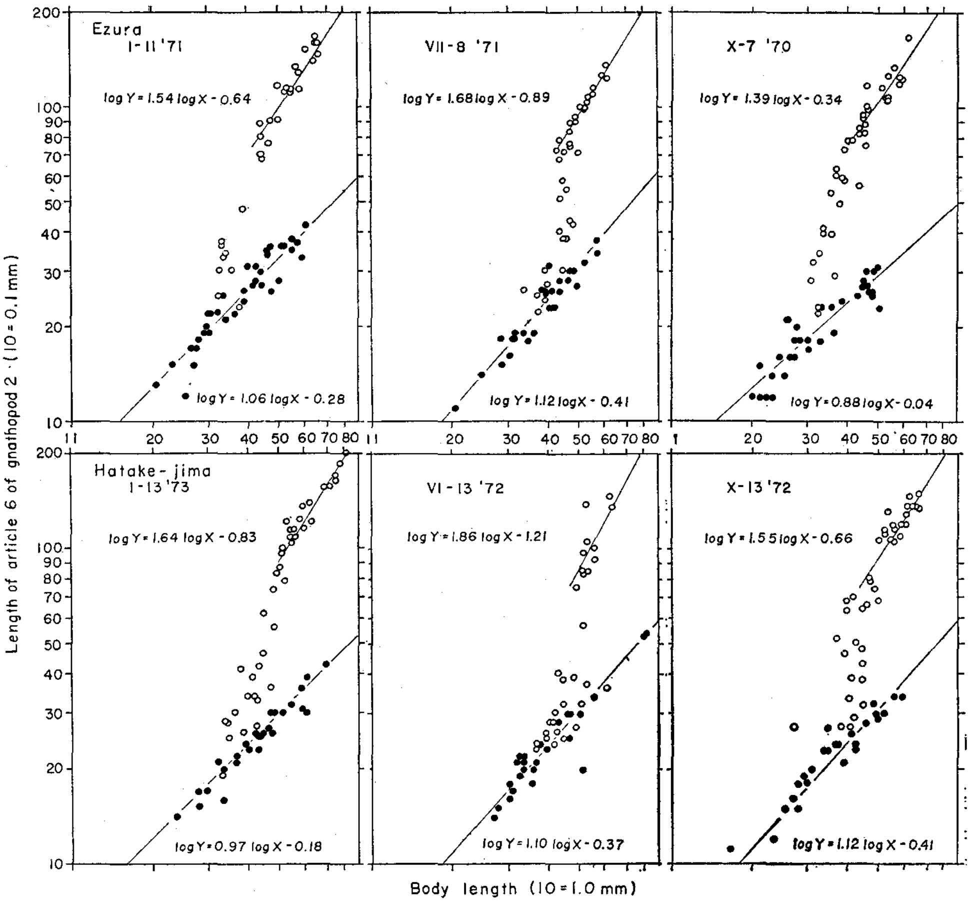

Fig. 4. Relations between body length and size of article 6 of gnathopod II. Solid circle: juvenile or female, hollow: male; from Tanabe Bay.

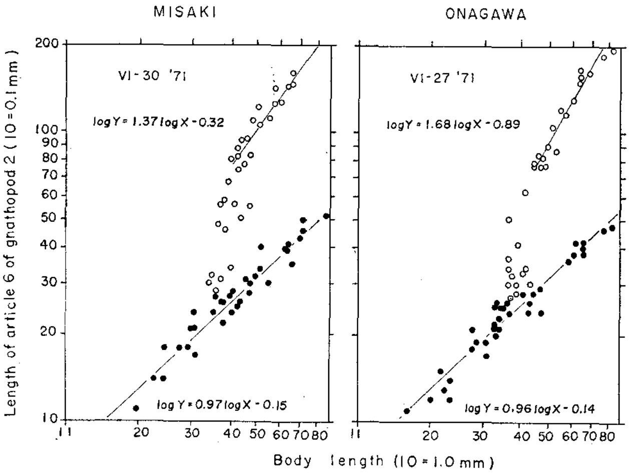

Fig. 5. Relations between body length and size of article 6 of gnathopod II, from Misaki and Onagawa.

intermediate phase. Namely the differentiation of the intermediate phase retards much in the summer population, in fact some fairly large males still bear mitten-like articles. Though, as the transitional steps are largely omitted, the attainment of massively developed articles is not influenced in parallel with the retardation. In addition, the body size whence the mature phase starts is smaller in October than that in the other months. In this case, the retardation of morphological differentiation is not appreciable, but moderate abbreviation of the transitional steps causes the minimal mature size to shorten. Although this trend of the seasonal variation is blurred by the individual variations in the population of Hatake-jima Island, general trend seems to concur with that of Ezura shore.

