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Ecological Information on *Oratosquilla oratoria* (Stomatopoda, Crustacea) with an Attempt to Estimate the Annual Settlement Date from Growth Parameters*1

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Ecology of a stomatopod crustacean, *Oratosquilla oratoria*, was studied in Hakata Bay, Japan. The relationship between carapace length (X, mm) and number of eggs spawned (Y) was $Y=0.04548X^{4.234}$. In the bay, the spawning season is from April to September and the peak month is June. Larvae were found mainly from August until October and the origin of the larvae collected seemed to be from the inner waters of the bay. Settlement of larvae mainly occurred in August or September. There was no obvious difference in the growth of the sexes and the growth rate at low temperatures (from November to the following April) was very low. Females spawned about two years after settlement. The life span after settlement was 3.0－3.5 years. Settlement date was estimated based upon the assumption that the ratio between the growth rates of metamorphosed individuals at two different water temperatures is equal to that between the embryonic development rates at these two water temperatures.

Oratosquilla oratoria (De Haan, 1844), a stomatopod crustacean, lives in the muddy bottom of bays and inlets in Japan, and is commercially important in these localities. Because an analysis of the population ecology of this species is useful for management of this resource, several studies have been carried out.

From Osaka Bay, Hayashi and Tsujino[1] reported the relationship between the size of *O. oratoria* and the number of eggs in the ovary. Komai[2] and Takamatsu *et al.*[3] counted the egg numbers present in a few egg masses nursed by the mother animal under natural conditions. A study estimating the relationship between size of females and egg numbers spawned, however, is lacking. Some reports have described the spawning season of *O. oratoria* in major fishing waters other than Hakata Bay, i. e., Ishikari Bay[4], Tokyo Bay[5,6], Osaka Bay[1], and the Seto Inland Sea[7].

Some authors have studied the larval ecology of *O. oratoria*. Komai[8] and Senta[9]

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reported that the larvae of this species were numerous in the coastal plankton of Japan. Information on the occurrence of these larvae has been reported from various areas around Japan, e. g. Ishikari Bay[10], Tokyo Bay[11], Osaka Bay[1], and the Seto Inland Sea[9]. None of the previous studies, however, have included detailed differentiation of the larval stages present. In other Stomatopoda, Morgan[12] and Williams *et al.*[13] classified the larval stages of *Squilla empusa* and *Heterosquilla tricarinata* larvae collected from the plankton, based on excellent monographs of their larval development[14, 15]. In this way they were able to study the temporal and spatial ecology of these larvae. Hamano and Matsuura[16, 17] described the larval development of *O. oratoria* from laboratory rearing and the terminally additive stage from nature. It is therefore possible to stage the larvae of *O. oratoria* captured in nature.

Regarding the growth of *O. oratoria*, there have been some reports from Tokyo Bay[5] and Osaka Bay[1, 18-21]. Growth estimation, however, has been unsatisfactory, because the reported modal trends of the size histograms of specimens captured in nature, although clear, have not provided a complete time series. Furthermore, a rearing technique for the species had not been established when these studies were conducted.

This paper consists of four main topics. First, the reproductive characteristics of *O. oratoria* are described by reporting the number of eggs spawned in aquaria, determining the spawning season in Hakata Bay based upon market sampling, and calculating the frequency ratio of spawning females to total females in each size-class to study maturation dynamics and help future resource estimation. Second, the growth of *O. oratoria* in Hakata Bay is reported, based on both growth analysis for immature animals captured using a bottom trawl and growth analysis for adults taken from a fish market. Third, the spatial and temporal appearance of *O. oratoria* larval stages in Hakata Bay is described. Fourth, a method for estimation of the annual settlement date of *O. oratoria* in nature is presented. To apply the method to natural populations, four elements were employed: growth equations for a constant water temperature of 25℃; equations describing the relationship between water temperature and embryonic development rate; daily water temperatures in nature; and an assumption that embryonic development and growth of metamorphosed animals have the same temperature dependence. The former two elements were described by Hamano and Matsuura[16, 22] and the latter two are presented here.

Materials and Methods

To estimate the relationship between body size and egg number, ovigerous *O. oratoria* were captured in Hakata Bay, northern Kyushu, in the western part of Japan, on May 8, 1985 and May 8, 1986. They were reared in large aquaria (Fig. 1 in Hamano and Matsuura[23]) containing many artificial burrows[24], 56mm × 600mm or 44mm × 450mm in diameter and length, under natural photoperiod and flowing water conditions. Krill, short-necked clams, and sardines were provided as food. Every day from the aquaria we collected any *O. oratoria*

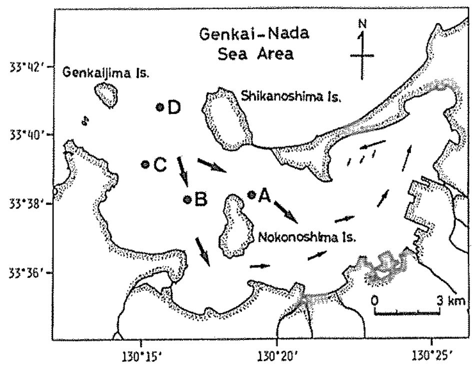

Fig. 1 Study stations A to D in Hakata Bay, Japan. The arrows show currents.

with a disc-shaped egg mass. The egg number in an egg mass was estimated as follows. (a) The egg mass was fragmented manually. (b) The eggs were placed in approximately 2*l* of water and the total volume, V_1, was measured in a volumetric cylinder. (c) The box-type, plankton sample dividing device of Motoda[25], was used to sub-divide the volume of suspended eggs four times. (d) The volume, V_2, of the subsample remaining in the device was measured and the number of eggs, N, in it was counted. (e) The total number of eggs, E, in the egg mass was calculated from $E = N\ (V_1 / V_2)$. (f) All subsamples were then reunited and steps (c) to (e), were then repeated. When two estimates of the total number of eggs, E_l and E_m satisfied the conditions $E_l > E_m$ and $E_l \times 0.9 < E_m$, the final estimate was calculated as $(E_l + E_m)/2$. For all egg number estimations, a difference between E_l and E_m of $< 10\%$ was always achieved between the first and second egg subcounts by steps (c) to (e).

