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著者	OMORI Michio, CHIDA Yoshio
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Comparison of Life History between Two Caridean Shrimps, *Heptacarpus rectirostris* and *Palaemon macrodactylus*, with Different Life Spans.

Michio OMORI and Yoshio CHIDA

Department of Fisheries, Faculty of Agriculture,
Tohoku University, Sendai Japan

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Summary

Life history of a caridean shrimp, *Heptacarpus rectirostris*, with a one-year life span in Matsushima Bay located in northern Japan was described and compared with that of another sympatric caridean shrimp, *Palaemon macrodactylus*, with a two-year life span, in relation to the adaptive significance of their life historical traits. The life history of *H. rectirostris* in Matsushima Bay was different from that in the Seto Inland Sea located in southern Japan. Most of the female *H. rectirostris* spawn only once during a short breeding season, and the shrimps assigned to the short-term generation hardly occurred. They invest a large quantity of energy in reproduction and produce small eggs after reaching maximum body size rapidly. Such life history seems to be extremely r-selective. On the other hand, *P. macrodactylus* invests a relatively smaller quantity of energy in reproduction. They repeat spawning several times during a long, annual breeding season for three years after maturing early in their lives. Such a life history also seems to be adaptive to the coastal environments which fluctuate unpredictably.

Kawasaki (1) remarked that the marine teleosts had differentiated their life histories adaptively into three separate types in the process of their evolution, and discussed the relation of each life historical type to the fluctuation pattern of population size. His theory seems to be applicable to the decapod crustaceans. Life span, or maximum age, has theoretical relation to the two fundamental factors determining the fluctuation pattern of population size, mode of growth and that of reproduction (2). The authors reported the relation of life historical traits of a caridean shrimp, *Palaemon macrodactylus*, with a two-year life span to their reproductive strategy (3, 4). In the present study, life historical traits of another caridean shrimp, *Heptacarpus rectirostris*, with a one-year life span are described and compared with those of *P. macrodactylus* which is sympatric with

* GSI, gonosomatic index, is the gonad weight as a percentage of the body weight.

it, from the viewpoint of comparative life history.

Materials and methods

Shrimps were caught in Matsushima Bay, Miyagi, by brash-trap fishery. Approximately thirty bundles of bamboo grass were sunk along a fringe of a *Zostera* belt 1.5 to 2.0 m deep. Animals hiding in the bamboo grass were dipped up with a net of 3.0 mm in mesh size every twenty days as a rule. Animals were preserved in ten percent formaline-sea water and *H. rectirostris* was sorted out in the laboratory. Carapace length was measured and the body and gonad weighed. Sex was discriminated by the presence or absence of appendix masculinas of the second pleopods. Clutch of ovigerous females was weighed and the major and minor axes of their carried eggs were measured. Clutch size was counted and the developmental stage of carried eggs was examined under a microscope after staining them with Delafield's hematoxiline to define their fine structures. In addition to this, eight body parts were measured for both sexes in order to examine relative growth.

Results

Growth and breeding season

Since the carapace length distribution of *H. rectirostris* has a single mode, growth curves were drawn by connecting mean carapace lengths freehand. The smallest group occurring on May 21, 1983 is undoubtedly a newcomer produced in the same year (Fig. 1). The life span is evidently one year. Although females were ovigerous in two separate seasons, from late November through early February of the next year and from late May through early June, those in the latter season were very few. Excepting the difference in maximum size, growth patterns for both sexes are similar to each other. They grow at a high rate till the first breeding without reducing the growth rate (Fig. 1). On the contrary, as mentioned in the previous paper, *P. macrodactylus* grows only during the breeding season, and yearly growth rates become lower with age. The proportion of ovigerous females of *H. rectirostris* was only 32.5 percent even at the peak of breeding (Fig. 2). On the contrary, most female *P. macrodactylus* go on carrying eggs for several months. GSI* of non-ovigerous females began to rise at a high rate in late November with a rising percentage of ovigerous females, peaking in early January (Fig. 3). On the other hand, GSI of ovigerous females remained low. This suggests that most females spawn only once in a breeding season, unlike *P. macrodactylus*.