Geographical variation of the pattern of development can also be demonstrated by comparing Fig. 5 with the middle figures in Fig. 4. Populations of Misaki and Onagawa show less steep intermediate line than those of Tanabe Bay, and their patterns rather resemble those of the winter or autumn populations in Tanabe Bay. It is not known whether the seasonal variation exists in the pattern of development or not in Misaki and Onagawa populations.

Appearance of Depression on Palmar Margin

As has been said above, larger males have the 6th article of the gnathopod II furnished with a depression on the palmar margin. Development of the depression is examined in relation to the size of the article. Fig. 6 shows that the size of the article showing the first sign of the depression tends to be smaller in July and October than in January and April at both localities of Tanabe Bay. The depression appears at about 1.0 to 1.1 mm in the article size in January and April, and it is at about 0.9 to 1.0 mm in July and October. The relationships in summer populations of Misaki and Onagawa are shown in Fig. 7. In Misaki population, the relationship is not different from that of Tanabe Bay, but the appearance of the depression in Onagawa population is retarded in relation to the article size as compared to populations of other localities. From above comparisons, it can be admitted that the depression appears in the smaller article under the warmer condition than under

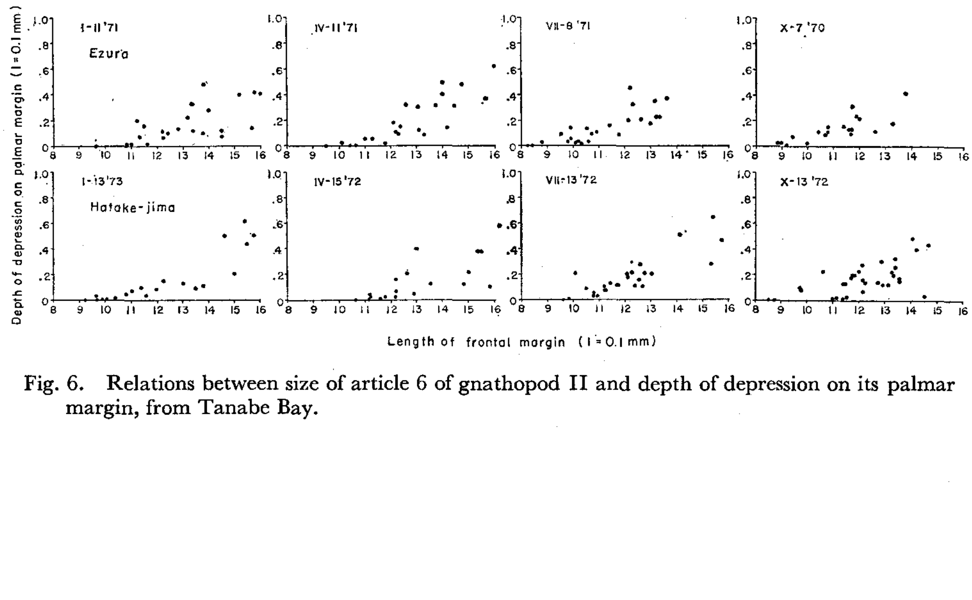

Fig. 6. Relations between size of article 6 of gnathopod II and depth of depression on its palmar margin, from Tanabe Bay.

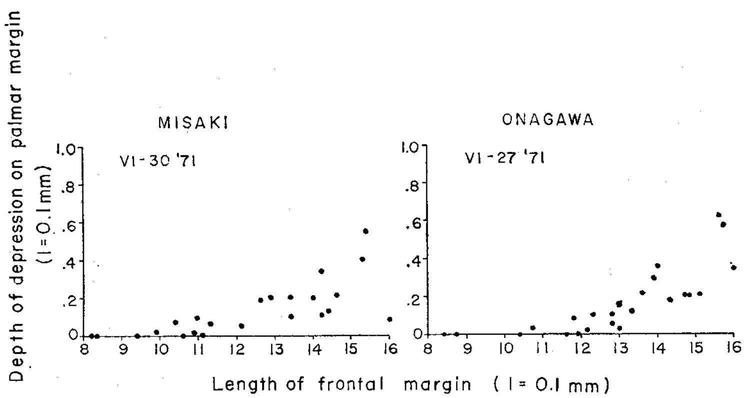

Fig. 7. Relations between size of article 6 of gnathopod II and depth of depression on its palmar margin, from Misaki and Onagawa.

Table 1. Variation of body length in male with 13 segmented flagella in antenna II.