The present species usually spawned within a week after the ovary on the ventral side of telson assumed the shape of an isosceles triangle[23]. To study the maturation dynamics of *O. oratoria* in Hakata Bay, their ovary shapes and carapace lengths (CLs) were monitored at the Meinohama Fish Market, where adults of the species, captured only in Hakata Bay, were landed. Two types of ovary were distinguished - undeveloped and developed, an advancement on the single triangular shape distinguished previously (Fig. 3 in our previous paper[23]). CL was also measured with a straight rule accurate to 1 mm. The frequency of females with a developed ovary in various market samples was summarized by CL size-class, at 1 mm size intervals, for each calendar month, irrespective of year, as follow. (a) For each market sample, frequencies of developed and total females in each size-class were calculated as moving means over three size-class intervals, so as to smooth length measurement errors. (b) Values for market samples in each calendar month, irrespective of year, were then amalgamated by size-class. (c) The occurrence of developed females in each size-class for each calendar month was then expressed as a percentage of all females in each class.

Specimens of *O. oratoria* larvae used in this study were collected by a larval net (diameter 1 m and mesh size 1 mm) deployed at four stations, A to D, in Hakata Bay (Fig. 1). The net was towed in the surface layer at each station for ca. 463 m (1.5 knots × 10 min). Collected animals were preserved in 5 % neutralized formalin. Then larvae of *O. oratoria* were removed from the plankton samples and their developmental stages were determined as described by Hamano and Matsuura[16, 17]. When the number of larvae captured in a haul exceeded 100 individuals, all larvae were counted, then 100 were selected at random and their stages identified; proportional conversions were then applied to the total count.

We employed three procedures to study the growth of *O. oratoria* in Hakata Bay. First, samples of immature animals were taken using a small bottom trawl (mesh size 8.7 mm) at Sts. A and B in the bay (Fig. 1). CLs of the collected specimens were measured with a slide caliper, accurate to 0.05 mm. The raw CL data were classified into size classes (width 2 mm, ≤CL<), and, then a Gaussian distribution was fitted to each frequency distribution, using a computer analysis based on Akamine's chi-squares minimum method[26]. Second, measurements were carried out at the Meinohama Fish Market mentioned above. The method of grouping individual CL was the same as that in the maturation study, described above. The size frequency distribution given by this method was assumed to reflect the typical distribution in a calendar month, and Gaussian distributions were then fitted by the computer method uesd above for immature animals. Finally, shell hardness was also examined. Soft-shelled individuals appeared rarely in this market, being unmarketable (fishermen discard both soft-shelled and juvenile animals). Nevertheless, we searched catches for soft-shelled individuals overlooked by the fishermen, because, in general, the incidence of these seemed to be in proportion to that of soft-shelled individuals captured in nature. We classified animals as soft-shelled, i. e. recently ecdysed, when the teeth on the telson could be bent by mild thumb pressure.

All field samplings were conducted at night once every month from October, 1982 to September, 1983 (detailed description of the sampling method is present in Hamano *et al.*[27]). Market samplings were conducted from June, 1983 to February, 1986. Specimens from the market were captured with bottom trawls from April to December and with gill nets in the other three months when trawling was prohibited.

In the present text, "CL" refers to carapace length measured along the midline excluding the rostral plate, which is illustrated and compared with other size measurements in Matsuura and Hamano[24].

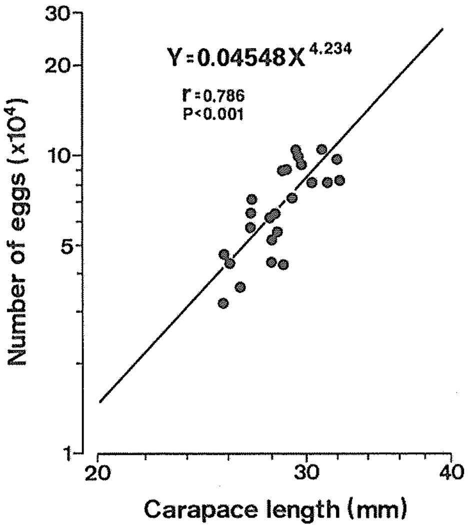

Fig. 2 Relationship between carapace length and number of eggs in the egg mass of *Oratosquilla oratoria* spawned in artificial burrows in aquaria.

Results and Discussion

Relationship between animal sizes and egg numbers

Egg numbers for 24 egg masses of *O. oratoria* were estimated. The range of CLs of spawning females was 25.7−31.9 mm and that of egg numbers was 32131 − 106379 eggs. A regression formula was applied to the relationship between the CL (X) of females and numbers of eggs spawned (Y) by the least squares method: $Y = 0.04548\ X^{4.234}$ ($r = 0.786$, $P < 0.001$) (Fig. 2).

For the present species, Hayashi and Tsujino[1] gave a regression equation between the body length (X: cm), shown as Kubo-BL by Matsuura and Hamano[24], and the numbers of eggs in ovary (Y), as $Y = (12.08\ X - 62) \times 10^3$. When we calculated the egg numbers produced by females of ca. 30mm CL using this equation and a regression between the CL and Kubo-BL, the values were similar to those calculated by our regression formula, given above. Therefore, we support Hayashi and Tsujinos' contention that *O. oratoria* extrude all eggs from the ovary in one spawning, i. e. that total fecundity is similar to relative fecundity. Although Komai[2] and Takamatsu *et al.*[3] reported that *O. oratoria* nursed $4 \times 10^4 - 5 \times 10^4$ eggs, we cannot comment on these numbers, because they did not describe the size of females.

Maturation dynamics in Hakata Bay

The total number of *O. oratoria* females examined was 3792 individuals in 64 samples. The females with a developed ovary on the ventral face of the telson appeared during April and September in Hakata Bay (Fig. 3). The peak month of occurrence was June. The spawning seasons of this species in various localities are summarized in Table 1. Based upon Table 1 we can conclude that in Japan, the spawning season of *O. oratoria* is during

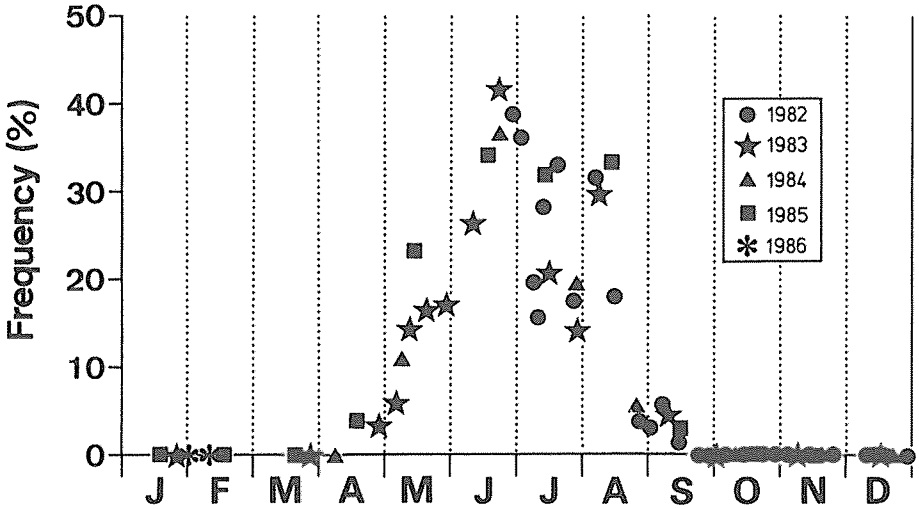

Fig. 3 Frequency (%) of occurrence of female *Oratosquilla oratoria* containing mature ovaries amongst all females larger than 20 mm carapace length (≒ the lower size limit for spawning females) in Hakata Bay. Maturation was established from the shape of the ovary on the ventral face of the telson. A total of 3792 females were examined in 64 samples from the Meinohama Fish Market, where fishermen land *O. oratoria* captured only in Hakata Bay.

