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Larval Stages of a Parthenopid Crab, *Parthenope validus*, Reared in the Laboratory and Variation of Egg Size among Crabs

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The larvae of Parthenopidae have long been known since Gourret[1] first mentioned in 1884 the zoeae of *Parthenope massena* (Roux) as *Lambrus massena*. However, until recently the studies have been limited to the first stage zoeae[2,3] or planktonic materials[4-6]. Yang[7] was the first who described in 1971 the complete larval development of any parthenopid crabs. He succeeded to rear the larvae of *Parthenope* (*Platylambrus*) *serrata* (H. Milne Edwards) from egg to crab stage in the laboratory. This report presents an additional information on the complete larval development of a parthenopid crab and on variation of egg size among crabs with respect to their phylogenetic relationships.

Hishi-gani, *Parthenope* (*Platylambrus*) *validus* De Haan, is very common on sandy bottoms of 30-50 m of water from Tokyo Bay to Kyushyu in Japan and further extends southward to Korea, China, Samoa, Singapore, Torres Strait and Queensland[8]. Recently, this species has been divided into three formae; *validus* De Haan, *laciniatus* (De Haan) and *intermedius* (Miers)[8]. The ovigerous female from which the present materials were obtained was attributed to forma *validus* De Haan.

Materials and Methods

An ovigerous female was trawled on August 6, 1975 from the eastern Seto Inland Sea off Akashi City, Hyogo Prefecture. This crab laid another two batches of egg during confinement in the laboratory for 38 days without males. Two or three days were required between each hatching and subsequent egg laying. The larvae which have hatched from the last batch of egg were reared as far as megalopa.

The newly hatched zoeae were reared in a 500 *l* black FRP tank with 300 *l* of filtered sea water which was aerated through an air difuser stone. Culture of *Chlorella* sp. was added to the rearing water at a concentration of 30 - 50×10^4 cells per ml. at the beginning of the rearing. The temperature of the rearing water ranged from 21.5°C to 25.0°C. The larvae were fed according to the following schedule.

Measurements were taken under a microscope with an ocular micrometer eyepiece. Length from spine to spine in zoeae refers to the perpendicular distance from tip of rostral tpine to tip of dorsal spine. The carapace length was measured in lateral profile from the anterior margin of the ocular peduncle to the mid-dorsal posterior margin. The

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Foods	Daily ration	Zoea 1	2	3	4	5	Megalopa
Marine G[a]	0.5 g/m^3	←	—	—	—	→	
Soy bean waste	2.0 g/m^3	←	—	—	—	→	
Rotifer[b]	10 ind./ml	←	—	—	—	—	→
Artemia nauplii	1-2 ind./larva		←	—	—	—	→
Minced clam meat juice[c]	2.0 g/m^3	←	—	—	—	→	
Minced clam meat particles[d]	10-15 g/m^3						←→

a) Organic paste made of marine products. b) *Brachionus pricatilis* cultured in separate tank. c) Juicy fine particles which passed through 40 mesh. d) Large particles which are retained by 40 mesh.

width of telson was measured at level of insertion of the outer pair of inner setae. The following table shows the chronology of development and survival rates.

Date	Stage	Survival rate(%)
Sept. 12	Zoea 1 (Hatchig)	100
16-17	Zoea 2	80
20-22	Zoea 3	60
24-27	Zoea 4	30
27-28	Zoea 5	?
Oct. 1-3	Megalopa	10

Description of Larval Stages

Zoea

The zoea has a poor coloration with faintly difused yellow over the whole body and speckled with small black chromatophores at the base of dorsal spine, at the base of lateral spine on each side, at hind end of abdominal somites 2-5, on the telson and along peduncle of maxilliped 1.

Five zoeal stages were recognized. The zoea has all the spines on carapace. They are smooth and considerably shorter than the carapace length. The rostral spine distinctly curves dorsally, while the dorsal spine curves posteriorly and slightly longer than the rostral spine. The lateral spines are almost straight and about 1/3 as long as the rosral spine. Dorsal protubelance between eyes is prominent, while that near the posterior end of carapace is inconspicuous. The ventral margin of carapace is smooth.