Changes in relative growth of males were observed about endo- and exopodites of the second pleopods, appendix masculinas of the second pleopods and rostrum (Fig. 4). The allometry changed at 3.5 mm in carapace length from positive to negative in the appendix masculinas and positive to isometric in the

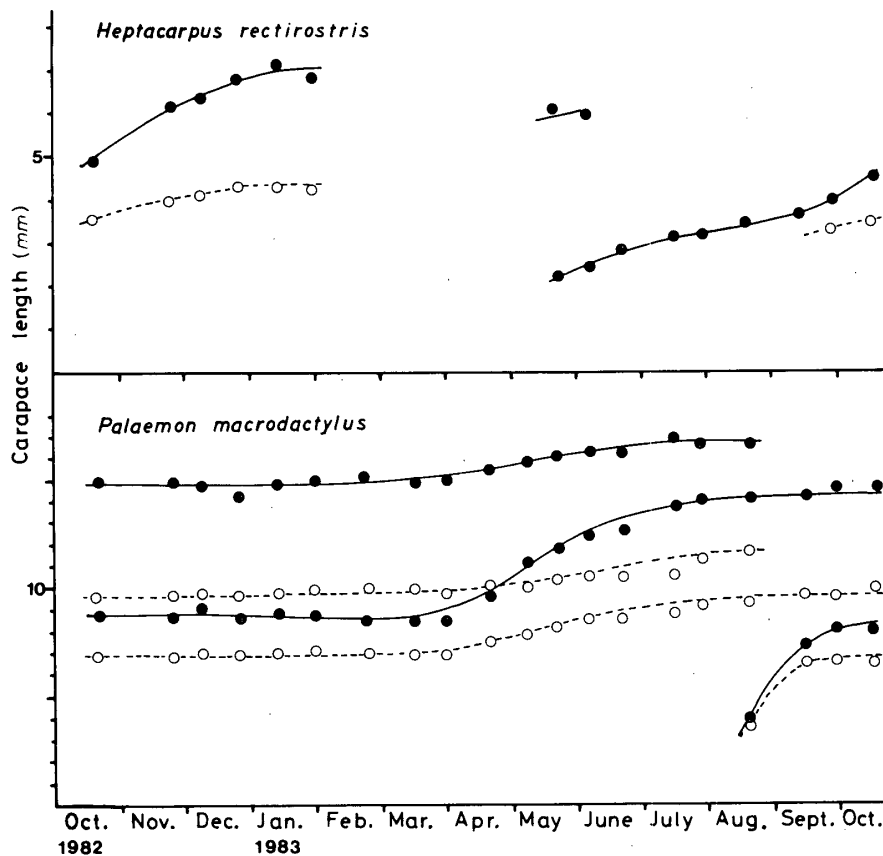


FIG. 1. Growth curves of two caridean shrimps, *Heptacarpus rectirostris* and *Palaemon macrodactylus*. Solid line: male; broken line: female.

endo- and exopodites of second pleopods. Morphological change of the rostrum was discontinuous, and a regression line adapted to larger shrimps shifted downwards parallelling that of smaller ones.

Three body parts of females showed changes in relative growth at 5.2 mm in carapace length. Regression lines adjusted to ovigerous and non-ovigerous females were clearly different from each other both in the height of pleuron and in the width of the second abdominal segment, showing discontinuity. On the other hand, the discontinuous change in regression lines was not true of the rostrum. The smallest size observed for ovigerous females was 5.2 mm in carapace length.

Clutch size and egg volume

The developmental stages of embryonic eggs were discriminated depending on a criterion proposed by the authors in a previous paper (3). Since most eggs of a clutch are in the same stage, they seem to be ovulated simultaneously.

The relation between clutch size and carapace length is shown in Fig. 5, with shrimps carrying Stage IV-V eggs excluded because of their considerably smaller clutch size. An allometric equation adjusted to *H. rectirostris* is $y = 2.7248x^{2.7461}$