Table 1. Spawning season of *Oratosquilla oratoria* in five different localities

Locality	Spawning season (peak month)	Reference
Ishikari Bay (western Hokkaido)	early June−mid June	Yorita[4]
Tokyo Bay (central Honshu)	mid May−early July (June)	Kubo *et al.*[5]
	May−August (late May−early July)	Hara *et al.*[6]
Osaka Bay (western Honshu)	mid May−mid September (May and August)	Hayashi and Tsujino[1]
The Seto Inland Sea (western Honshu)	May−early September	Senta *et al.*[7]
Hakata Bay (northern Kyushu)	April−September (June)	present study

Table 2. Expected egg numbers spawned by a female of *Oratosquilla oratoria* and frequency (%) of occurrence of females containing developed ovaries amongst all females in each size-class. Females with developed ovaries were distinguished by ovarian shape on the ventral face of the telson; they usually spawn within a week in aquaria[23]. No spawning females occurred in other months or size-classes

Carapace length (mm)	Number of eggs expected*	Frequency (%)					
		April	May	June	July	August	September
20	14668	0	0	5.00	0	0	2.77
21	18034	0	0	10.00	0	0	2.08
22	21960	0	0	32.86	8.33	3.57	1.28
23	26507	0	0	29.10	16.66	11.66	0
24	31742	0	5.00	35.25	23.55	18.29	3.62
25	37731	0	16.66	32.91	23.41	19.64	4.16
26	44546	0	10.00	36.74	22.52	18.04	5.00
27	52265	0	12.91	39.01	24.44	15.63	4.27
28	60965	1.66	15.52	40.31	29.76	19.69	5.40
29	70731	1.25	17.46	39.01	33.90	26.25	6.64
30	81649	1.47	18.39	29.17	31.53	26.22	7.59
31	93809	1.72	16.86	30.78	34.72	24.56	8.69
32	107306	2.77	21.11	30.14	38.88	23.89	0
33	122238	5.55	20.38	38.88	46.42	39.68	0
34	138708	5.00	36.90	25.00	53.57	22.50	0
35	156821	7.14	16.66	16.66	16.66	20.00	0
36	176687	0	16.66	5.00	0	12.50	0
37	198420	0	0	0	0	5.00	0

* Calculated by a regression formula: $Y = 0.04548 X^{4.234}$, where X(mm) is carapace length and Y is egg number.

summer, especially around June.

Table 2 represents the frequency of females with a developed ovary in each size-class during each month of the spawning season. The size of the smallest female was 20mm CL; females of this size were present in June and September. There are three previous reports on the size, as body length, of the smallest spawning female of *O. oratoria*. From these reports, female size as CL was calculated using regression formulae[24], giving 24.8 mm for Tokyo Bay[5], 21.8 mm for Osaka Bay[1], and 20.1 mm for the Seto Inland Sea[7]. Including Hakata Bay, where the smallest female having a developed ovary was 20mm CL, we can conclude that ca. 20mm CL is the smallest size at which females can spawn in nature.

Table 2 also shows maturation dynamics for each size-class. In April, the size of the smallest female with a developed ovary in the telson was 28mm CL. Those in May and June, however, were 24mm and 20mm, respectively.

This indicates that generally larger *O. oratoria* start to spawn earlier than smaller individuals. We observed that the second egg laying of this animal occurred about 40 days after the first spawning, at 25℃ in aquaria[23]. Consequently, in Hakata Bay, females which spawned early in the spawning season can spawn again in the same season since the water temperature of the bottom water is still sufficiently high[28].

Distributional ecology of larvae in Hakata Bay

The total number of *O. oratoria* larvae collected in this study was 3900. Many copepods, chaetognaths, a sergestid shrimp, *Lucifer penicillifer*, were captured, as well as several fish larvae, decapods, and other stomatopods.

O. oratoria larvae in Hakata Bay occurred mainly from August until October (Table 3). During this period, the greatest number of larvae occurred in the inner bay area (Sts. A and B). Currents flow from the mouth of the bay into the inner waters by way of both northern and southern routes around Nokonoshima Island, and then circulate counterclockwise growing weak in the inner waters[29] (Fig. 1). During this season, however, in the mouth of the bay, Sts. C and D, larvae were older than those in the inner waters, Sts. A and B. These facts suggest that the origin of pelagic larvae of *O. oratoria* described here were from the inner waters of the bay.

Most individuals were in the fifth to seventh larval stages in August, when larvae were most abundant. Larvae in these stages required 19 − 32 days to metamorphose at 21 − 28 ℃[16]. Water temperatures in the surface layer of the bay were very high in August (Table 3), thus planktonic larvae present on August 10 in this bay, would be expected to metamorphose to juveniles within one month.

During later larval stages, the *O. oratoria* larvae float near the bottom in nature[9] and in aquaria[16]. All specimens used in this study were collected from surface water layers, consequently the low numbers of later stage larvae captured at each station (Table 3) may be underestimates. We have previously reported that *O. oratoria* appears to have considerable flexibility for adaptation to various environments likely to be experienced during larval life[16]. As a part of that phenomenon, long-lived larvae occurred in December and January. Similarly some larvae in the terminally additive stage[17] were present in Hakata Bay, during September and December.

Growth in Hakata Bay

The growth of a single year-class cohort was followed at both Sts. A and B (Fig. 4). Animals were captured in September for the first time, newly settled on the sea bottom, and showed little growth from November to the following April. A remarkable decrease in the numbers of animals occurred between June and August at St. A, and July and August at St. B. This was also observed in other benthic animals and Hamano *et al.*[27] thought it was due to migration to better habitats, away from eutrophied areas.

In this study, 6495 individuals were examined from 64 market samples. There was no obvious differences in growth between sexes of *O. oratoria* (Fig. 5). A cohort with a mean of about CL 22 mm occurred first in market samples during November. Although the cohort grew little from November to the following April, growth recommenced in May and mean CL reached over 30 mm by November. Again, size remained unchanged until April and growth recommenced in May. Subsequently, the cohort grew to CL 33 mm after five months, and then it disappeared from catches. Growth rate was always at a high level from September to November (Fig. 5).