Abdomen is moderately long with lateral knobs on somites 2 and 3. There are postero-lateral spines with rounded tip on somites 3-5. Those on somite 5 become very long in later stages. The telson is robust and assumes a form of a lyre. It is, less fork, much wider than long. The fork is smooth and strongly upturned distally. Its length is slightly less than the width of telson. There is small dorsal spine near the proximal end of the fork. This spine tends to be less prominent in later stages and is seemed, judging from its position, to represent the third outer spine in the primitive form. Its insertion is distinctly behind to that of the first inner seta. An another very minute spine may be present in early stages on the outer edge anterior to the dorsal spine. There are no extra inner setae in all but the last stage, in which an unpaired short extra seta may be present near the center. The second inner seta is distinctly longer than the others and is almost 1/2 as long as the fork. The central indentation on the hind margin of the telson is very shallow but wide and slightly less than 1/4 as wide as telson.

Antennule is simple and unjointed in all but the last stage in which it is bifurcated. Antenna is about 1/2 or somewhat less as long as the rostral spine. The spinous process bears two rows of spinules. Exopod ends in two spines, of which the inner is about 3 times as long as the outer, almost reaching tip of the spinous process. Endopod appears from stage 3, exceeding spinous process in the last stage.

Mandible is well developed with cutting and grinding teeth. A small unointed palp appears in the last stage. Maxillule has an endopod of two segments with 1 rudimentary seta on proximal segment which may be very difficult to see in early stages, and 6 setae in 2 or 3 groups near the tip of the distal segment. There is a feathered outer seta on basis from stage 3 and a simple seta on coxa in the last stage. Endopod of maxilla is unsegmented but 3 lobed on the inner edge with 2,2 and 3 setae from proximal to distal lobe. Endopod of maxilliped 1 is of 5 segments, and that of maxilliped 2 of 3 segments. Exopod of both maxilliqeds bears only 10 swimming setae each in the last stage. Pleopod buds appear from stage 4.

Stage 1. Length from spine to spine is 0.9 mm. Eyes are sessile. Abdomen is of 5 segments plus telson. Postero-lateral spines on abdominal somites 3-5 are small but distinct (Fig. 1, A and B). Telson, including fork, is only slightly longer than wide (Fig. 2, A). There are no endopod on antenna (Fig. 1, G), no palp on mandible, and no outer seta on maxillule. Scaphognathite of maxilla ends proximally in a feathered seta. Maxillipeds have 4 swimming setae on exopod. Rudiments of maxilliped 3 and legs are very minute.

Stage 2. Length from spine to spine is 1.1 mm. Eyes are stalked. Postero-lateral spines on abdominal somite 5 are almost as long as the somite. Maxillule has an outer feathered seta. Proximal end of scaphognathite is rounded. Maxillipeds have 6 swimming setae on exopod (Fig. 1 ; C).

Stage 3. Length from spine to spine is 1.4 mm. Abdominal somite 6 is segmented off from the telson. Postero-lateral spines on abdominal somites are elongated, those on somites 3 and 4 are almost as long as their respective somite and those on somite 5 are distinctly longer than the somite, well exceeding the hind end of somite 6 (Fig. 1, D). Antenna has a small endopod (Fig. 1, I). Maxillipeds have 8 swimming setae on exopod.