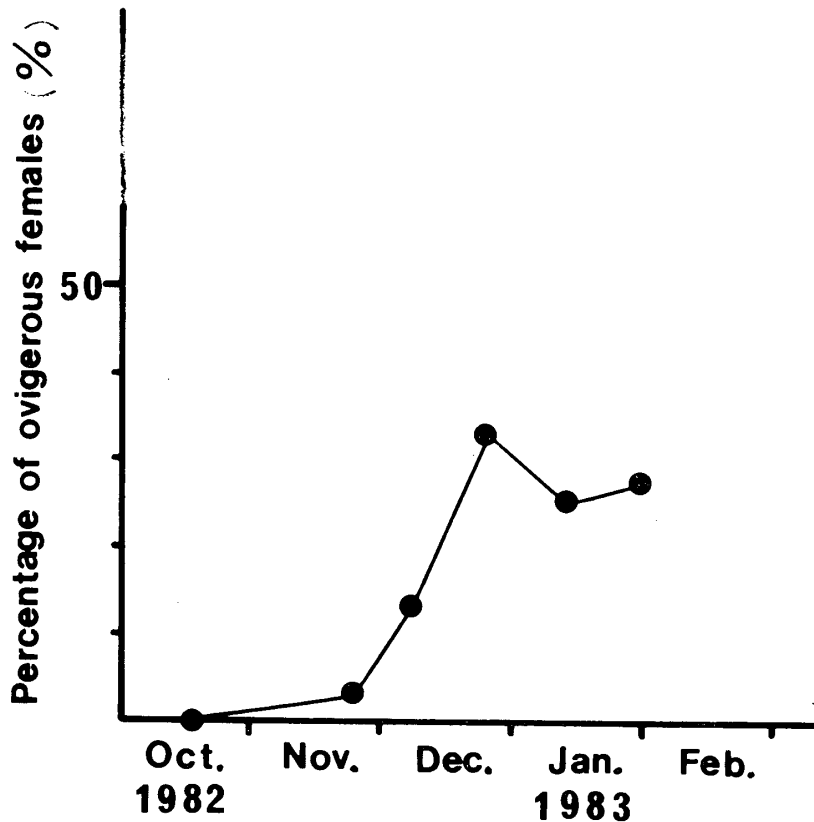


FIG. 2. Seasonal change in percentage of ovigerous females of *H. rectirostris*.

(Fig. 5), where x and y are carapace length and clutch size, respectively. Clutch size-carapace length relation for *P. macrodactylus* differs from age to age, and O+ females have the largest size-specific clutch size (3), for which the allometric equation is $y=0.0621x^{4.0455}$. When the clutch size is compared between *H. rectirostris* and O+ *P. macrodactylus*, that for the former is 2.7 to 3.5 times larger than the latter.

Mean volume of eggs within a clutch was estimated for 100 eggs, on the assumption that the egg is ellipsoidal.

The seasonal trend of the mean egg volume and environmental temperature are shown in Fig. 6. Egg size became larger with falling water temperature in late November, reaching a maximum in late December when the temperature was 8°C. Although the water temperature went on falling thereafter, egg size remained unchanged. Since *H. rectirostris* spawns once and grows little during its short breeding season, the temperature at gametogenesis seems to be closely related to the size of eggs to be ovulated, like *P. macrodactylus* (3).

The egg size of *H. rectirostris* is considerably smaller than that of *P. macrodactylus* with maximum and minimum volumes of 0.103 mm³ and 0.061 mm³ for the former and 0.171 mm³ and 0.102 mm³ for the latter.