Table 4 gives the incidence of soft-shelled *O. oratoria*. The occurrence of many soft-shelled individuals from September to November indicates that ecdysis occurred frequently during these months, corresponding to the high growth rate from September to November determined from size distribution

Table 3. Occurrence of larvae of *Oratosquilla oratoria* at four study stations in Hakata Bay. Specimens were collected by towing a larva net (diameter 1 m and mesh size 1 mm) in the surface layer at each station for ca. 463 m (1. 5 knots × 10 min) at night. When number of larvae collected in a haul exceeded 100 individuals, all larvae were counted, then 100 were selected at random and their stages identified; proportional conversions were then applied to the total count

Date	St.	Surface water temp.(℃)	Number of larvae per haul	Larval stages by Hamano and Matsuura[16,17]											
				I	II	III	IV	V	VI	VII	VIII	IX	X	XI	TAS*
June 14, 1983	A	18.1	2	—	—	—	—	—	2	—	—	—	—	—	—
	B	19.8	3	—	—	—	—	—	3	—	—	—	—	—	—
	C	18.1	1	—	—	1	—	—	—	—	—	—	—	—	—
	D	18.8	0	—	—	—	—	—	—	—	—	—	—	—	—
July 13, 1983	A	25.6	15	—	—	9	1	3	1	1	—	—	—	—	—
	B	25.3	1	—	—	1	—	—	—	—	—	—	—	—	—
	C	24.8	1	—	—	1	—	—	—	—	—	—	—	—	—
	D	24.2	2	—	—	—	1	—	—	—	—	1	—	—	—
Aug. 10, 1983	A	29.7	1023	—	—	—	41	327	348	205	61	41	—	—	—
	B	29.4	1014	—	—	—	112	314	233	243	81	20	10	—	—
	C	29.5	320	—	—	—	3	48	90	131	42	6	—	—	—
	D	28.0	514	—	—	—	—	82	170	175	62	15	10	—	—
Sep. 30, 1983	A	24.3	197	—	—	—	—	4	2	12	73	49	33	18	8
	B	24.2	86	—	—	—	—	—	—	7	33	14	21	7	4
	C	24.5	11	—	—	—	—	—	—	3	6	—	1	1	—
	D	24.5	41	—	—	—	—	—	1	—	12	14	7	4	3
Oct. 13, 1982	A	22.1	369	—	—	—	—	7	66	144	114	18	15	4	—
	B	22.1	211	—	—	—	—	6	6	32	63	51	40	6	6
	C	22.2	72	—	—	—	—	1	1	6	39	17	7	—	1
	D	21.7	6	—	—	—	—	1	—	2	2	1	—	—	—
Nov. 16, 1982	A	18.5	0	—	—	—	—	—	—	—	—	—	—	—	—
	B	19.1	1	—	—	—	—	—	—	—	—	—	—	1	—
	C	19.4	3	—	—	—	—	—	1	—	1	1	—	—	—
	D	19.2	1	—	—	—	—	—	—	1	—	—	—	—	—
Dec. 10, 1982	A	13.8	1	—	—	—	—	—	—	1	—	—	—	—	—
	B	15.8	1	—	—	—	—	—	—	—	—	—	—	—	1
	C	14.5	0	—	—	—	—	—	—	—	—	—	—	—	—
	D	15.8	0	—	—	—	—	—	—	—	—	—	—	—	—
Jan. 11, 1982	A	10.0	1	—	—	—	—	—	—	—	—	1	—	—	—
	B	11.4	4	—	—	—	—	—	1	1	1	1	—	—	—
	C	13.9	2	—	—	—	—	—	—	2	—	—	—	—	—
	D	13.4	0	—	—	—	—	—	—	—	—	—	—	—	—

* The terminally additive stage.