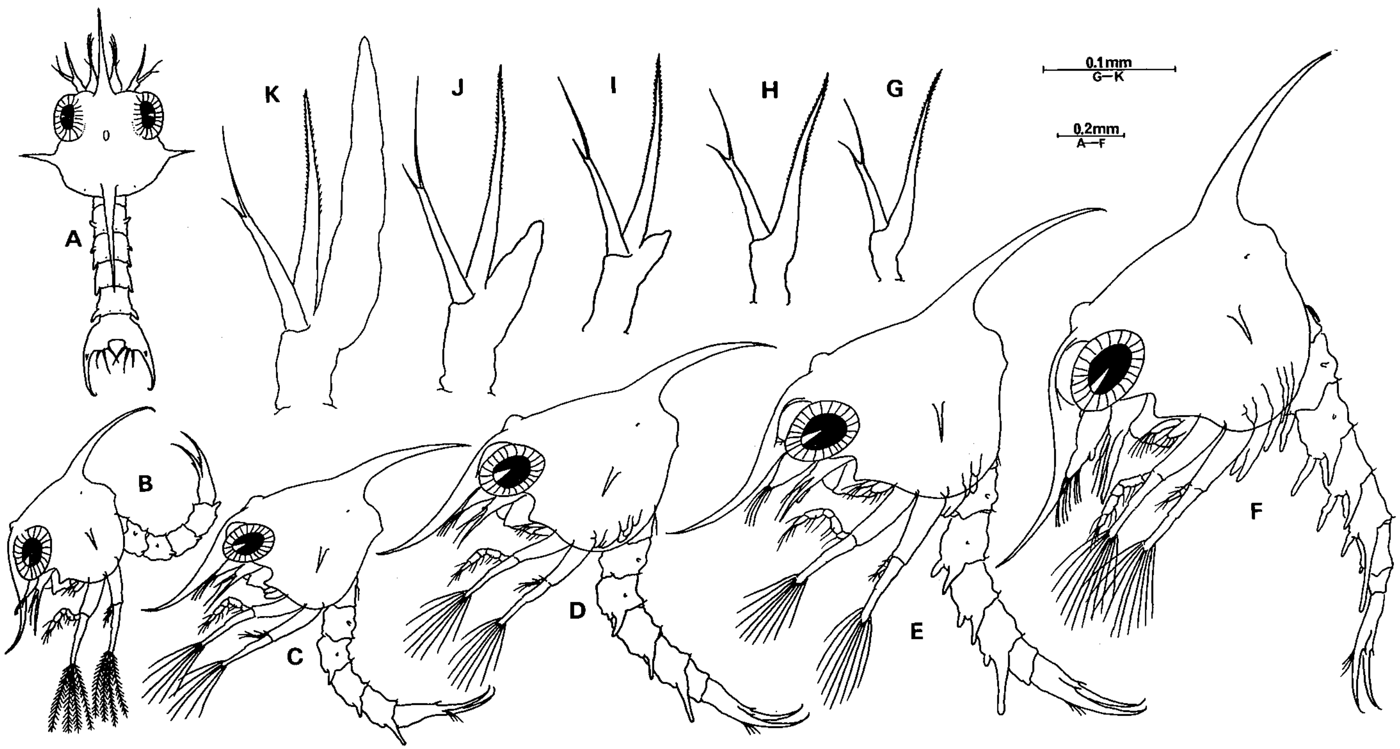

Fig. 1. *Parthenope validus,* zoeae. A, stage 1, dorsal; B-F, stages 1-5, lateral; G-K, antenna, stages 1-5.