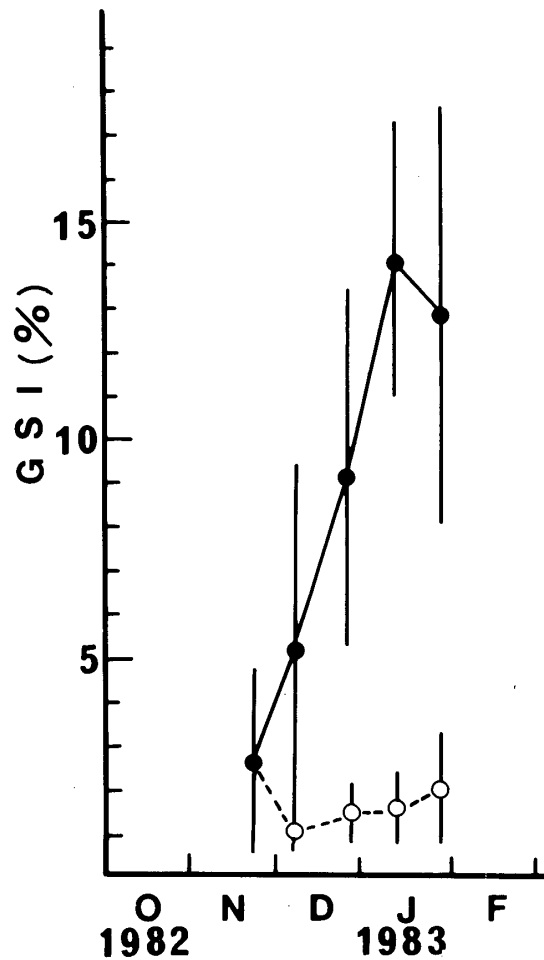


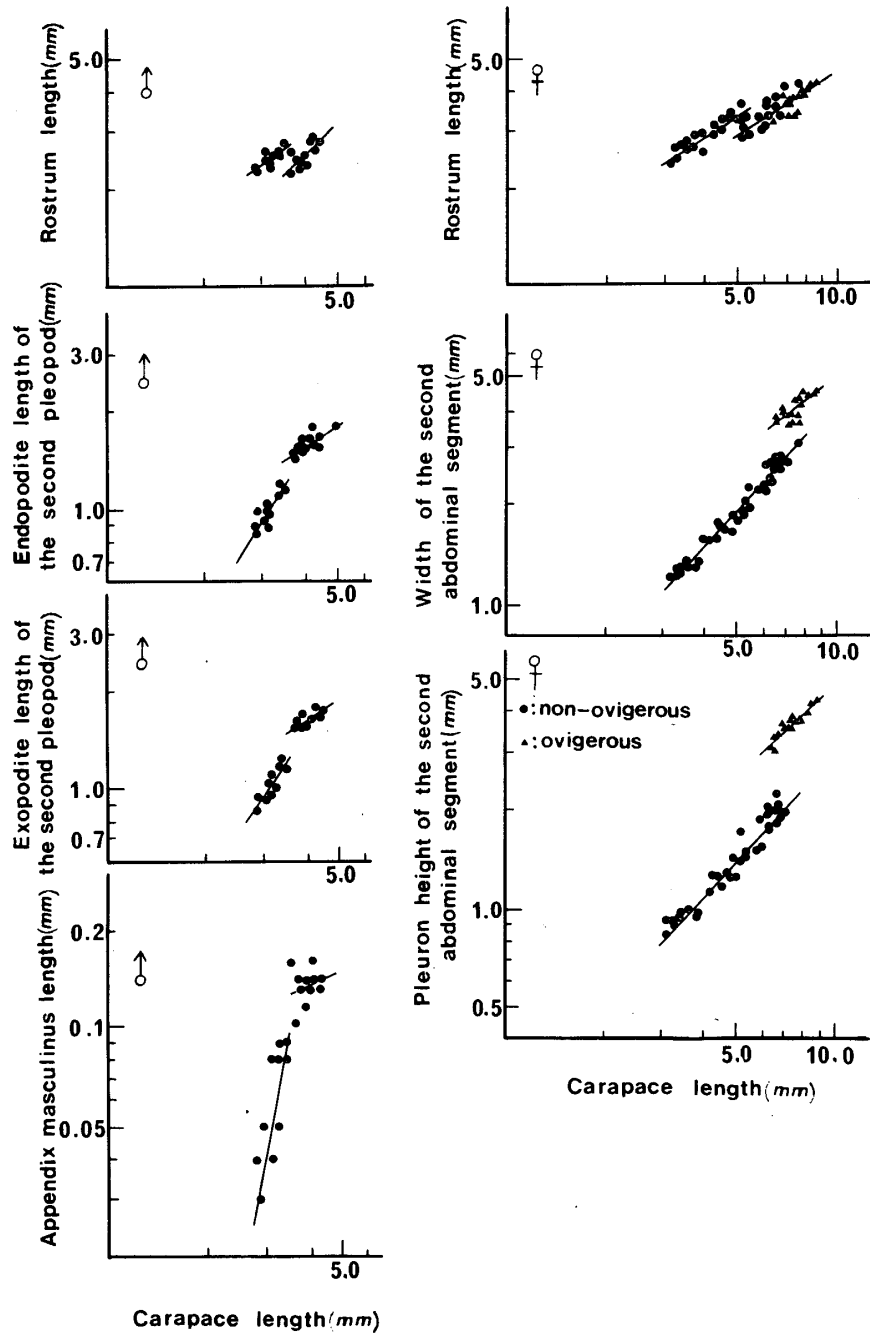
FIG. 3. Seasonal change in GSI of ovigerous and non-ovigerous females of *H. rectirostris*. Closed circle: ovigerous; open circle: non-ovigerous.