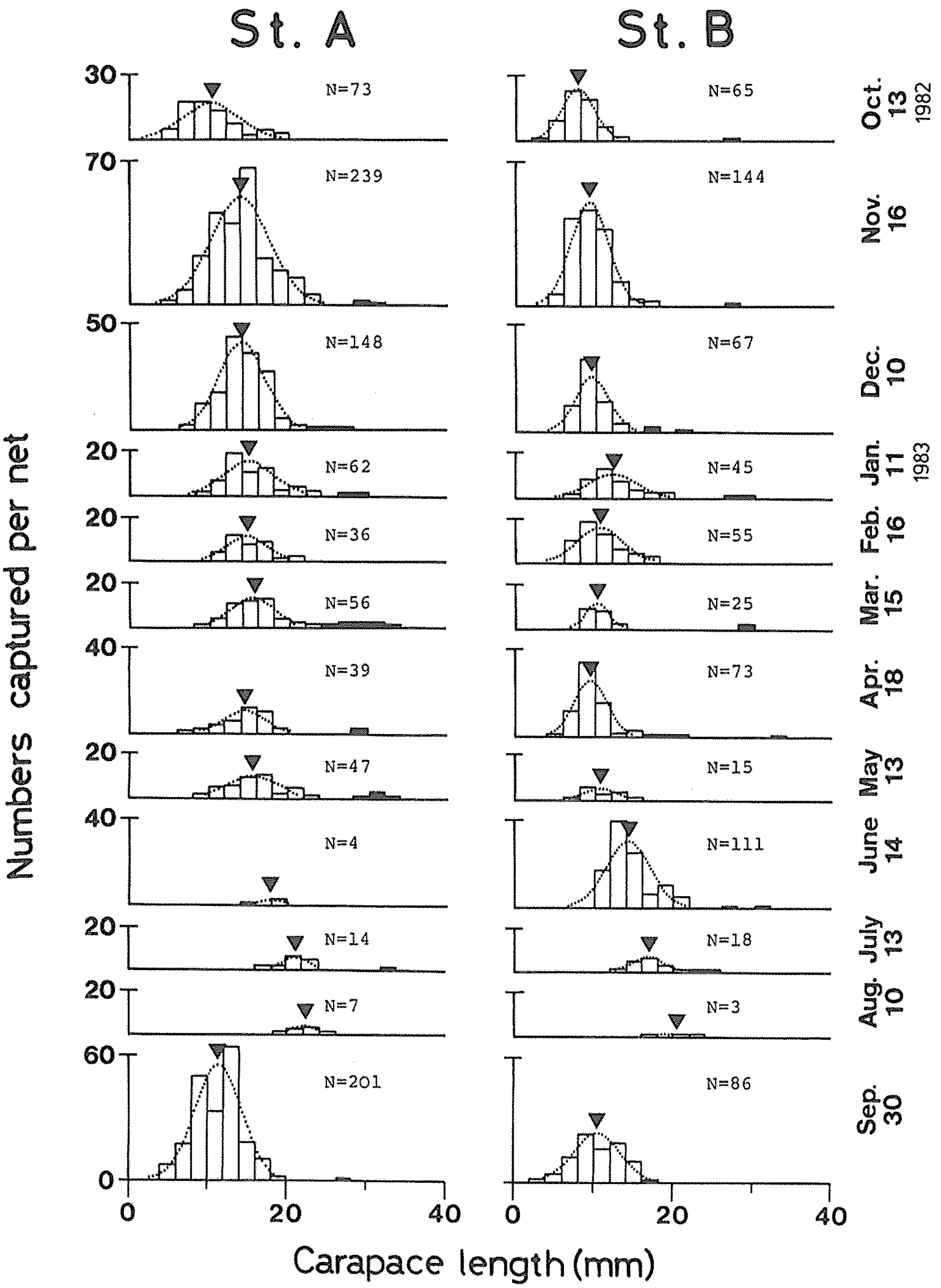

Fig. 4 Size distribution of *Oratosquilla oratoria* captured using a small bottom trawl in Hakata Bay. Triangles show the means of the fitted Gaussian distributions.

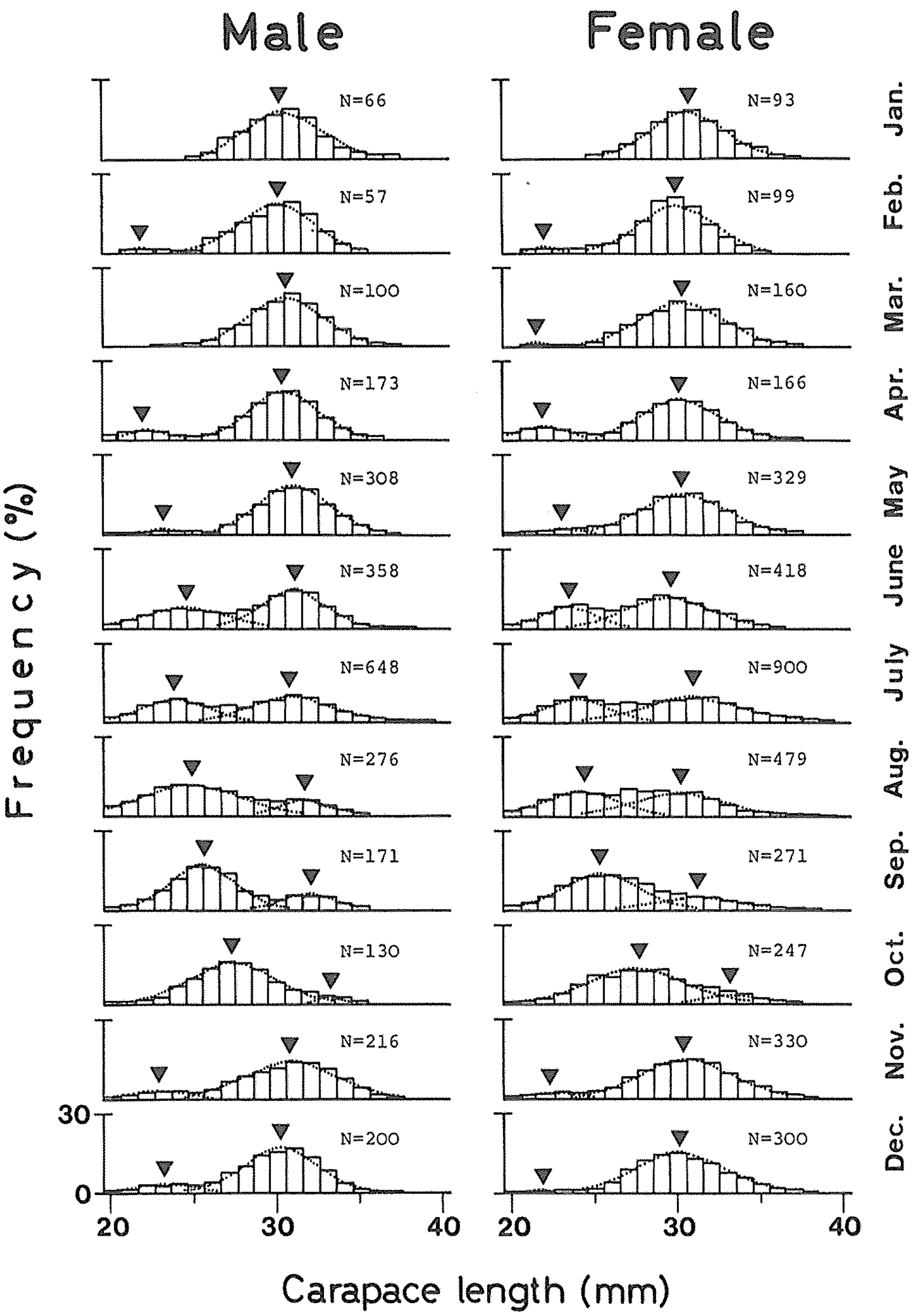

Fig. 5 Size distribution of *Oratosquilla oratoria* landed at the Meinohama Fish Market from Hakata Bay. Classification method is described in text. Triangles are the means of the Gaussian distributions.

Table 4. Incidence of soft-shelled *Oratosquilla oratoria* at Meinohama Fish Market from Hakata Bay. Investigations were carried out from 1982 to 1986

Month	Number of samples	Sex	Number of animals examined (A)	Number of soft-shelled animals (B)	B/A × 100 (%)
Jan.	3	♂	66	0	0
		♀	93	1	1.1
Feb.	2	♂	57	1	1.8
		♀	99	3	3.0
Mar.	2	♂	100	0	0
		♀	160	0	0
Apr.	3	♂	173	0	0
		♀	166	0	0
May	6	♂	308	0	0
		♀	329	0	0
June	5	♂	358	0	0
		♀	418	1	0.2
July	11	♂	648	2	0.3
		♀	900	5	0.6
Aug.	7	♂	276	0	0
		♀	479	0	0
Sep.	6	♂	171	5	2.9
		♀	271	3	1.1
Oct.	7	♂	130	1	0.8
		♀	247	6	2.4
Nov.	6	♂	216	2	0.9
		♀	330	9	2.7
Dec.	6	♂	200	4	2.0
		♀	300	1	0.3

analysis.

In the present study, each cohort of *O. oratoria* showed a wide range of individual sizes (Figs. 4 and 5). This was due to the protracted spawning season, from April to September in Hakata Bay, and the adaptative flexibility of larval life, whereby the larva delays metamorphosis and stays in a terminally additive stage until bottom conditions become favourable[16, 17].