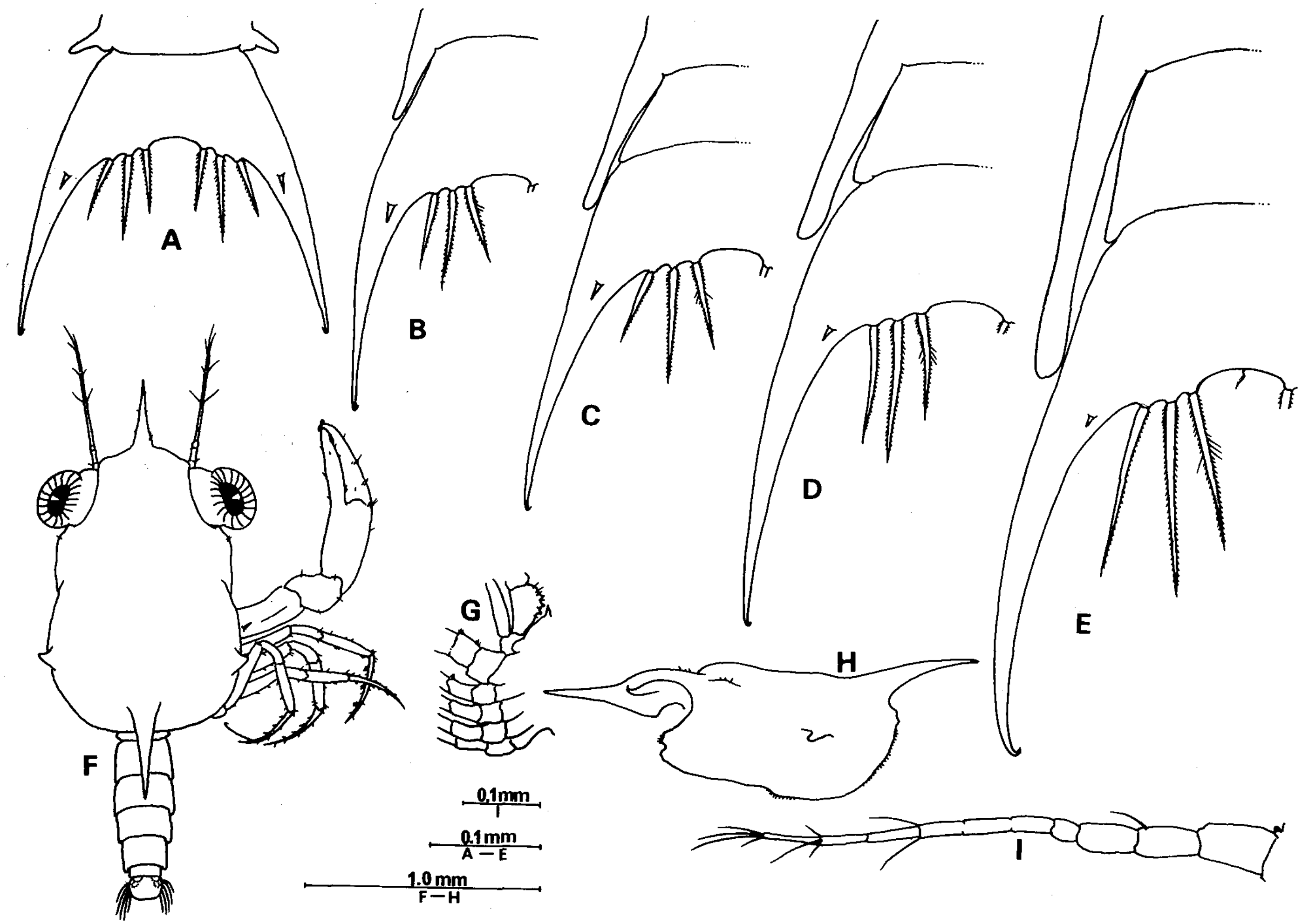

Fig. 2. *Parthenope validus*. zoeae(A-E) and megalopa(F-I). A-E, telson, stage 1-5; F, dorsal; G. Thorax and proximal segments of legs, ventral; H, crapace, lateral: I, antenna.

Stage 4. Legth from spine to spine is 1.7 mm. Antennal endopod is enlarged and slightly shorter than exopod less apical spines (Fig. 1, J). Maxilliped 1 has 9 swimming setae while maxilliped 2 has 10 on respective exopod. Leg buds are partly exposed from ventral margins of carapace. There are small pleopod buds on abdominal somites 2-5 (Fig. 1, E).

Stage 5. Length from spine to spine is 2.1 mm. Telson may has a short extra inner seta near the center of the hind margin (Fig. 2, E). Antennule is jointed with a small conical bud of the inner flagellum. Antennal endopod is very large, well exceeding tip of the spinous process (Fig. 1, K). Mandible has a small unjointed palp. Maxillipeds has 10 swimming setae on exopod. Pleopod buds are almost as long as the respective somite (Fig. 1, F).

Megalopa

Carapace length is 1.5 mm. Rostrum is squarish projecting almost horizontally in the center into a large spine. There is a dorso-median spine, projecting behind and being almost as large as the rostral spine, and a pair of small lateral spines on carapace. The carapace is, otherwise, comparatively smooth (Fig. 2, F and H).

Abdomen is of 6 segments plus telson. It is somewhat shorter than carapace less rostrum. The telson is semicircular and wider than long. There is a pair of well developed pleopods on abdominal somites 2-5. Uropods are very short, almost rudimentary with 5 seae.