Locality	Data	Body length[1)] (mm)	Sample size
Hatake-jima Island	III-13, '72	5.7±0.56	16
	IV-15	6.3±0.49	25
	V-12	6.2±0.57	13
	VI-13	5.5±0.49	19
	VII-13	5.3±0.52	20
	VIII-14	5.0±0.34	38
	IX-15	4.6±0.45	14
	X-13	4.9±0.33	19
	XI-13	5.4±0.64	25
	XII-13	5.3±0.44	66
	I-13,'73	5.6±0.63	28
	II-15	5.5±0.50	11
	III-20	5.7±0.46	18
Misaki	VI-30,'71	5.8±0.51	9
Onagawa	VI-27,'71	5.7±0.45	7

1) Body length is measured from the tip of head to postero-medial edge of pereionite VII.

the colder one. Table 1 shows the seasonal variation of the body length of the male. It is smaller in the warmer season than in the colder one. Since there is no appreciable differences in the relationship of the article size to the body length in the mature phase throughout the year, there exists a superficial parallelism between the mode of the seasonal variation of the body length and that of the critical size at which the diagnostic character is recognizable, after the mature phase is attained.

Discussion

It is of interest that the retardation of differentiation of a male sexual character in male is superficially corresponding to the seasonal fluctuation of female sexual character and activity. Female reproductive activities decline in summer, particularly in July, and this is caused by retardation of sexual maturation (Morino, 1978). Observed seasonal variations of sexual characters parallel in both sexes might be assignable to the same environmental factor, that is, "fluctuating temperature" (Morino, 1978).

Before going into taxonomical evaluations and phyletic considerations of gnathopod II and its variation, probable functions of the appendage will be mentioned.

Functions of Gnathopod II

The function of the gnathopod II has been suggested from behavioral observations. Since it shows a drastic sexual dimorphism during growth in the species of *Orchestia*, etc., it is reasonable to allocate to the appendage some particular functions inherent to each sex.

In the male, the enlarged "amplexing type" gnathopod is said to serve in seizing the female in the copulation. Williamson (1951) observed the mating behavior of *Orchestia gammarellus, O. mediterranea, Talorchestia deshayesii, T. brito* and *Talitrus saltator* in the laboratory. In these five species, only *Talitrus saltator* does not have an amplexing type gnathopod II, but a mitten-shaped one as in the female. He witnessed both the gnathopod II and the antenna II being used in holding the female during the amplexus and/or copulation in those four species, and the gnathopod II in *Orchestia mediterranea* in fighting against a second male for a female. Meanwhile, Morino (1972) observed mating behavior in *O. platensis* and said: "It was observed in *Orchestia platensis* that the male carried the female by use of the gnathopod I,..." Whether the gnathopods I or II is used in the copulation may thus depend on the species. In any case, enlarged gnathopod II is not indispensable for the copulatory behavior in the talitrid species, as is also demonstrated by the fact that the male of *Talitrus saltator* carries the female throughout the copulation with his long antennae.

Female gnathopod II has well developed pellucid lobe on the 6th article, which makes the appendage rather odd looking appearance. It is a semitransparent, non-masculated highly vascularized lobe with a scabrous surface (Hurley, 1968). The peculiar surface is furnished with a great number of minute finger-like scales. Graf and Sellen (1970) examined the fine structure and distribution of this semitransparent surface in *Orchestia cavimana, O. gammarellus, O. mediterranea* and *O. montagui.* They emphasized that the adult male had also the peculiar surface on the gnathopod I, whose gnathopod II was deprived of it. By taking into account the fact that the surface is not calcified but permeable to salts and oxygen, they assumed some physiological function. At the same time, they did not deny some mechanical function of the scabrous surface, such as taking foods or cleaning the mouth parts.

Meanwhile, a few investigators alluded to the function by direct observations of the behavior. McIntyre described it being used to comb oöstegites and Duncan has seen it being used to turn the eggs (Hurley, 1968). I had a chance to watch under the binocular microscope the behavior of a female with her youngs in her brood pouch. The gnathopod II was used to scrape eagerly the surface of the sand grains just in front of the head, and then directed into the brood pouch where youngs fidgeted in crowds. It was, as if, she fed them with food particles on the sand grains and drew up youngs in order. These observations strongly suggest that the female gnathopod II has a nursing function. The non-masculated, highly vascularized structure, as well as peculiar scales on the surface of the pellucid lobe, might be suited for the function.

Taxonomic Evaluation

In general, classification of species has been done on adult specimens; thus diagnoses of species are mostly of adult characters. This is mainly because distinguishing characters are generally better developed in adults than when in the young. There seems to be no theoretical ground to assign the biological weight to adults, except that they are direct carriers of the next generation. It goes without saying that in taxonomy it is desirable that every developmental stage of any species is definable. However, so far as morphological characters are used in defining taxa, the same diagnosis can not hold good for all the stages of growth.