To establish the settlement period of *O. oratoria* larva in this bay, we used the mean CLs of young animals in September 30 (CL 10 − 11 mm) and October 13 (CL 8 − 10 mm) (Fig. 4). Juveniles of *O. oratoria* required 50−60 days and 40−50 days after metamorphosis to grow to these sizes, respectively, at a constant 25 ℃[22]. The temperature of bottom water in

Hakata Bay is ca. 25 ℃ in September and ca. 22 ℃ in October[28], and therefore the mean settlement period of *O. oratoria* larvae is probably in August or September as suggested above.

For the 24 immature and 45 adult mean CLs of cohorts (Figs. 4 and 5) of *O. oratoria* in Hakata Bay, a growth curve can be drawn by eye (Fig. 6). From June to August at St. A and from July to August at St. B, with the migration of benthic animals to better habitats[27], the number of *O. oratoria* decreased considerably (Fig. 4). Therefore the three values from June to August at St. A, and the two values for July and August at St. B should be removed from Fig. 6 to obtain a more realistic curve. With this correction, the slope of the curve from ca. CL 13 mm in May to ca. CL 20 mm in August in Fig. 6 is less pronounced.

In this paper, we estimated the smallest size of spawning females to be ca. CL 20 mm, and the spawning season of *O. oratoria* in Hakata Bay to be from April to September. From Fig. 6 and indications described above, this species takes a year to grow to CL 20 mm after settlement on the bottom. By the time they reach this size, however, the spawning season is almost over, so there is insufficient time for female maturation and spawning. Therefore, they must spawn for the first time ca. two years after settlement. Females can also spawn again ca. three years after settlement. In general, the female survives two spawning seasons in Hakata Bay and seems to spawn once or twice a spawning season. Thus, we can conclude that generally a female of *O. oratoria* experiences spawning two to four times in this bay during its life.

Table 5 shows a comparison of the growth rate of *O. oratoria* in three different localities. In general, the life span of the species is three years, or so, in Japan. Growth was

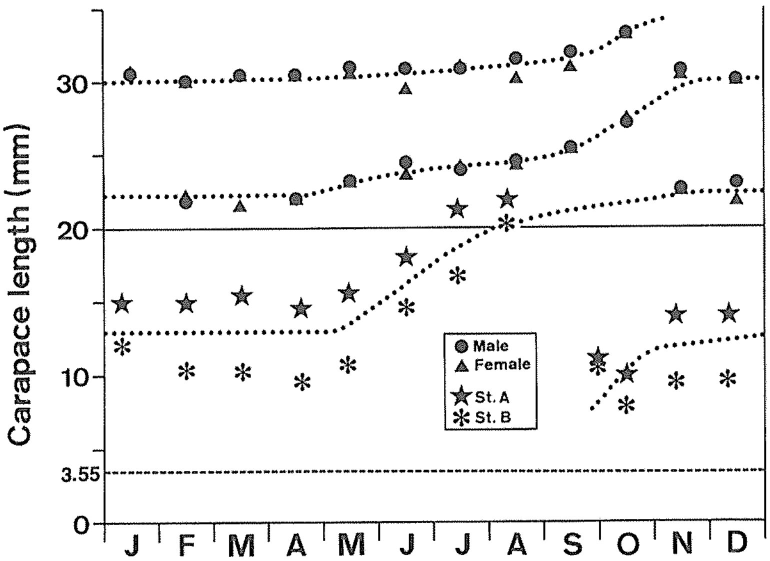

Fig. 6 Growth curve of *Oratosquilla oratoria* in Hakata Bay. The curve was fitted by eye. The 24 immature (triangles in Fig. 4) and 45 adults (those in Fig. 5) mean in the cohort were used. A broken line shows the mean size of juveniles newly settled on the bottom, after Hamano and Matsuura[16].

Table 5. Comparison of the growth rate of *Oratosquilla oratoria* in Tokyo Bay, Osaka Bay, and Hakata Bay. The body length (Kubo-BL) in other studies was converted to carapace length with the regression formula given by Matsuura and Hamano[24]. The values, excepting Hakata Bay, were calculated by growth equations and those from Hakata Bay were estimated by eye in Fig. 6

Locality	Hatching date	Age after hatching				Reference
		1 year	2 years	3 years	4 years	
Tokyo Bay	June 1	18.1	25.9	31.6	—	Kubo *et al.*[5]
Osaka Bay	June 1*1	20.2	31.6	39.1	—	Hayashi and Tsujino[1]
	June 1	14.4	23.5	29.9	34.3	Ishioka[18]
	June 1	24.2	35.3	40.3	—	Ishioka *et al.*[19] Ishioka[20]
	June 1	25.0	37.6	—	—	Ishioka *et al.*[21]
Osaka Bay	August 1*2	16.9	29.1	36.6	—	Hayashi and Tsujino[1]
Hakata Bay	July 15*3	18.5	24.1	30.8	—	present study

*1 The early hatching group.
*2 The later hatching group.
*3 The day was roughly estimated by referring to the duration of larval life under rearing condition given in Hamano and Matsuura[16] and the settlement day: September 1 (= mid way over August and September).

overestimated by Ishioka *et al.*[21], because the water temperature of bottom waters in Osaka Bay, where their study was conducted, is under 20 ℃ on the average in a year (calculated from the data by Hayashi and Tsujino[1]) and even the animals reared at a constant 25 ℃ could not grow to CL 25 mm over a year from settlement[22]. There are also some differences between previous values and ours in Table 5. We cannot make further comment, however, because of errors in the conversion from the body length to CL and because the populations studied are very different in time and place from each other. Furthermore, there has been no field work which clearly explains the growth pattern of the species in these bays.

From this study, the following conclusions can be drawn for the typical growth and life cycle of *O. oratoria* in Hakata Bay: there was no obvious difference in the growth of the sexes; settlement of larvae occurred in August or September; the growth rate at low temperatures (from November to the following April) was very low; the female spawned about two years after settlement; and the life span after settlement was 3.0—3.5 years.

Application of theoretical growth to the populations in Hakata Bay

We applied the following growth equations which Hamano and Matsuura[22] established previously to describe the laboratory growth of *O. oratoria* at 25 ℃:

$Lt \leq 15$ mm

$$Lt = (\sqrt{f})^{-1} \ln[2f(t-c) + 2\sqrt{f^2(t-c)^2 + fa}] + d \quad (1)$$

coefficient $a = 32.7066$, $c = 47.0217$, $d = 5.10445$, $f = 0.0767384$

$Lt \geq 15$ mm

$$Lt = 11.9473 + 0.0319893t \quad (2)$$

where Lt is CL (mm) at age t (days) after settlement and ln is the natural logarithm.