Antennule is composed of peduncle of 3 segments, outer flugellum of 5 segments with many aesthetes and setae, and inner flagellum of 1 segment. Antenna is composed of a peduncle of 3 segments and a flugellum of 7 segments of which the segments 2-4 are still fused (Fig. 2, I), excceeding tip of the rostral spine by its distal 3 segments. Mandible is well calcified and assumes a form of a cutting tooth with a 2 segmented palp. Endopods of maxillule and maxilla are degenerated retaining a few rudimentary setae. Maxilliped 3 in armed along the inner margin of ischium with 3 teeth (Fig. 2, G).

Chiliped is large and stout, much longer and havier than the walking legs, with a spine at proximal dorsal edge of merus. Chela is about 1/4 as wide as long. Fingers are nearly as long as palm. The walking legs are of the same structure and markedly smaller than chiliped. Their dactyli are about 1.7 times as long as respective propodi, each with 3 barbed spines along the ventral edge and a pair of subterminal spines. The last leg has a feeler. There is a large epipod on maxilliped 1 and 3, 1 arthrobranch on maxilliped 3 and legs 2 and 3, while leg 1 (cheliped) has 2 arthrobranchs.

Discussion

Yang[7] observed, in *Parthenope serrata* reared singly in compartment boxes, that either fifth or sixth stage zoea changed into megalopa. He assumed that the six-staged zoeal development to be normal. In the present work on *P. validus*, on the other hand, many larvae were reared together in a large container, and the five-staged zoeal development was seemed to be normal inasmuch as no sixth stage zoeae were rocognized among samples taken every 3 or 4 days.

It is well known that the number of larval stages is not always constant in many decapods and the different rearing conditions such as temperature[9,10] and amount of available food[11-13] may cause intraspecific variation in larval development pattern. The last stage zoea of *P. validus* is very well comparable to the sixth stage zoea of *P. serratus* in development except the number of swimming setae on maxillipeds.

There is a good deal of evidences showing that the Oxyrhyncha is quite heterogeneous with respect to the larval characteristics. The known larvae of Hymenosomatidae, Majidae and Parthenopidae which constitute Oxyrhyncha in most recent taxonomy, have little in common with one anther as are summarized in the following table.

Larval characters	Hymenosomatidae	Majidae	Parthenopidae
Number of zoeal stages	2-3	2	5-6
"Anterior setae"	Absent	Present	Absent
Spines on carapace	Dorsal and lateral lost, while rostral persisted	Tend to lose either lateral, rostral or dorsal spine	All spines persisted
Antennal exopod	Rudimentary or absent	Ends in 3 spines or spinous as a whole	Ends in 2 spines
Abdominal somite: lateral knobs	On somite 2 only or absent	On somite 2 only or on somites 2 & 3	On somites 2 & 3
Telson	Parallel sided, indentation absent	Wider posteriorly, indentaion absent, narrow and shallow or wide and deep	Lunate, indentation wide but shallow
Outer spine of telson	0-2, when present, spine 1 persist.	1-3, spine 1 tends to persist	1-2, spine 3 tends to persist
Megalopa	Benthic	Pelagic	Pelagic
Source of data	Al-Kholy[14] Boschi *et al*[15] Lucas[16] Muraoka[17]	Kurata[18]	Yang[7] present paper

The most fundamental characters of zoeae of Parthenopidae which distinguish them from those of the other two families seem to be in the greater number of zoeal stages, the tendency to retain all the spines on carapace, the tendency to retain the third outer spine on telson, and the wide but shallow central indentation on the hind margin of telson. Apparently, the zoea of Parthenopidae is much more Brachyrhynch than Oxychynch.