Reproductive effort

In the present study, "reproductive effort" is defined as the energy invested for gametogenesis and expressed in GSI. Distribution of GSI of *H. rectirostris* and that of O+ *P. macrodactylus* are shown in Fig. 7. The highest GSI of the former species was 1.2 times higher than that of the latter in spite of scattered observations. When clutch weight/body weight was compared between the two species, the maximum for *H. rectirostris* was 1.6 times larger than that for *P. macrodactylus*. From these facts, the reproductive effort of *H. rectirostris* appears to be relatively larger than that of *P. macrodactylus*.

Discussion

Several papers on ecological aspects of *H. rectirostris* from southern Japan have been published to date (5-8). According to Takeda (5), *H. rectirostris* in captivity repeats spawning six to seven times in its long breeding season from late

FIG. 4. Relative growth of *H. rectirostris*.

December through late June of the next year, and 75 percent of ovigerous females carry developed ovaries in the nature, showing recurring spawning. Kojima (8) also mentioned that the breeding lasted for six months from January to June. On the other hand, the breeding concentrated in two months in Matsushima Bay, and most ovigerous females did not carry developed ovaries. Yasuda (7) stated that a population of *H. rectirostris* in the Seto Inland Sea consists of two subpopula-

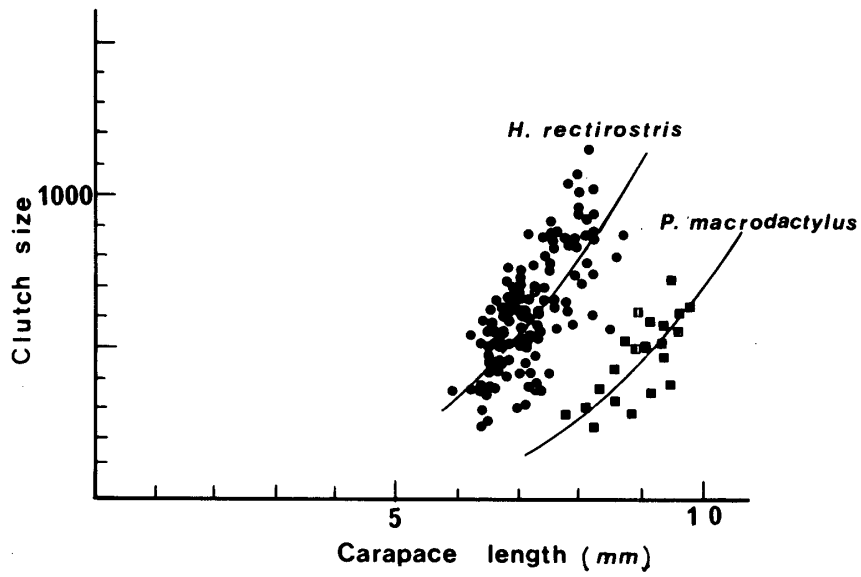


FIG. 5. Clutch size-carapace length relation of *H. rectirostris* and O+*P. macrodactylus*.