These equations describe growth rate at 25 ℃; however, the bottom water temperature in nature varies throughout a year.

To overcome this difficulty, it was assumed that the ratio between the growth rates of metamorphosed individuals at two different water temperatures is equal to that between the embryonic development rates at these two water temperatures.

Two equations proposed for the embryonic development of *O. oratoria* by Hamano and Matsuura[16] were,

$$te(w_i) = 58.39 - 1.85w_i \quad (3)$$
$$te(w_i) = 111.40/(w_i - 15.26) \quad (4)$$

where te (w_i) is the duration (days) of incubation between spawning and hatching at a mean water temperature w_i (℃).

Following the assumption stated previously,

$$tm(w_2)/tm(w_1) = te(w_2)/te(w_1) \quad (5)$$

where, tm (w_i) is time taken (days) for a metamorphosed individual to grow a certain amount at water temperature w_i ℃ and te (w_i) is duration (days) of embryonic development (= duration of incubation) at water temperature w_i ℃. Combining equations (3), (5) and (4), (5), respectively,

$$tm(w_2) = tm(w_1) \times (58.39 - 1.85w_2)/(58.39 - 1.85w_1) \quad (6)$$

and

$$tm(w_2) = tm(w_1) \times (111.40/(w_2 - 15.26))/(111.40/(w_1 - 15.26)) \quad (7)$$

when w_1 is 25 ℃, equations (6) and (7) are written as

$$tm(w_2) = tm(25) \times (58.39 - 1.85w_2)/12.14 \quad (8)$$

and

$$tm(w_2) = tm(25) \times (111.40/(w_2 - 15.26))/11.44 \quad (9)$$

Here, tm (w_2) is the time taken (days) at a water temperature w_2 for a metamorphosed individual to grow a certain amount in size. This growth increment is specified by the equation as the amount of growth over one day at 25℃. Therefore, the term tm (25) is 1 (= one day) and equations (8) and (9) simplify to

$$tm(w_2) = (58.39 - 1.85w_2)/12.14$$
: equation I

and

$$tm(w_2) = (111.40/(w_2 - 15.26))/11.44$$
: equation II

Lt, the CL at *t* days after settlement in nature, was calculated in the following sequence: (a) Daily water temperature values for each of the *t* days after a possible settlement date were estimated. (b) The daily value for tm (w_2) in equation I, or equation II, was calculated for each of the above daily water temperature during the *t* days after settlement, and then these values were summed. (c) The total value calculated in (b) was employed as the time parameter, *t*, in the growth equations, (1) and (2) for *Lt*.

Twelve monthly cohort values of mean CL of *O. oratoria* were collected from Sts. A and B (Fig. 1). But because only nine mean values at St. A (excluding those from June to August) and ten at St. B (excluding July and August) were realistic as described above, the present theoretical growth model could only be applied to these nineteen mean CLs from the two stations.

The annual cycle and characteristic, daily values of bottom water temperature at each of the stations in Hakata Bay were interpolated from monthly values recorded over the sampling year (broken lines in Fig. 7).

The closest fitting growth curve was found by varying the settlement date. Briefly, the iterative procedure for arriving at the best fit curves, shown in Fig. 7, was as follows. (a) The nine CL values from St. A and the ten CL values from St. B were arranged so as to represent seasonal cohort growth. (b) The

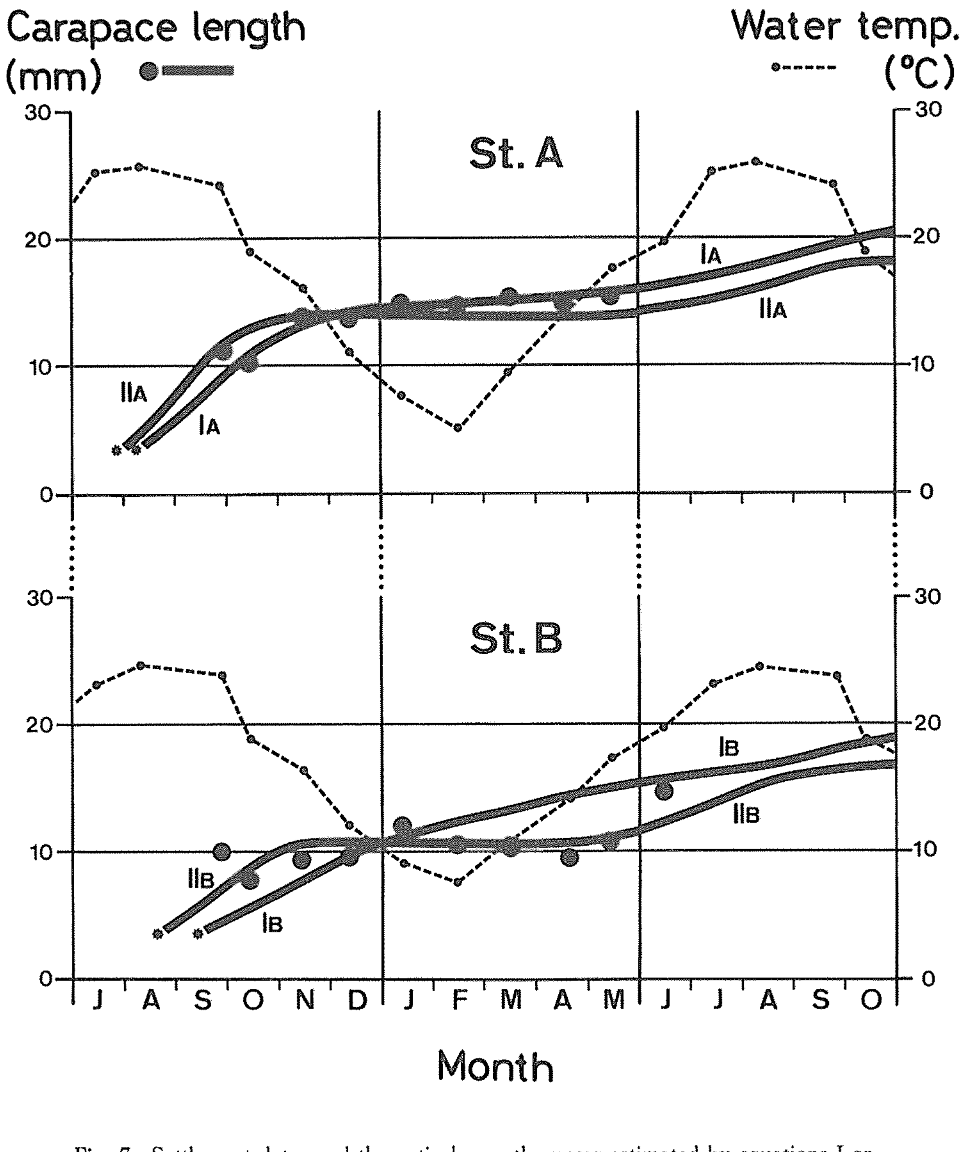

Fig. 7 Settlement dates and theoretical growth curves estimated by equations I or II, for *Oratosquilla oratoria* and temperature of bottom water at Sts. A and B in Hakata Bay. Asterisks show settlement dates. Large black circles are the means of Gaussian CL distributions of specimens.