The character of zoeal antenna of Parthenopidae ending in 2 spines of different

Table 1. Diameter of crab eggs across long axis. Species are arranged according to Sakai's classification[8)]

Species	Egg diameter in mm.
Subsection Drcmiacea	
Superfam. Dromiidea	
Fam. Dromiidae	
Petalomera wilsoni (Fulton and Gcant)	0. 85
P. granulata Stimpson	0. 81
Superfam. Homolidea	
Fam. Latreillidae	
Laterillia phalangium De Haan	0. 31
Subsection Oxystomata	
Fam. Dorippidae	
Paradorippe granulata (De Hann)	0. 37
Fam. Leucosiidae	
Subfam. Philyrinae	
Philyra pisum De Haan	0. 33
Myra fugax (Fabricius)	0. 33
Subfam. Leucosiinae	
Leucosia obtusifrons De Haan	0. 46
L. anatum (Herbst)	0. 46
Fam. Calappidae	
Subfam. Calappinae	
Calappa lophos (Herbst)	0. 31
Subsection Oxyrhyncha	
Fam. Hymenosomatidae	
Halicarcinus orientalis Sakai	0. 44
Trignoplax unguiformis (De Haan)	0. 58
Fam. Majidae	
Subfam. Inachinae	
Camposcia retusa Latreille	0. 78[2)]
Macrocheira kaempferi (Temminck)	0. 74
Pleistacantha sanctijohannis Miers	0. 62
Subfam. Oregoninae	
Chionoecetes opilio (O. Fabricius)	0. 66
Subfam. Acanthonychinae	
Pugettia quadridens quadridens (De Haan)	0. 50
P. incisa (De Haan)	0. 41
Huenia proteus De Haan	0. 45
Subfam. Pisinae	
Phalangipus hystrix (Miers)	0. 55
Hyastenus diacanthus (De Haan)	0. 49
H. elongatus Ortmann	0. 55
Pisoides ortmanni (Balss)	0. 33
Subfam. Majinae	
Menaethius monoceros (Latereille)	0. 32[2)]
Leptomithrax edwardsi (De Haan)	0. 76
L. bifidus Ortmann	0. 65
Schyzophrys aspera (H. Milne Edwards)	0. 73
Chlorinoides longispinus (De Haan)	1. 18
Subfam. Mithracinae	
Micippa thalia (Herbst)	0. 41
Fam. Parthenopidae	
Parthenope (Platylambrus) validus validus De Haan	0. 26

Table 1 (continued)

Subsection Brachyrhyncha	
Fam. Portunidae	
Subfam. Portuninae	
Portunus (*Portunus*) *trituberculatus* Miers	0.41
P. (*P.*) *sanguinolentus* (Herbst)	0.29
P. (*Monomia*) *gladiator* Fabricius	0.31
Charybdis (*Charybdis*) *acuta* (A. Milne Edwards)	0.30
Ch. (*Ch.*) *miles* De Haan	0.31
Ch. (*Goniohellenus*) *truncata* (Fabricius)	0.26
Ch. (*G.*) *bimaculata* (miers)	0.33
Thalamita prymna (Herbst)	0.35
Th. *picta* Stimpson	0.27
Subfam. Caphyrinae	
Lissocarcinus polybioides Adams and White	0.36
Fam. Xantidae	
Subfam. Xanthinae	
Atergatis floridus (Linnaeus)	0.37
A. *reticulatus* De Haan	0.49
Actaea savignyi (H. Milne Edwards)	0.52
Subfam. Chlorodinae	
Chlorodiella nigra (Forskal)	0.43[1]
Subfam. Pilumninae	
Pilumnus minutus De Haan	0.34
Fam. Goneplacidae	
Subfam. Carcinoplacinae	
Carcinoplax longimana (De Haan)	1.10
Eucrate crenata De Haan	0.33
Fam. Pinnotheridae	
Subfam. Pinnotherinae	
Ostrachotheres tridacnae Ruppel	0.65[1]
Subfam. Astenognathinae	
Tritodynamia japonica Ortmann	0.36
Fam. Ocypodidae	
Subfam. Macrophthalminae	
Macrophthalmus (*Macrophthalmus*) *dilatatus* De Haan	0.23
M. (*Mareotis*) *japonicus* De Haan	0.27
Subfam. Scopimerinae	
Scopimera globosa De Haan	0.33
Ilyoplax pusillus (De Haan)	0.30
Fam. Grapsidae	
Subfam. Grapsinae	
Grapsus strigosus Herbst	0.35[1]
Planes cyaneus Dana	0.39
Subfam. Varuninae	
Acmaeopleura parvula Stimpson	0.36
Eriocheir *japonicus* De Haan	0.45
Hemigrapsus sanguineus (De Haan)	0.38
H. *longitarsis* (Miers)	0.32
Subfam. Sesarminae	
Sesarma (*Holometopus*) *haematocheir* (De Haan)	0.33
Subfam. Plagsiinae	
Plagusia dentipes De Haan	0.36