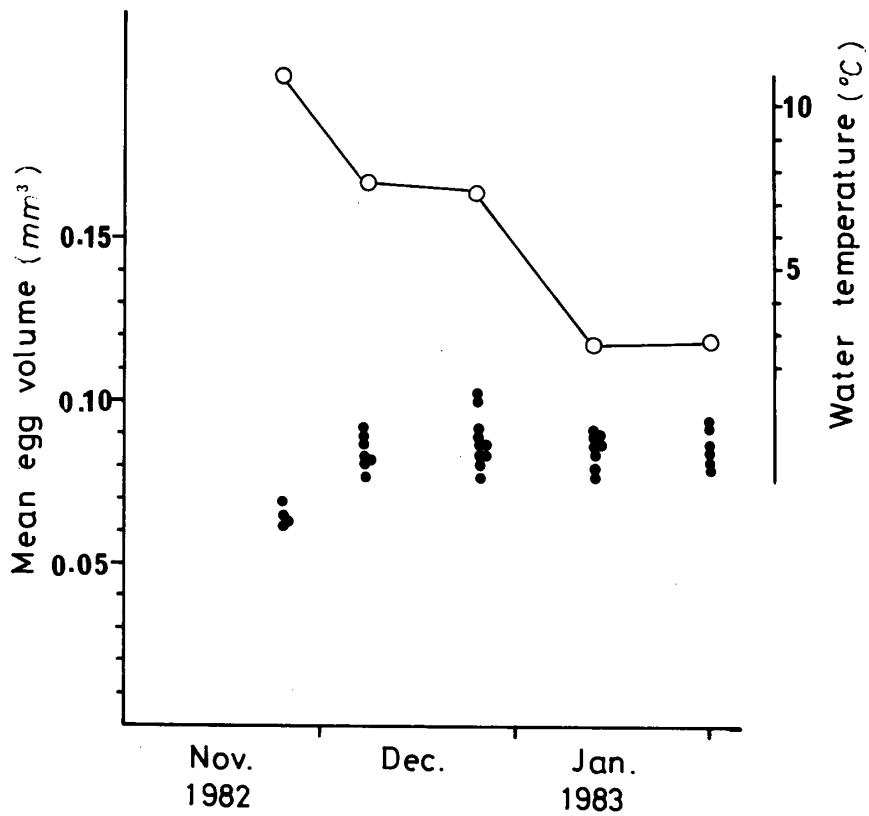


FIG. 6. Seasonal change in egg volume of *H. rectirostris* and ambient water temperature.