growth curve for any chosen settlement date was calculated by the method described above and the residual sum of squares (RSS) for the values was taken as the measure of the goodness of fit to the monthly CL values. (c) Settlement dates were varied from January 1 to December 31, repeating (b). (d) The best fitting growth curve was taken, finally, as that giving the minimum RSS. The RSS of the successive growth curves decreased smoothly as a result of advancing the settlement date from January 1 and reached a minimum on the date shown in Table 6. After that date, the RSS increased smoothly. These calculations were carried out by using a computer and a BASIC program.

The four growth curves each giving a settlement date for one of the two stations from either equation I or II are shown (as solid curves) in Fig. 7.

The population dynamics and temporal appearance of larvae of *O. oratoria* in Hakata Bay indicated that the settlement of most larvae occurred in August or September in this bay. The settlement dates estimated from the present model were between July 27 and September 13, and, thus, estimation of the settlement date using either equation I or II seemed effective. However, when the mean CLs of older year-class cohorts of *O. oratoria* population from market samplings were considered and the four growth curves in Fig. 7 were extrapolated to

Table 6. Results of estimations of the settlement date of *Oratosquilla oratoria* at Sts. A and B in Hakata Bay

St.	Equation	The settlement day	RSS*
A	I	August 10	6.21
	II	July 27	15.82
B	I	September 13	102.92
	II	August 20	19.51

* Residual sum of squares.

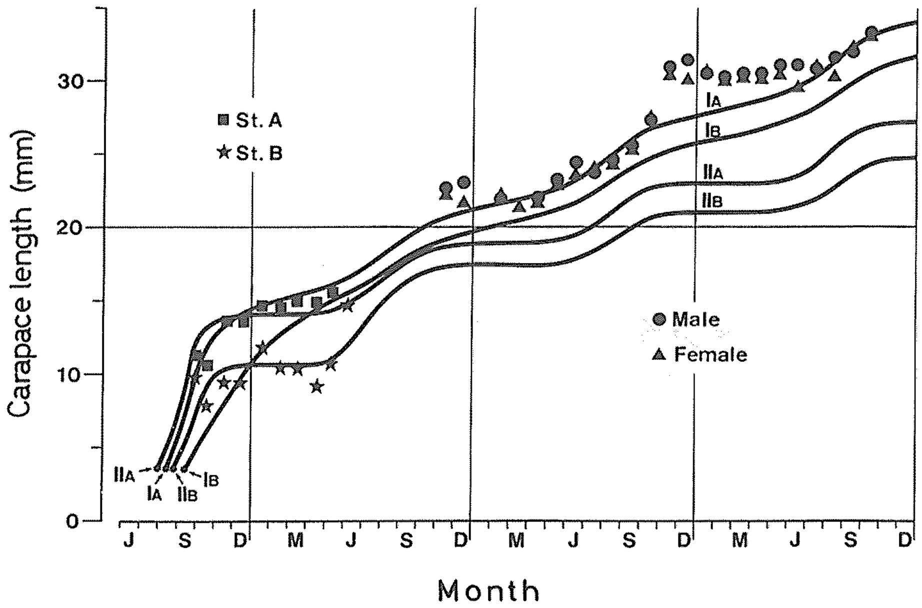

Fig. 8 Theoretical growth curves of *Oratosquilla oratoria* extrapolated in time from those in Fig. 7 so as to observe fit to the mean values of Gaussian CL distributions of older specimens obtained from market samplings.

overlap them in time (Fig. 8), the growth curves based upon equation II were (II_A and II_B) inadequate to describe the subsequent growth of the species. Consequently, the settlement dates given by equation I are considered to be more realistic than those by II.

Support for the theoretical basis of our model is also shown by field observations on the annual "resting", or zero growth, period due to low water temperatures. Since the equation (4) was derived from the law of total effective temperature, the constant term, 15.26, in this equation and equation II, represents the critical lower temperature (℃) for embryonic development of *O. oratoria.* The estimated temperatures of the bottom water in Hakata Bay were lower than 15.26℃ from November 20 to the following April 25 at St. A and from November 23 to April 25 at St. B (Fig. 7). Consequently, the animal would show zero growth during these periods based on the theoretical calculation using equation II (II_A and II_B in Fig. 8). In the field, simultaneous "resting" periods were present in the annual growth of the year-class cohorts represented in our samplings at Sts. A and B (Fig. 7) and the market (Fig. 8). There was generally little indication of growth from November to the following April. These observations indicate also that the critical lower temperature for ecdysis of metamorphosed individuals is similar to that for embryonic development.

In summary, there is good support for the descriptive model that the growth of *O. oratoria* essentially progresses along a growth curve well represented by equation I and that ecdysis usually commences above 15.26℃.

The growth curves described here were based on the assumption that the ratio between growth rates of the metamorphosed individual at two different water temperatures is equal to that between the embryonic development rates at these two water temperatures. Size increase of the metamorphosed individual and development of the embryo are both categorized as growth; the former, however, is dependent on the environment for nutrition, while the latter utilizes endogenous nutrients (yolk). Differences in growth under these and other dietary conditions, e.g. in nature and under captivity, where equations (1) and (2) were derived, have been disregarded here. There does, however, appear to be a fundamental similarity between the temperature dependence of embryonic development rate and the growth rate of metamorphosed individuals. Consequently, better fitting growth equations based on this idea can be developed by resolving these problems.

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シャコの生態学的知見および成長パラメータから着底日を推定する試み

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博多湾に産するシャコは，産卵雌の頭胸甲長(X, mm)と産出卵数（Y）の間に，$Y=0.04548X^{4.234}$ の関係があった。産卵期は4～9月で，盛期は6月であった。幼生は，主として8～10月に出現したが，これらは内湾部で孵化したと推察された。また，幼生の多くは，8月か9月に着底すると考えられた。成長には性差がほとんどなく，低水温期である11月から翌年4月の間の成長速度は非常に小さかった。雌は着底後約2年を経過したのち産卵を行った。寿命は着底後3.0～3.5年であった。最後に，異なる二つの水温下での成長速度の比は胚発生速度の比に等しいという仮定のもとに着底日の推定を試みた。