1) Cited from Gohar and Al-Kholy[26]

2) Cited from Gohar and Al-Kholy[27]

lengths is fairly common among zoeae of Brachyrhyncha such as Portunidae[19,20], Calappidae[21] and Sesarminae[22,23], and may be derived from the first type antenna of Majidae in which the exopod ends in 3 spines of different length[18].

One of the reliable distinguishing characters of Parthenopidae zoeae from Brachyrhyncha zoeae having the same type of antenna is the distinctly upturned rostral spine on carapace. The same character was observed in *Heterocripta granulata* (Gibbes)[24] and seemed to be common among Parthenopidae zoeae, though it was not mentioned by the other authors[2,3,6,7] who reported larvae of Parthenopidae.

The presence of many larval stages in Parthenopidae deserves further discussion. Williamson[25], in the study of origin of crabs, proposed a hypothesis that, with the exception of primitive families, "all the Brachyura are descended from forms in which there were only two zoeal stages. The Majidae and fam. nov.? have retained this pattern of development but in nearly all other families of the Brachyura the number of zoeal stages has been secondarily increased". According to this hypothesis, Parthenopidae should be more advanced in evolution than Majidae. It is intersting to note here, in this connection, that certain members of Majidae produce large eggs, while the other members of Oxyrhyncha including Parthenopidae as well as many of Brachyrhyncha produce small eggs (Table 1). In addition, majid crabs which produce large eggs have, according to Kurata[18], zoea larvae of primitive characters with all the spines on carapace and original three outer spines on telson. In the other species of Majidae and all of the known Parthenopidae which produce small eggs, the zoeae are more or less modified in external characters with fewer spines on carapace and on telson than in the primitive forms.

These evidences strongly suggest that the ancestral crabs would produce large eggs and the general trend of evolution among crabs was toward the decrease in egg size to maximize the reprodutive rate. This strategy seems to have been successful to establish a large population of certain of the Portunidae, Cancridae and Xanthidae in the nutrient rich coastal waters in temperate and tropical regions where the interspecific competition is much more severe than in cold or deep waters. *Macrocheira* and *Chionoecetes* among Majidae which still retain the strategy of ancestral crabs producing large eggs, are confined in cold or deep waters and never be found in any appreciable quantity in the competitive environments.

The adoption of new strategy against straggle for existence in the nutrient rich environments should involved the production of small eggs in maximum possible number which, in turn, has resulted in the production of small zoeae less forward in development, so that a greater number of stages was required to reach metamorphosis.

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ヒシガニ，*Parthenope validus,* の飼育幼生と カニ類における卵径の変異

倉田　博・松田　泰嗣

実験室内でふ化・飼育した幼生にもとずいて，ヒシガニ幼生の外部形態の特徴を記載した。幼生期はゾエア5期とメガロパ1期とからなる。

ゾエアは甲に額角棘，背棘および側棘があり，額角棘は上方に，背棘は後方に湾曲する。腹節は，第2・3節に側突起，第3～5節に鈍頭の後側突起がある。尾節はたて琴の形をなし，幅広く，尾叉基部の背縁に各1棘がある。第2触角は額角棘の約1/2長で，外肢は2異長棘に終る。

メガロパは，額角中央が大きな棘となり，後方に背中棘と1対の側棘とがある。腹部は6腹節と尾節とからなり，尾肢に5毛がある。鉗脚は歩脚より著しく長大で，長節背縁に1棘がある。第4歩脚先端に1触毛がある。

現存するカニ類には，大卵小産と小卵多産の傾向が分化しており，前者はより原始的な生存戦略を，後者は栄養が豊富で競合がきびしい環境におけるより進歩した生存戦略を反映していることを論じた。ヒシガニ類は幼生の特徴に関する限り尖頭亜区（Oxyrhyncha）よりもむしろ方頭亜区（Brachyrhyncha）に近い。