In the taxonomy of the Amphipoda, the situation is severe because the animals of this group change their structural characters by molting, and "the different growth-stages of a species may be, and often are, described as so many different species, or sometimes even as different genera" (Sexton, 1924). In hope to find structural characters which are stable for every developmental stage, she examined the structural change during growth in *Gammarus chevreuxi* by gathering and comparing complete series of exuviae from a single newly hatched animal in the laboratory. She gave a taxonomical comment in conclusion, saying "It is at present not possible to establish specific characters which will hold good for both sexes at all stages of their growth, nor is it possible to distinguish the youngest stages of closely allied species by any structural character... The sideplates which may undergo less change than the other external parts, appear to be the most reliable characters for distinguishing the species of a genus, at least as far as *Gammarus* is concerned."

Theoretically, this suggestion of Sexton's should be supported. In practical taxonomy, however, characters which show the most drastic change during growth have often been used for this group of animals, because of the fact that these characters usually show much more diversity and are easier to be distinguished than those showing less changes. Taxonomical application of characters showing the drastic changes during growth is apparently limited to some size or age groups of the taxon in question. In these cases, the developmental stage where the diagnostic characters develop and appear can be specified.

Orchestia platensis has been clearly distinguished from the other Japanese species of the genus by the presence of the depression on the palmar margin of the 6th article of gnathopod II (Morino, 1975). This character, however, is shared with *Orchestia pickeringi* Dana known from the Hawaiian Islands (Barnard, 1955). Thus the character is not species-specific though still useful in recognizing the local faunules.

The development of the appendage bearing the diagnostic character shows marked seasonal variation in the population in Tanabe Bay. That is, the molting age when the appendage begins to transform greatly delays in summer population. However, the variation is compensated by abbreviation of the intermediate stages, and well-developed appendage appears at more or less similar size to those of the other seasons. In well-developed gnathopod II, the appearance of the diagnostic character on the 6th article is not strictly correlated with the size of the animals which fluctuates seasonally. Parallelism between seasonal variation of age-specific body length and the critical size where the character emerges, as has been stated above, suggests the correlation of the latter with molting age. In fact, in almost all males, irrespective of the body length, having more-than-13 segmented flagella of the antenna II, the diagnostic character has clearly developed. The demonstrated fact gives a significance to the character, which is of use in distinguishing closely related forms including the terrestrial ones, although other characters that are independent of sex and instar would be more useful taxonomically.

Sexual Dimorphism

Bulycheva (1957) critically reviewed the beach hoppers and allied groups in the world in the light of functional morphology and possible evolutionary pathway. She amalgamated several terrestrial genera into the *Talitrus* and confined the family Talitridae to embrace only four genera; *Talitrus, Talorchestia, Orchestoidea* and *Orchestia.* In them, *Talitrus,* characterized by little sexual dimorphism in gnathopod II, was regarded as the most primitive genus by the author.

Meanwhile, Hurley (1957) made an extensive taxonomic survey on terrestrial talitrids in New Zealand and suggested further subdivision of the genus *Orchestia* into supralittoral and terrestrial groups. In 1959, he noted that some terrestrial species of the genus *Orchestia* show gradual steps of modification of male gnathopod II from the supralittoral form to a "form not far removed from the terrestrial *Talitrus* gnathopod". By comparing the interspecific gradation of the appendages in *Orchestia* with developmental stages in *Talorchestia bottae,* he suggested the neotenic loss of the enlarged gnathopod II in the supralittoral *Orchestia* species.

Bousfield (1968) also mentioned that terrestrial talitrids in the world were composed of two types, one with distinct sexual dimorphism that was related to sea-shore species, and the other with suppressed sexual dimorphism that was not directly related to sea-shore talitrid species.

Recently Bousfield and Howarth (1976) described a new genus *Spelaeorchestia* from Hawaiian lava tubes, characterized by the gnathopod II of mitten-like shape in both sexes. They suggested that the male gnathopod II of the species "might be derived from *Orchestia* or *Parorchestia* by neotenic loss or failure to develop of the powerfully subchelate condition in gnathopod II of the male."

These notions advanced mainly as a result of recent taxonomical analyses of terrestrial forms seem to suggest that sexual dimorphism in gnathopod II has been suppressed in several independent phyletic lines currently recognized of the Talitridae.

The development of sexual dimorphism of gnathopod II in *Orchestia platensis* is subject to a marked variation, and some adult males at maturity still retain mitten-like shape. The same developmental variation of male gnathopod II is expected to be proved in other species of the other genera. The sexual dimorphism seems to be more or less liable to be suppressed in ontogeny. This fact favors the possibility of phylogenetic suppression or neotenic loss of the sexual dimorphism in the Talitridae.

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