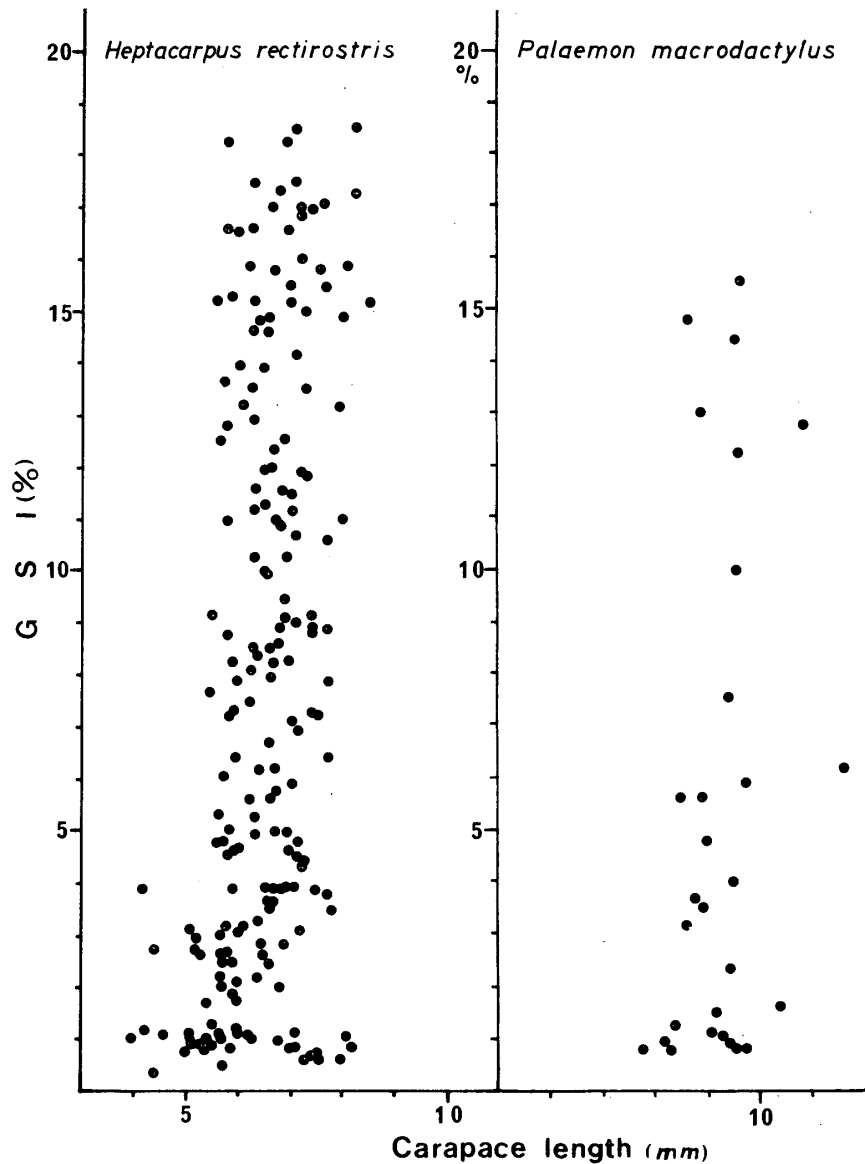


FIG. 7. Comparison of female GSI between *H. rectirostris* and *O + P. macrodactylus*.

tions with different generation times. The one is called short-term generation, which is produced early in the breeding season and dies after breeding in their first year. The other is called long-term generation, which is produced late in the season and mature in the next year. Ovigerous females caught on May 7 and June 6 would be assigned to the short-term generation, judging from their size and breeding time, but few of them were observed. Population size of the short-term generation of carideans is extremely different depending on place (5), and the number of females of *P. macrodactylus* spawning in their first year of life is influenced by the duration of warm climate suitable for breeding (3, 4). Although the genetic differences between local populations have not been found, a variety of phenotypes of life historical traits of caridean shrimps would occur in

a variety of environments where they have lived separately for a long time. The difference in life historical traits of *H. rectirostris* between southern Japan and Matsushima Bay located in northern Japan might be explainable from this point.

All of the relative growth lines of males inflect where the carapace length is 3.5 mm. The regressive relation of appendix masculina on carapace length convert there from positive to isometric, showing that the shrimp becomes adult.

Inflexion of all of relative growth lines of females occur at 5.2 mm in carapace length, where the smallest ovigerous females are observed. A discontinuous change in the relative growth of width and pleuron height of the second abdominal segment, or the expansion of the brood chamber, was ascribed to the adaptive morphological change caused by parturient molting by Kamiguchi (9) and the present authors (3), indicating that the shrimp become adult at 5.2 mm.

Generally speaking, larger eggs tend to bring larger larvae with well-developed feeding organs and higher tolerance to environmental stresses (10, 11). Since the egg of *P. macrodactylus* is larger than that of *H. rectirostris*, recruitment of the former would be more successful than the latter in the unpredictably fluctuating environments.

H. rectirostris inhabiting Matsushima Bay reproduces once during its short breeding season. On the other hand, *P. macrodactylus* repeats spawning five to nine times every year during its long breeding season. Brown and Russell-Hunter (12) demonstrated that the semelparous molluscs invest more effort in reproduction than the iteroparous ones. This would also be true of *H. rectirostris* and *P. macrodactylus*.

H. rectirostris continues to grow at a steady rate till maturation, but yearly growth rates of *P. macrodactylus* become lower with age. Provided that the asymptotic body size, L_{∞} , and size at first maturity, L_m , are approximated by the maximum size in Fig. 1 and size at puberty molt, respectively, the ratio, L_m/L_{∞} , will be 0.78 for *H. rectirostris* and 0.51 for *P. macrodactylus*, suggesting that the former grows more slowly once it matures but the latter continues a sustained growth (1).

Life historical traits of the two species are summarized in relation to their adaptive significance, as follows.

H. rectirostris which lives for a year lays smaller eggs once after reaching its maximum size quickly, investing a large quantity of energy in reproduction at the cost of future survival. Such a life history seems to be extremely r-selective and adaptive to the unpredictably fluctuating environment, as mentioned on marine teleosts by Kawasaki (1). As stated in previous papers by the present authors (3, 4), I+ and II+ female *P. macrodactylus* repeats spawning 6-9 times in the long breeding season in spite of spawnings once or twice in the short breeding season by O+ ones. The iteroparity of the former seems to lead to a high probability of recruitment success, even under the unpredictably fluctuating

environmental conditions. On the other hand, the latter could produce more offspring if the environmental conditions were suitable, in compensation for the low recruitment success. They, I+ and II+ females in particular, would have to keep their reproductive effort lower in order to adapt themselves to iteroparity. Such a life history, we think, is also adaptive to the unstable coastal environments.

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